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Small mammal diversity along two neighboring Bornean mountains

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Biodiversity across elevational gradients generally follows patterns, the evolutionary origins of which are debated. We trapped small non-volant mammals across an elevational gradient on Mount (Mt.) Kinabalu (4,101 m) and Mt. Tambuyukon (2,579 m), two neighboring mountains in Borneo, Malaysia. We also included visual records and camera trap data from Mt. Tambuyukon. On Mt. Tambuyukon we trapped a total of 299 individuals from 23 species in 6,187 trap nights (4.8% success rate). For Mt. Kinabalu we trapped a total 213 animals from 19 species, in 2,044 trap nights, a 10.4% success rate. We documented the highest diversity in the low elevations for both mountains, unlike previous less complete surveys which supported a mid-elevation diversity bulge on Mt. Kinabalu. Species richness decreased gradually towards the highlands to a more even community with different species (high turnover), less rich but with the highest levels of endemism. These patterns suggest that an interplay of topography and climatic history of the region were drivers of the diversity gradient, in addition to standing climatic and spatial hypothesis.

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Abstract

Biodiversity across elevational gradients generally follows patterns, the evolutionary origins of which are debated. We trapped small non-volant mammals across an elevational gradient on Mount (Mt.) Kinabalu (4,101 m) and Mt. Tambuyukon (2,579 m), two neighboring mountains in Borneo, Malaysia. We also included visual records and camera trap data from Mt. Tambuyukon. On Mt. Tambuyukon we trapped a total of 299 individuals from 23 species in 6,187 trap nights (4.8% success rate). For Mt. Kinabalu we trapped a total 213 animals from 19 species, in 2,044 trap nights, a 10.4% success rate. We documented the highest diversity in the low elevations for both mountains, unlike previous less complete surveys which supported a mid-elevation diversity bulge on Mt. Kinabalu. Species richness decreased gradually towards the highlands to a more even community with different species (high turnover), less rich but with the highest levels of endemism. These patterns suggest that an interplay of topography and climatic history of the region were drivers of the diversity gradient, in addition to standing climatic and spatial hypothesis.

Key words: Mt. Kinabalu, Mt. Tambuyukon, Shannon index, Southeast Asia, mountain endemics, elevational gradient

Introduction

We surveyed the diversity of the non-volant small mammals along the elevational gradients of two neighboring mountains on the island of Borneo: Mt. Kinabalu (4,101 m) and Mt. Tambuyukon (2,579 m). Previous surveys of elevational transects have measured diversity along altitudinal gradients on Mt. Kinabalu for a wide diversity of taxa: moths (Beck & Chey 2008), ants (Brühl *et al*. 1999; Malsch *et al*. 2008), plants (Kitayama 1992; Aiba & Kitayama 1999; Aiba *et al*. 2005; Grytnes & Beaman, 2006; Grytnes *et al*. 2008), Oribatid mites (Hasegawa *et al*. 2006), and small mammals (Nor 2001). These studies have recovered a decline in diversity with elevation, which seems to fit a global pattern (Rahbek 1995). This decline is also compatible in some cases with the mid-domain effect (MDE). Such evidence has been reported for small mammals on Mt. Kinabalu, which could be related to the incomplete sampling of low elevations. On a broader scale, the MDE hypothesis predicts highest diversity at middle elevations, but in mammals it is only partially supported by other worldwide data (McCain 2005, 2007a). Alternative mechanisms have been proposed to explain diversity gradients on mountains, as climatic (McCain 2007b), or ecological (total area and diversity of habitats; Rozenweig 1992). Contrary to all theoretical hypotheses, some mammal communities have been observed to have peak diversity at the highest elevation, which could be explained by historical factors (i.e. rodents in Peru, Patterson & Stotz ,1998, and Dreiss *et al.*, 2015). Overall, the drivers of diversity in elevational gradients are not clearly defined and the patterns do not respond to a universal rule (Rahbek 1995; Patterson & Stotz 1998; Heaney 2001; Li *et al.* 2003; McCain 2007a, 2009; Li *et al*. 2009; Dreiss *et al*. 2015).

The goals of this study were (1) to better characterize the diversity of the small mammal community along elevational gradients in Kinabalu National Park, (2) to evaluate whether the

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MDE previously described is robust to incomplete sampling of the low-elevations, (3) to determine if the same pattern of diversity across the altitudinal transect is the same on the two mountains, and (4) to discuss evolutionary and historical factors that could have driven small mammal diversity with elevation in this context.

Materials & Methods

Study sites

Mt. Kinabalu and Mt. Tambuyukon are two neighboring peaks inside Kinabalu National Park in the Malaysian state of Sabah, Borneo (Figure 1). This park covers 764 square kilometers. Mt. Kinabalu is the tallest peak in Borneo at 4,101 meters above sea level (m), and is home to thousands of endemic plant and animal species (van der Ent 2013). Mt. Tambuyukon (the 3rd highest peak in Borneo, 2,579 m; Figure 1), despite being only 18 km away, is far less scientifically explored. The vegetation zones as described by Kitayama (1992) for Mt. Kinabalu have been used for simplicity as well as for consistency with previous elevational surveys (Nor, 2001): lowland (>1,200 m), lower montane (1,200-2,000 m), upper montane (2,000-2,800 m) and subalpine (2,800 m -3,400).

The geology of Kinabalu Park is complex, with recent uplift events (~1.5 million years ago) leading to the modern appearance of Mt. Kinabalu, including 13 jagged granite peaks along the summit (Jacobson 1978). Mt. Tambuyukon is a much older mountain, and is currently eroding away, while Mt. Kinabalu continues to rise (Cottam *et al.* 2013). This area of Sabah, Malaysia, also houses a great expanse of ultramafic outcrops (nickel and magnesium rich soils with more basic pH). Associated with these soils are unique and rich floral assemblages which tolerate the high concentration of ions (van der Ent 2011, 2015): there are at least 2,542 ultramafic associated species. Mt. Tambuyukon contains a higher proportion of ultramafic soils than Mt. Kinabalu (van

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der Ent & Wood 2013). The extent of ultramafic soils causes Mt. Tambuyukon to have more compressed and less productive vegetation zones than Mt. Kinabalu (van der Ent *et al.* 2015). The lowland dipterocarp forest dominates both mountains from the lowest elevations up to 1,200 m. Above this elevation begins lower montane oak forest of 10-25 m trees up to around 1,800-1,900 m on both Mt. Kinabalu and Mt. Tambuyukon. On Mt. Tambuyukon at 1,440 m there is a sharp break to an ultramafic outcrop and the vegetation changes to a low productivity forest with shorter trees. The mossy or cloud forest begins at around 2,000 m on both mountains. This zone is usually immersed in clouds and moss covers most surfaces and pitcher plants (genus *Nepenthes*), epiphytes, orchids and climbing bamboos are abundant. At 2,350 m on Mt. Tambuyukon and 2,600 m on Mt. Kinabalu there is a fast transition to an open stunted forest dominated by *Dacrydium* and *Leptospermum* species. At these elevations the vegetation develops a sclerophyllous and microphyllous syndrome (van der Ent 2011). At 2,800 m the subalpine vegetation appears on Mt. Kinabalu, which is absent on Mt. Tambuyukon.

Field survey

Surveys were conducted in two consecutive field seasons along elevational gradients following climbing trails along Mt. Tambuyukon and Mt. Kinabalu. We targeted small non-volant mammals and further included opportunistic observations and data from trail cameras. Species identification was performed according to Payne *et al*. (2007). During the first field season we surveyed Mt. Tambuyukon in June-August 2012. Surveys for the second field season were conducted on select locations on Mt. Tambuyukon and along the full elevational gradient of Mt. Kinabalu in February-April 2013.

We set traps from ~331 -2,509 m on Mt. Tambuyukon, and from 503-3,466 m on Mt. Kinabalu (Supplementary File S1). The taxa we expected in the small mammal trap surveys included members of the families Soricidae (shrews), Erinaceidae (gymnures), Tupaiidae (treeshrews), and rodents in the family Muridae (mice and rats) and Sciuridae (squirrels). Trapping was conducted following ethical standards according to the guidelines of the American Society of Mammalogists (Sikes *et al.* 2016). Animal care and use committees approved the protocols (Smithsonian Institution, National Museum of Natural History, Proposal Number 2012-04 and Estación Biológica de Doñana Proposal Number CGL2010-21524). Field research was approved by Sabah Parks (TS/PTD/5/4 Jld. 45 (33) and TS/PTD/5/4 Jld. 47 (25)), the Economic Planning Unit (100-24/1/299) and the Sabah Biodiversity Council (Ref: TK/PP:8/8Jld.2).

Line transects were set at approximately every 400-600 m in elevation. On Mt. Tambuyukon, transects were placed along the mountaineering trail markers (placed every 1 kilometer along the trail) as follows: from Monggis substation to Km 1 at 500 m, 900 m (Km 7.5), 1,300 m (Km 10.3), 1,600 m (Km 11), 2,000 m (Km 12.6) and 2,400 m (Km 13.5). On Mt. Kinabalu the 500 m and 900 m transects were located at Poring Hot Springs from the entrance and along the trail to the Langanan Waterfall. The next elevation transect for Mt. Kinabalu was set at ~1,500 m at the Park Headquarters, ~2,200 m along the Timpohon mountaineering trail (Km 2, Kamborangoh), 2,700 m (Km 4, Layang-Layang), and 3,200 m (around Waras, Pendant hut and Panar Laban). Transect locations were rounded to the closest hundred meters in elevation for diversity analysis. The distribution range in elevation was compared to Nor's (2001) dataset from Mt. Kinabalu.

We set traps at approximately 5-10 m intervals for a total of around 40 traps per transect. Transect locations are shown in Figure 1. Collapsible Tomahawk live traps (40 cm long), collapsible Sherman traps (two sizes used: 30 cm and 37cm long), and local mesh-wire box traps were used. We considered traps as 'terrestrial' if set below approximately 3 meters off the ground. Anything above that was considered 'arboreal'. A bait mixture (of varying composition) consisting of bananas, coconuts, sweet potatoes, palm fruit and oil, vanilla extract, and dried fish was placed in each trap. A small number of pitfall traps were distributed from 500-2,000 m on Mt. Tambuyukon.

Each trapping location had a total of 2-4 transects. The highest elevation had a lower number of trap nights due to the smaller area available for placement of traps. Coordinates for trapping locations were recorded using Garmin eTrex® series and Garmin GPSmap 60CSx. The minimum number of trap nights was based on the saturation rates obtained from Nor (2001) at approximately 300 trap nights.

We set up 4 camera traps (Reconyx rapid fire RC55 cameras, and ScoutGuard HCO cameras) along the mountaineering trail on Mt. Tambuyukon. Camera 1 was placed at 500 m, at the first kilometer marker for the hiking trail. Cameras 2 and 3 were placed along the Kepuakan River near Km 8 and at approximately 900 m. Camera 4 was placed at approximately 1,300 m near Km 10.5. No cameras were deployed along the Mt. Kinabalu trail due to the large number of day hikers and mountain climbers.

Additionally, while on Mt. Tambuyukon we opportunistically recorded mammalian observations while walking to, from and along our trap lines, while setting cameras, or while in our campsite.

Diversity analyses

Diversity indices were calculated for all elevations to quantify the differences in species diversity associated with forest zones. We used the Community Ecology Package 'vegan' (Dixon 2003) in R (v. 3.2.1) to calculate the Shannon diversity index (H') and Simpson's diversity index. Pielou's evenness index (J') was calculated as $J'=H'/H_{max}$, and species richness (S) as the number of species. All indices were calculated per altitude and per mountain. We used the LOWESS smoother (*stats::lowess* function, in R) to visualize the change of these indexes with elevation (Figure 2).

We calculated the beta diversity for each mountain using a Sorensen-based dissimilarity index (β_{SOR}) and its turnover (β_{SIM}) and nestedness (β_{NES}) components (Baselga 2010), with function beta.multi, package *betapart* 1.3 (Baselga & Orme 2012), in R. We evaluated the relationship between the similarity in the community composition and the elevation with a Mantel test in R (mantel function in the Community Ecology Package 'vegan' v 3.2.1). We did a cluster analysis to evaluate the community relatedness between mountains, and elevations using and Bray-Curtis (Bray & Curtis 1957) dissimilarity *(vegan::vegdist*, R). UPGMA dendrograms were generated using *stats::hclust*, in R.

Results

Field survey

On Mt. Tambuyukon, we trapped a total of 295 different individuals (not including recaptured animals) from 21 different species (Supplementary File S1) over 5,957 trap nights, for a total of 5.0% trap success (not including arboreal or pitfall trapping; Table 1). Trap success at each elevation ranged from 2.1% at 1,600 m to 9.6% at 2,400 m. We trapped 21 species including one carnivore, a Kinabalu ferret-badger (*Melogale everetti*). The trap success calculations were done excluding pitfall traps and arboreal traps (due to inconsistent placement of traps). The accumulation of species across trap nights varied across elevations, and appeared near saturation in all elevations (Figure 3). A white toothed shrew (*Suncus sp.*) was collected in a pitfall trap, and a gray tree rat (*Lenothrix canus*) in an arboreal trap, bringing the total species to 23 (Table 2).

On Mt. Kinabalu, we trapped a total of 209 different individuals over 2,022 trap nights, for an average trap success of 10.3%. We trapped a total of 19 species, including a Kinabalu ferret-badger at 3,200 m (Table 2). The trap success across elevations was much higher on Mt. Kinabalu, ranging from 5.6% (at 900 m), to 15.4% (at 2,700 m) (Table 1). This overall higher capture rate resulted in species saturation with a lower number of trap nights on Mt. Kinabalu than on Mt. Tambuyukon (Figure 3).

Species distribution

Trapping

The distribution and abundance of species was not even across all elevations surveyed (Figure 4). A complete list of the animals trapped is reported in Supplementary File S1. The mountain treeshrew, *Tupaia montana,* was the most frequently caught species (35.7 % of all catches) and it had a wide elevational distribution from 836-3,382 m. On Mt. Kinabalu, the Bornean mountain ground squirrel (*Sundasciurus everetti,* formerly *Dremomys everetti,* see *Hawkins et al. 2016*) was also trapped from 944-3,263 m on Mt. Kinabalu, and from 1,397-2,477 m on Mt. Tambuyukon. The long-tailed giant rat (*Leopoldamys sabanus*), from 348-2,757 m, and Whitehead's spiny rat (*Maxomys whiteheadi*) from 334-2,050 m, also had large elevational distributions on both mountains. The lesser gymnure (*Hylomys suillus*) was also distributed on both mountains but only found at high elevations: 2,263-3,382 m on Mt. Kinabalu, and 2,050 m on Mt. Tambuyukon. All other species were found at one to three elevations (Figure 4). Nine species were trapped only at a single elevation and mountain: *Callosciurus prevostii pluto* (~515 m, Poring Hot Springs, Mt. Kinabalu), *Chiropodomys pusillus* (=*C. gliroides* in Payne et al. 2007; 524 m Mt. Tambuyukon), *Crocidura* sp. (1,531 m, Mt. Tambuyukon), *Suncus* sp. (517 m, Mt. Tambuyukon), *Lenothrix canus* (526 m Mt. Tambuyukon), *Rattus exulans* (347 m Mt. Tambuyukon), *Sundasciurus lowii* (843 m Mt. Tambuyukon), *Sundasciurus jentinki* (990 m, Poring Hot Springs, Mt. Kinabalu), and *Tupaia minor* (516 m, Poring Hot Springs, Mt. Kinabalu). The lowland (<1,000 m) terrestrial small mammal community was the most diverse with 19 species trapped. We trapped 15 species in the community associated with montane forest between 1,000 m- 2,400 m and only 7 species at 2,400 m and above (*Rattus baluensis*, *Hylomys suillus*, *Maxomys alticola*, *Tupaia montana*, *Sundasciurus everetti*, *Melogale everetti*, and *Leopoldamys sabanus*). This high elevation community, despite having fewer species, was mostly composed of Bornean montane endemics (Figure 5). We recorded for the first time on another peak the summit rat (*Rattus baluensis*), which was thought to be endemic to Mt. Kinabalu. *Maxomys alticola* and *Sundasciurus everetti* are endemic to northern Borneo, and *Tupaia montana* is more widespread across mid to high elevation areas of Borneo. The last two species, *Hylomys suillus* and *Sundamys infraluteus*, have distributions very similar to *Maxomys alticola* and *Sundasciurus everetti* on Borneo, but are also reported elsewhere in Sundaland.

We captured a single animal that was identified as *Suncus* sp. after a trapping effort of 176 pitfall trap nights. A less intensive tree trapping effort of 76 trap nights yielded six small mammal species identified as: *Tupaia montana* (n = 2), *Lenothrix canus* (n = 1), *Callosciurus prevostii* (n = 1), *Sundasciurus jentinki* (n = 1), *Sundamys muelleri* (n = 1) and *Tupaia minor* (n = 1). Despite the smaller effort of arboreal trap nights, we still captured two species that were not trapped elsewhere (*Lenothrix canus* and *Sundasciurus jentinki*). The forest has a complex threedimensional structure, with vines and logs used by terrestrial animals to reach zones slightly off the forest floor. Arboreal species also sometimes frequent structures closer to the ground. We used a threshold of three meters off the ground to consider a trap arboreal. However, we also caught arboreal species in ground traps or traps close to the ground (< 3m): *Chiropodomys pusillus*, *Callosciurus prevostii* and *Tupaia minor*.

Camera traps

We set 4 trail cameras on Mt. Tambuyukon to document larger mammals not targeted by our traps. They documented an additional 8 species of mammals (Table 3; Supplementary File S2). The number of species captured on the cameras varied from one to five, with the camera at 500 m exhibiting the most diversity, both in number of species and number of independent visits (Table 3). The species documented on the camera survey for Camera 1 (500 m) included a pig-tailed macaque (*Macaca nemestrina*), a common porcupine (*Hystrix brachyura*), a mouse deer (*Tragulus* sp.), a muntjac (*Muntiacus* sp.), and sambar deer (*Rusa unicolor*). Of these species, the pig-tailed macaque and the sambar deer were documented with direct observation, but the other three species were not detected in any other manner. Camera 2 (900 m) captured two different series of the Malay civet (*Viverra tangalunga*) and one of the banded linsang (*Prionodon linsang*); the latter was not documented in any other location. Camera 3 (also 900 m) captured a single series of a Malay civet and Camera 4 (1,300 m) captured another Malay civet as well as a masked palm civet (*Paguma larvata*).

Direct observations

On Mt. Tambuyukon, several species were detected only through direct observation. These include many diurnal mammals like squirrels, *Callosciurus baluensis, C. notatus, Sundasciurus jentinki* (~1,400 m), *Exilisciurus whiteheadii* (~ 900 m), *Reithrosciurus macrotis* (~800 m) and

Ratufa affinis, and primates, *Pongo pygmaeus* (~1,400 m)*, Hylobates muelleri, Macaca fascicularis* and *Presbytis rubicunda* (~1,400 m) as well as a sighting of a bearded pig (*Sus barbatus*, 1,300 m, and sambar deer *Rusa unicolor* (Table 4). Of these sightings many were documented only a single time, including the orangutan (*Pongo pygmaeus*), the Bornean giant tufted ground squirrel (*Reithrosciurus macrotis*), Whitehead's squirrel (*Exilisciurus whiteheadii*) and the bearded pig (*Sus barbatus*). The Bornean gibbon (*Hylobates muelleri*) was heard singing on an almost daily basis, but only directly observed a single time. The sambar deer (*Rusa unicolor*) was heard vocalizing once at 1,400 m. Only one observation was made of a carnivore, the Malay civet (*Viverra tangalunga*), which was observed during a late night walk. The Malay civet was the most common carnivore observed, as it was identified at three different camera trap locations as well as a visual sighting. The visual observations increased the diversity of species documented, especially for primates and tree squirrels. The complete list of species identified on Mt. Tambuyukon can be found in Table 4.

Diversity analyses

Both mountains showed a similar pattern for the diversity estimates across elevations (Figure 2; Table 5). Species richness and Shannon diversity were maximum in low elevations and decreased gradually towards high elevations. However, evenness was lowest at middle elevations (U-shaped) (Figure 2; Table 5). The high dominance of some species at middle elevations (e.g. T*upaia montana*) leads the Shannon diversity to sink at around 1,500 m in both mountains. However, Shannon diversity increases again towards the highest elevations due to the more even frequency of the species in the small mammal communities at these altitudes, despite species richness being lower (Figure 2; Table 5).

Variation in the species composition assemblages, or beta diversity, was similar for both mountains (β_{SOR} = 0.75 on Mt. Kinabalu and β_{SOR} = 0.74 on Mt. Tambuyukon). Most of this beta diversity derived from the turnover component (β_{SIM} =0.71 for Mt. Kinabalu and 0.65 for Mt. Tambuyukon). The nestedness component was very low on both mountains (β_{NES} = 0.04 for Mt. Kinabalu and 0.09 for Mt. Tambuyukon).

A Mantel test on the Bray-Curtis dissimilarity indices across elevations revealed that the closer mammal communities are in elevation, the higher the similarity between them (Mt. Kinabalu: r = 0.63, p = 0.003; Mt. Tambuyukon: r = 0.70, p = 0.006; Supplementary File S3). In the same way, the UPGMA dendrogram revealed that community composition between comparable elevations across the two mountains were more similar than between proximate elevations within the same mountain (Figure 6). The clustering analysis generated from both Jaccard's and Bray-Curtis methods resulted in a dendrogram with the same topology. The communities at 1,600 m on Mt. Tambuyukon and 3,200 m on Mt. Kinabalu were in independent branches.

Discussion

Mt. Tambuyukon

Despite being the third highest peak in Borneo (2,579 m), the mid-elevation and high areas of Mt. Tambuyukon had not previously been systematically surveyed for small mammals. Some important sightings included the orangutan (*Pongo pygmaeus*), which has an estimated population of only 50 individuals within Kinabalu Park boundaries (Ancrenaz *et al.* 2005). The Kinabalu ferret-badger (*Melogale everetti*) was a significant finding since it is the first official record of this species on Mt. Tambuyukon (Wilting *et al.* 2016, Payne *et al.* 2007). We trapped this species at 2,051 m on Mt. Tambuyukon and 3,336 m on Mt. Kinabalu. We also identified a population of the summit rat, *Rattus baluensis* on Mt. Tambuyukon, previously only known from

Mt. Kinabalu. This species was common at high elevations and has it lower distribution limit at around 2,000 m. A population genetic analysis of the summit rats from Mt. Kinabalu and Mt. Tambuyukon demonstrated that they are currently genetically isolated (Camacho-Sanchez *et al.* accepted).

We caught all described Sabahan terrestrial murids associated with non-perturbed habitats except for *Maxomys baeodon*, *M. tajuddinii* and *Rattus tiomanicus* (Phillipps and Phillips 2016). We did not catch other murids associated with more disturbed habitats, such as *Rattus norvegicus, Rattus rattus, Rattus argentiventer,* or *Mus musculus*. We did not catch either native climbing mouse, *Chiropodomys major* or *Haeromys margarettae*, probably because our trapping was not focused to survey these tree specialists. We put less trapping effort on shrews and still captured species from two different genera, *Crocidura* and *Suncus*. Trapping shews in Borneo is challenging as densities are low. Because of this, there is little comparative material in natural history collections and their taxonomy is likely to change soon, as new comparative material is included in molecular and morphological studies, as has happened with other Sunda shrews (Demos *et al*. 2016). We did not catch or observe moonrats (*Echinosorex gymnura*), although they are common in lowlands (Phillipps and Phillips 2016).

The identification of new populations and the high level of endemism (Figure 5) inside the best surveyed national park on Borneo highlights the importance of continuing to conduct surveys and explore and document the natural diversity in the region and also the important role that Kinabalu Park plays in the ongoing conservation of biodiversity on Borneo.

The Mid-Domain Hypothesis: a matter of sampling?

Colwell & Lees (2000) suggested that a mid-domain effect (species richness is greatest in middle elevations in mountains) should constitute the null hypothesis over which deviations should be interpreted. However, this point of view is far from universal (Rahbek 1995, McCain 2007a, 2009). The mechanisms that lead to a mid-elevation bulge are not clear and could relate to more favorable climatic variables (McCain 2007b), or a purely mid-domain effect defined as “the increasing overlap of species ranges towards the center of a shared geographic domain due to geometric boundary constraints in relation to the distribution of species’ range sizes and midpoints” (Colwell & Lees 2000). Non-standardized sampling can also lead to biased gradients in species richness (Rahbek 1995).

A previous survey with a very similar scheme to ours on Mt. Kinabalu by Nor (2001) found a mid-elevation bulge in species richness, consistent with the mid-domain hypothesis. According to our trapping of ground species we recorded the highest species richness in low elevations, which gradually decreased towards high elevations in both mountains, showing the species-accumulation curves saturation at all elevations. Our results highlight the importance of a comprehensive sampling for more precise inference of biogeographical patterns. The effects of an incomplete sampling should be more acute in elevations with more habitat heterogeneity (Rosenzweig 1995), usually lowlands. We identified 11 more species as compared to Nor (2001), including a climbing mouse, *Chiropodomys pusillus*, a tree rat *Lenothrix canus*, Prevost’s squirrel, *Callosciurus prevostii*, Jentink’s squirrel, *Sundasciurus jentinki*, the rats *Maxomys rajah*, *M. alticola*, *Rattus exulans* and *Sundamys muelleri*, two species of treeshrews *Tupaia longipes* and *T. minor*, and two species of shrews, one trapped in a small Sherman trap, *Crocidura* sp., and one in a pitfall trap, *Suncus* sp.

Our results are consistent with the spatial hypothesis which states that (1) at the regional level larger areas, such as the lower elevations in mountains, where extinction is lower and speciation is favored since there are more chances for natural barriers and hence for allopatric speciation (Rosenzweig 1992), whereas at the local scale (2) larger areas have more types of different habitats, leading to greater species diversity (Rosenzweig 1995). Possibly, the relationship between area and diversity on elevational gradients along large mountains falls somewhere between these processes (McCain 2007a). These patterns together describe a mammal community more diverse in lowlands in terms of species number and evenness. Shannon diversity plunged towards middle elevations. This was mainly due to a combination of a decrease in species richness together with the high dominance of some species in this habitat, such as *Tupaia montana*, which accumulated up to 59% of the captures at middle elevations. The number of species was lowest at the highest elevations, which is cohesive with global patterns of species richness described by Rahbek (1995). However, the diversity remained similar or even higher than in middle elevations because of the high evenness in the community composition in highlands.

Although we trapped most of the expected species of small terrestrial mammals, our sampling of the diversity was far from complete. For example, we only captured a fraction of regional diversity for some taxa such as tree and flying squirrels (Nor 2001, Payne *et al.* 2007). Many species of squirrels were observed, but never trapped, which we attributed to the lack of systematic arboreal traps and/or trapability of the species. The high canopy species were rarely observed, and without substantial effort to place cage traps in the highest strata of the forest they are very difficult to trap in cage traps (most historical museum specimens were collected via firearms). The home range size may also affect the likelihood of trapping those species. Regional and local diversity are usually positively correlated (Caley & Schluter 1997) but local circumstances can profoundly affect the local community structure (Ricklefs 1987). However, there are few data for some groups such as shrews, small carnivores and tree and flying squirrels, to relate the regional diversity to local community assemblages. A replicated sampling scheme

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taking into account these regional-local relationships in diversity is important to overcome biases in the description of diversity along elevational gradients.

Historical and phylogenetic constrains in diversity

The turnover component of the beta diversity (β_{SIM}) was very high with respect to its nestedness component (β_{NES}) on both mountains (Mt. Kinabalu $\beta_{SIM} = 0.71$ vs $\beta_{NES} = 0.04$; Mt. Tambuyukon $\beta_{SIM} = 0.65$ vs $\beta_{NES} = 0.09$). That is, the assemblages at different elevations are not the product of species loss from the richest assemblages. Instead, they are singular assemblages with different species compositions.

The small mammal communities found in the high elevations of both Mt. Kinabalu and Mt. Tambuyukon had very similar species composition. These species are largely endemic to high mountain habitat in northern Borneo. This is in striking contrast to the lowland community, which is comprised primarily of widespread species, many of which are also distributed across other Sundaland landmasses such as Sumatra and the Malay Peninsula. This pattern could be even more pronounced as some of the highland taxa also found on other islands in Sunda are revised (i.e. *Hylomys suillus* and *Sundamys infraluteus*; Camacho Sánchez 2017). The observed high levels of endemism on the higher slopes is partially attributed to speciation from lowland taxa, a pattern which has been identified in other groups in Kinabalu (Merckx *et al.* 2015). The structure of this diversity along the elevational gradients could be maintained by the lower extinction rates for mammals in the tropics compared to temperate regions (Rolland et al. 2014). Additionally, the presence of high-elevation mountains such as Mt. Kinabalu, could have acted as a refugium for some highland endemics during periods of Quaternary climatic fluctuations (Camacho-Sánchez *et al.* accepted).

Conclusions

We report a decline in small mammal diversity from low to high elevations on both Mt. Kinabalu and Mt. Tambuyukon. This pattern differs from the previously described mid-elevation bulge for Mt. Kinabalu, highlighting the relevance of complete sampling of the regional diversity for biogeographical inferences. Instead, the pattern we found seems supported by the larger heterogeneity and larger areas in lowlands, which could promote speciation and decrease extinction. Additionally, the particular climatic history and elevation of the mountain range and extinction/speciation rates could play a major role in structuring mammal diversity along this elevational gradient. However, most tropical mammals have been poorly studied, and deeper ecological and evolutionary history insights are needed to better understand the processes that shape mammalian diversity along mountains.

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Supplementary Information

Supplementary File S1: Data of animals sampled and trapping effort.

Supplementary File S2: Photographs from camera traps.

Supplementary File S3: Mantel test.

Table 1(on next page)

Trap success across all elevations.

Trap success across all elevations. The number of animals caught is in column N, followed by number of trap nights, and the overall trap success per altitude.

Table 1: Trap success across all elevations. The number of animals caught is in column N, followed by number of trap nights, and the overall trap success per altitude.

		Including arboreal and pitfall traps			Excluding arboreal and pitfall traps		
	Elev. (m)	N	Trap nights	Trap success	N	Trap nights	Trap success
Kinabalu	500	33	300	11.0%	30	285	10.5%
	900	20	360	5.6%	20	360	5.6%
	1,500	36	360	10.0%	36	360	10.0%
	2,200	35	434	8.1%	34	427	8.0%
	2,700	60	390	15.4%	60	390	15.4%
	3,200	29	200	14.5%	29	200	14.5%
	Totals	213	2,044	10.4%	209	2,022	10.3%
Tambuyukon	500	78	1713	4.6%	75	1588	4.7%
	900	24	992	2.4%	24	956	2.5%
	1,300	53	712	7.4%	52	702	7.4%
	1,600	22	1036	2.1%	22	1,025	2.1%
	2,000	55	1036	5.3%	55	988	5.6%
	2,400	67	698	9.6%	67	698	9.6%
	Totals	299	6,187	4.8%	295	5,957	5.0%

Table 2(on next page)

Small mammals trapped at each trapping location.

Table 2: Small mammals trapped during field surveys. Mt. Tambuyukon was surveyed at 500, 900, 1,300, 1,600, 2,000 and 2,400 m. Mt. Kinabalu was surveyed at 500, 900, 1,500, 2,200, 2,700, 3,200 m. Columns are headed with the elevation (m), where the same (or similar) elevation was sampled between the two mountains (Mt. Tambuyukon/Mt. Kinabalu).

Table 2: Small mammals trapped during field surveys. Mt. Tambuyukon was surveyed at 500, 900, 1,300, 1,600, 2,000 and 2,400 m. Mt. Kinabalu was surveyed at 500, 900, 1,500, 2,200, 2,700, 3,200 m. Columns are headed with the elevation (m), where the same (or similar) elevation was sampled between the two mountains (Mt. Tambuyukon/Mt. Kinabalu).

	500	900	1,300	1,600 /1,500	2,000/ 2,200	2,400	2,700	3,200	Total
Callosciurus prevostii	0/2	-	-	-	-	-	-	-	2
Chiropodomys pusillus	1/0	-	-	-	-	-	-	-	1
Crocidura sp.	-	-	-	1/0	-	-	-	-	1
Hylomys suillus	-	-	-	-	3/2	-	3	3	11
Lenothrix canus	1/0	-	-	-	-	-	-	-	1
Leopoldamys sabanus	7/0	1/3	4	1/5	0/2	-	1	-	24
Maxomys alticola	-	-	-	1/0	12/3	11	5	-	32
Maxomys ochraceiventer	0/1	4/5	-	-	3/0	-	-	-	13
Maxomys rajah	19/1	2/1	2	-	-	-	-	-	25
Maxomys surifer	1/1	2/1	-	-	-	-	-	-	5
Maxomys whiteheadi	15/5	4/0	4	3/3	2/0	-	-	-	36
Melogale everetti	-	-	-	-	1/0	-	-	1	2
Niviventer cremoriventer	4/13	1/0	1	-	-	-	-	-	19
Niviventer rapit	-	-	-	1/0	0/1	1	-	-	3
Rattus baluensis	-	-	-	-	2/0	20	15	11	48
Rattus exulans	1/0	-	-	-	-	-	-	-	1
Suncus sp.	1/0	-	-	-	-	-	-	-	1
Sundamys infraluteus	-	-	-	0/4	1/0	-	-	-	5
Sundamys muelleri	23/7	1/0	-	0/1	-	-	-	-	32
Sundasciurus everetti	-	0/1	11	2/2	7/7	4	11	7	52
Sundasciurus jentinki	-	0/1	-	-	-	-	-	-	1
Sundasciurus lowii	-	1/0	-	-	-	-	-	-	1
Tupaia longipes	2/1	2/0	-	-	-	-	-	-	5
Tupaia minor	0/2	-	-	-	-	-	-	-	2
Tupaia montana	-	3/8	31	13/21	24/20	31	25	7	183
Tupaia tana	3/0	3/0	-	-	-	-	-	-	6
Number of species:	15	13	6	9	11	5	6	5	26

Table 3(on next page)

Results of camera trap survey.

Results of camera trap surveys, with relative abundance calculated for 100 trap nights.

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Table 3: Results of camera trap surveys, with relative abundance calculated for 100 trap nights.

Camera	Elevation (m)	Common Name	Species	No. of series	Camera nights	Relative abundance
1	500	Pig-tailed Macaque	*Macaca nemestrina*	1	42	2.38
		Common Porcupine	*Hystrix brachyura*	2		4.76
		Mouse Deer	*Tragulus* sp.	2		4.76
		Muntjac	*Muntiacus* sp.	1		2.38
		Sambar Deer	*Rusa unicolor*	1		2.38
2	900	Malay Civet	*Viverra tangalunga*	2	42	9.52
		Banded Linsang	*Prionodon linsang*	1		2.38
3	900	Malay Civet	*Viverra tangalunga*	2		----
4	1,300	Malay Civet	*Viverra tangalunga*	1	29	3.45
		Masked Palm Civet	*Paguma larvata*	1		3.45

Table 4 (on next page)

All species recorded on Mt. Tambuyukon.

All species recorded on Mt. Tambuyukon.

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Table 4: All species recorded on Mt. Tambuyukon.

Number	Family	Common name	Scientific name	Method(s) of detection
1	Cercopithecidae	Pig-tailed Macaque	*Macaca nemestrina*	camera trap/ observation
2	Cercopithecidae	Long tailed Macaque	*Macaca fascicularis*	observation
3	Cercopithecidae	Maroon Langur	*Presbytis rubicunda*	observation
4	Cervidae	Muntjac	*Muntiacus* sp.	camera trap
5	Cervidae	Sambar Deer	*Cervus unicolor*	camera trap/ observation
6	Erinaceidae	Lesser Gymnure	*Hylomys suillus*	live trap
7	Hylobatidae	Bornean Gibbon	*Hylobates muelleri*	observation
8	Hystricidae	Common Porcupine	*Hystrix brachyura*	camera trap
9	Muridae	Common Pencil-tailed Tree Mouse	*Chiropodomys pusillus*	live trap
10	Muridae	Grey tree rat/ Sundaic Lenothrix	*Lenothrix canus*	live trap
11	Muridae	Long-tailed giant rat	*Leopoldomys sabanus*	live trap
12	Muridae	Bornean Mountain Maxomys	*Maxomys alticola*	live trap
13	Muridae	Chestnut-bellied spiny rat	*Maxomys ochraceiventer*	live trap
14	Muridae	Brown Spiny Rat	*Maxomys rajah*	live trap
15	Muridae	Red Spiny Rat	*Maxomys surifer*	live trap
16	Muridae	Whitehead's Rat	*Maxomys whiteheadi*	live trap
18	Muridae	Dark-tailed tree rat	*Niviventer cremrioventer*	live trap
19	Muridae	Mountain long tailed rat	*Niviventer rapit*	live trap
20	Muridae	Summit Rat	*Rattus baluensis*	live trap
21	Muridae	Polynesian/Pacific rat	*Rattus exulans*	live trap
22	Muridae	Giant Mountain Rat	*Sundamys infraluteus*	live trap
23	Muridae	Muller's Rat/ Sundamys	*Sundamys muelleri*	live trap
24	Mustelidae	Kinabalu ferret-badger	*Melogale everetti*	live trap
25	Pongidae	Bornean Orangutan	*Pongo pygmaeus*	observation
26	Sciuridae	Bornean Mountain Ground Squirrel	*Sundasciurus everetti*	live trap
27	Sciuridae	Low's squirrel	*Sundasciurus lowii*	live trap
28	Sciuridae	Plantain Squirrel	*Callosciurus notatus*	observation
29	Sciuridae	Kinabalu Squirrel	*Callosciurus baluensis*	observation
30	Sciuridae	Giant Squirrel	*Ratufa affinis*	observation
31	Sciuridae	Jentink's Squirrel	*Sundasciurus jentinki*	live trap
32	Sciuridae	Whitehead's Squirrel	*Exilisciurus whiteheadi*	observation
33	Sciuridae	Giant Bornean Tufted Ground Squirrel	*Reithrosciurus macrotis*	observation
34	Soricidae	Shrew	*Crocidura* sp.	live trap

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35	Soricidae	Shrew	*Suncus* sp.	live trap
36	Suidae	Bearded Pig	*Sus barbatus*	observation
37	Tragulidae	Mouse Deer	*Tragulus* sp.	camera trap
38	Tupaiidae	Common treeshrew	*Tupaia longipes*	live trap
39	Tupaiidae	Lesser treeshrew	*Tupaia minor*	live trap
40	Tupaiidae	Mountain treeshrew	*Tupaia montana*	live trap
41	Tupaiidae	Large treeshrew	*Tupaia tana*	live trap
42	Viverridae	Malay Civet	*Viverra tangalunga*	camera trap
43	Viverridae	Banded Linsang	*Prionodon linsang*	camera trap
44	Viverridae	Masked Palm Civet	*Paguma larvata*	camera trap

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Table 5 (on next page)

Diversity indices per mountain and trapping site.

Diversity calculations for both mountains, across elevations (H’, Shannon diversity index; D, Simpson diversity index; S, species richness; J’, Pielou’s evenness index).

Table 5: Diversity calculations for both mountains, across elevations (H’, Shannon diversity index; D, Simpson diversity index; S, species richness; J’, Pielou’s evenness index).

	Elevation (m)	H’	D	S	J’
Mt. Kinabalu	500	1.75	0.24	9	0.79
	900	1.60	0.26	7	0.82
	1,500	1.30	0.38	6	0.73
	2,200	1.28	0.38	6	0.71
	2,700	1.45	0.28	6	0.81
	3,200	1.40	0.27	5	0.87
Mt. Tambuyukon	500	1.89	0.20	12	0.76
	900	2.27	0.11	11	0.95
	1,300	1.23	0.40	6	0.69
	1,600	1.36	0.38	7	0.70
	2,000	1.66	0.26	9	0.76
	2,400	1.24	0.33	5	0.77

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Figure 1(on next page)

Trapping locations

Map of Kinabalu Park, Sabah, Malaysia with trails followed and trapping locations

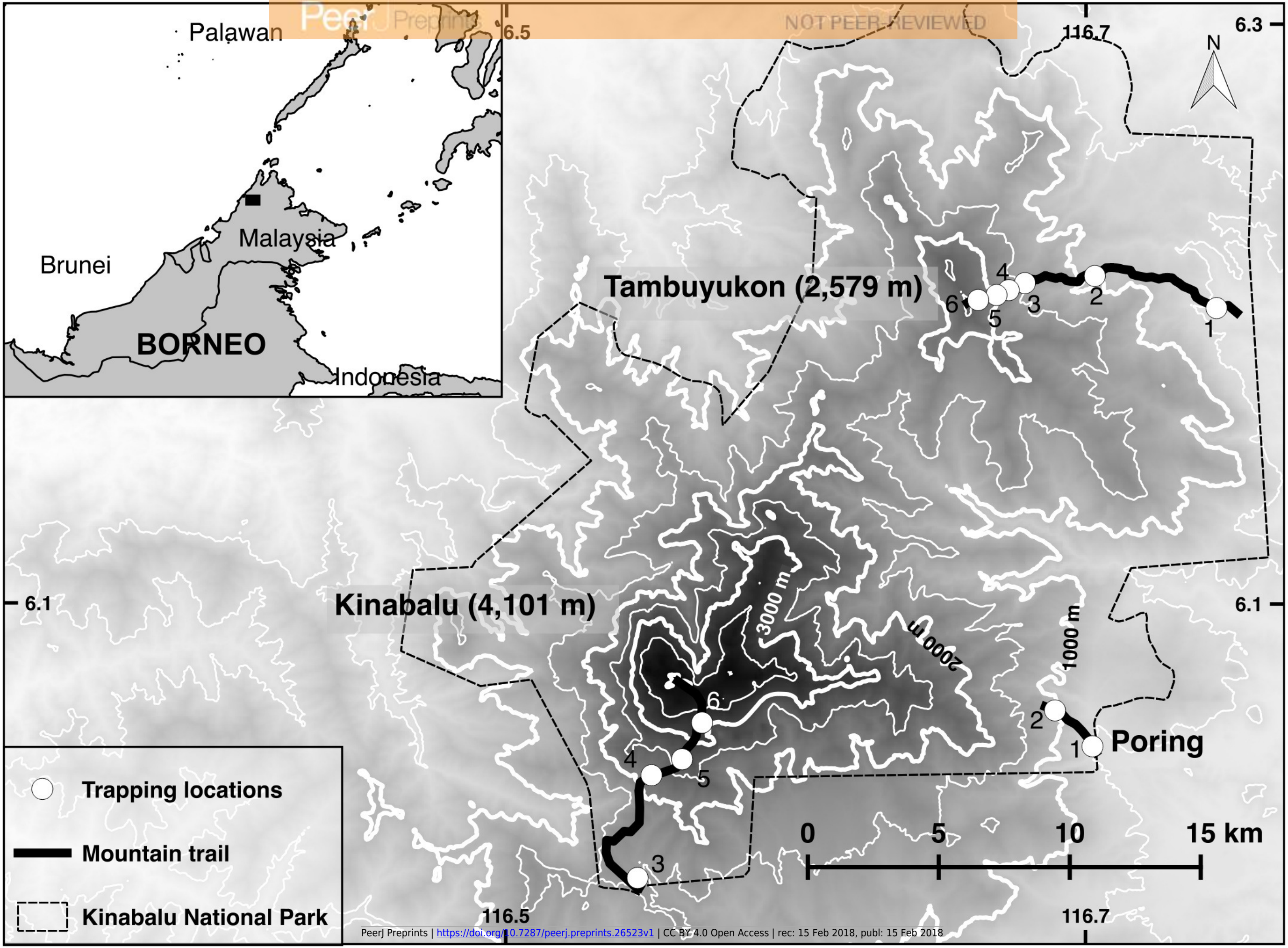
Palawan
Malaysia
Brunei
BORNEO
Indonesia
6.5
116.7
6.3
N
Tambuyukon (2,579 m)
1
2
3
4
5
6
Kinabalu (4,101 m)
3000 m
2000 m
1000 m
6.1
6.1
Poring
1
2
3
4
5
6
Trapping locations
Mountain trail
Kinabalu National Park
0
5
10
15 km
116.5
116.7

Figure 2

(on next page)

Diversity indices across elevations.

Diversity indices across elevations for Mt. Kinabalu (circles) and Mt. Tambuyukon (triangles) with loess regressions (Mt. Kinabalu, solid line; Mt. Tambuyukon, dashed line).

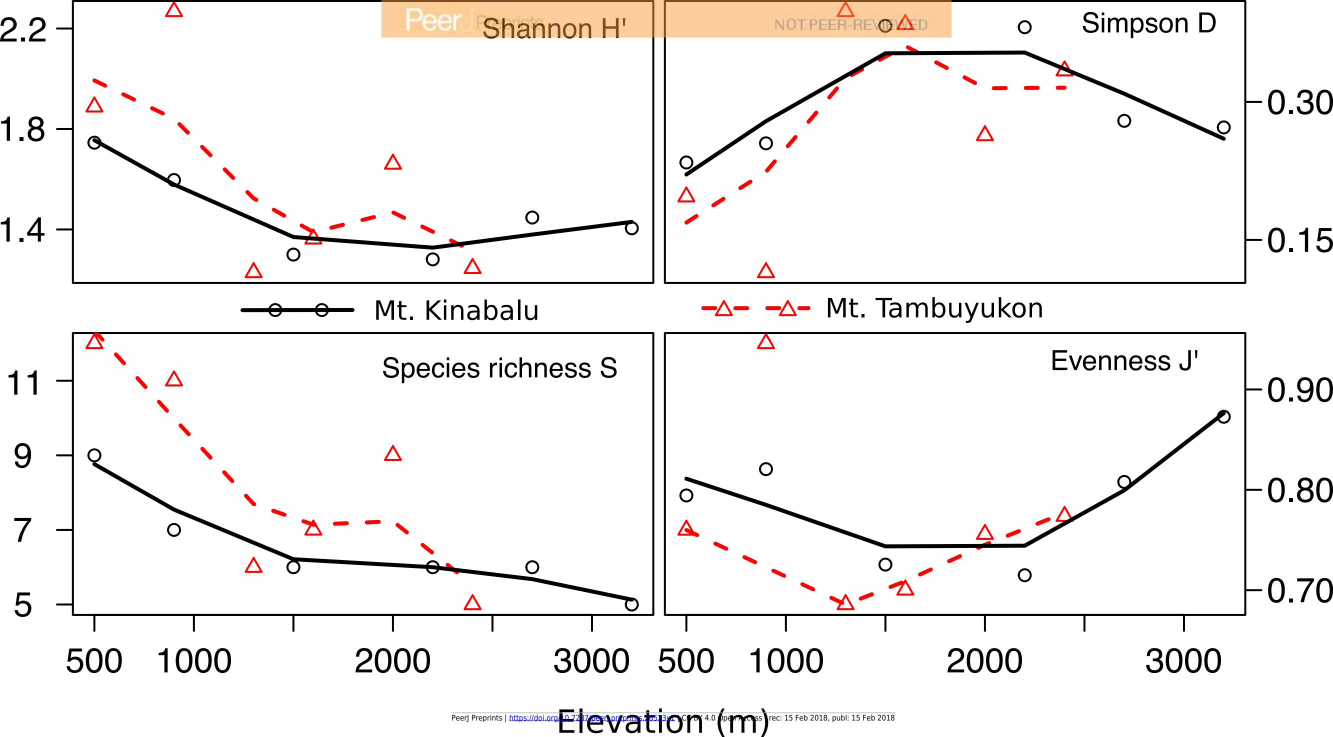
Shannon H'
Simpson D
Species richness S
Evenness J'
Mt. Kinabalu
Mt. Tambuyukon
2.2
1.8
1.4
0.30
0.15
11
9
7
5
0.90
0.80
0.70
500
1000
2000
3000
Elevation (m)

Figure 3 (on next page)

Species accumulation curves.

Species accumulation curves in both mountains and across elevations (solid lines, Mt. Kinabalu; dotted lines, Mt. Tambuyukon).

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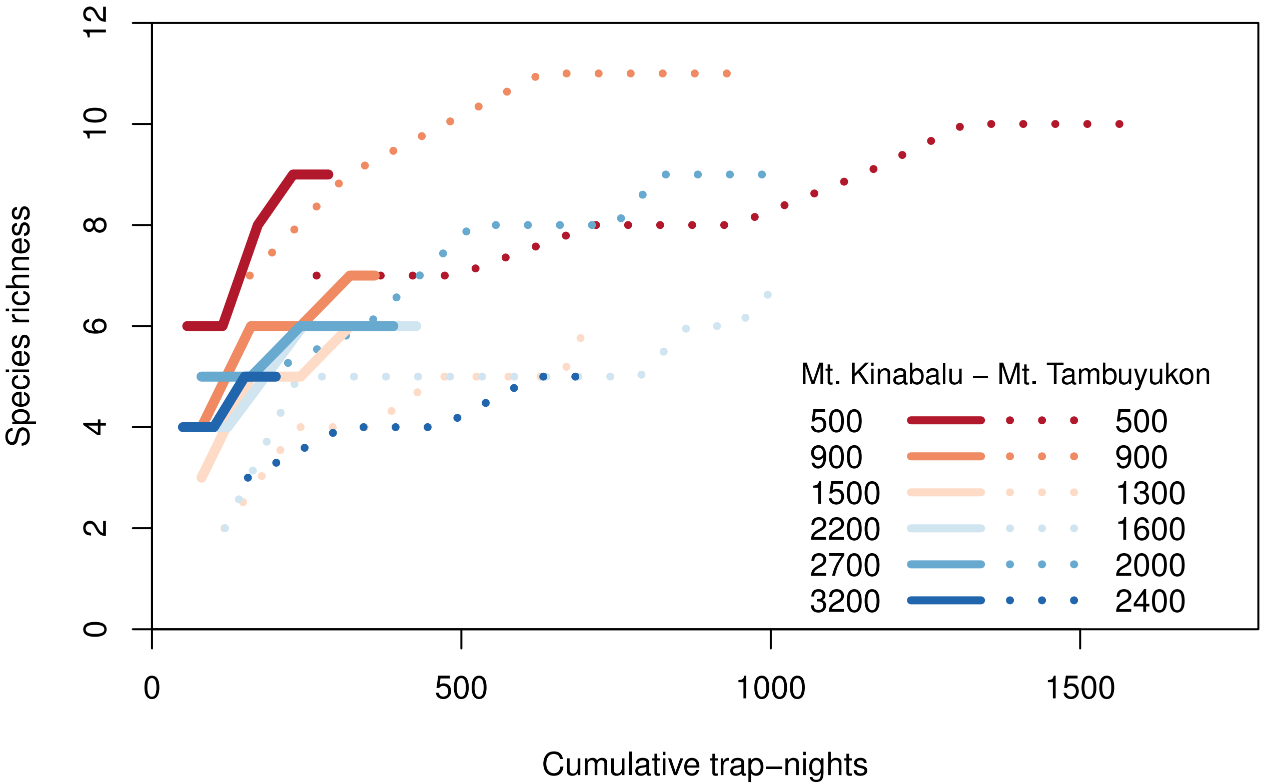
Species richness
Cumulative trap–nights
0
2
4
6
8
10
12
0
500
1000
1500
Mt. Kinabalu – Mt. Tambuyukon
500 500
900 900
1500 1300
2200 1600
2700 2000
3200 2400

Figure 4(on next page)

Species distribution across elevations.

Species distribution across elevations. Our two field surveys are represented by triangles (Mt. Kinabalu), and squares (Mt. Tambuyukon), together with a previous small mammal survey of Mt. Kinabalu (open circles; Nor 2001). The accumulated trapping effort for each mountain is shown on the upper horizontal axis. We have represented the vegetation levels as described in Kitayama (1992) for Mt. Kinabalu in greyscale in the background.

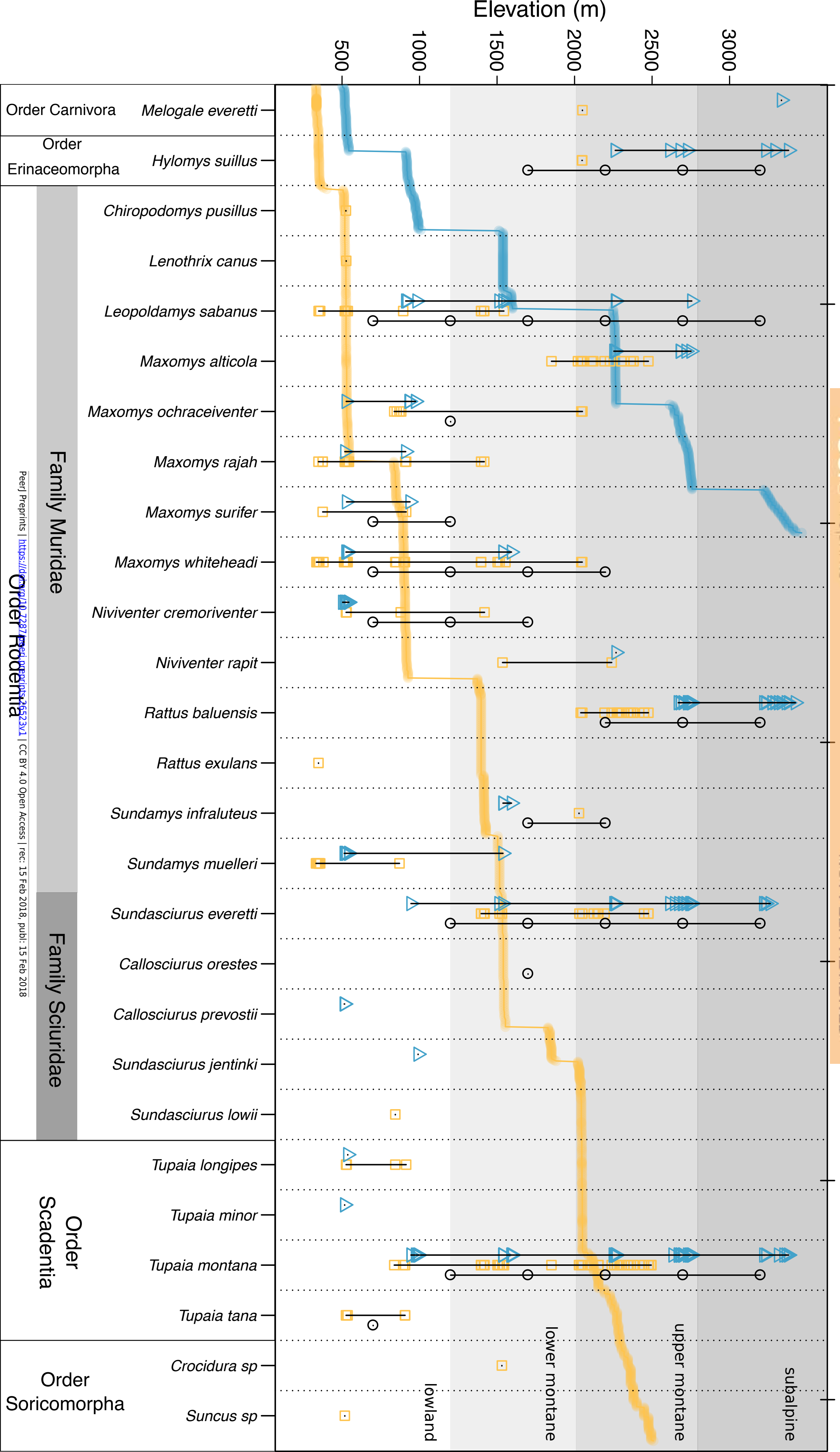
Elevation (m)
500
1000
1500
2000
2500
3000
Trap nights
0
1000
2000
3000
4000
5000
6000
Order Carnivora
Melogale everetti
Order Erinaceomorpha
Hylomys suillus
Order Rodentia
Family Muridae
Chiropodomys pusillus
Lenothrix canus
Leopoldamys sabanus
Maxomys alticola
Maxomys ochraceiventer
Maxomys rajah
Maxomys surifer
Maxomys whiteheadi
Niviventer cremoriventer
Niviventer rapit
Rattus baluensis
Rattus exulans
Sundamys infraluteus
Sundamys muelleri
Family Sciuridae
Sundasciurus everetti
Callosciurus orestes
Callosciurus prevostii
Sundasciurus jentinki
Sundasciurus lowii
Order Scadentia
Tupaia longipes
Tupaia minor
Tupaia montana
Tupaia tana
Order Soricomorpha
Crocidura sp
Suncus sp
lowland
lower montane
upper montane
subalpine

Figure 5(on next page)

Relation of endemism and altitudinal range of small mammals trapped.

Distribution range (km^2) (IUCN 2016) for the mammals trapped related to their elevational range in Kinabalu National Park. Dots represent the mid-point of their elevational range. Bornean endemics are filled in gray. Black vertical lines represent elevational ranges from the literature (Musser 1986; Nor 2001; IUCN 2016), and over-plotted vertical grey bars are the elevational ranges we found in this survey.

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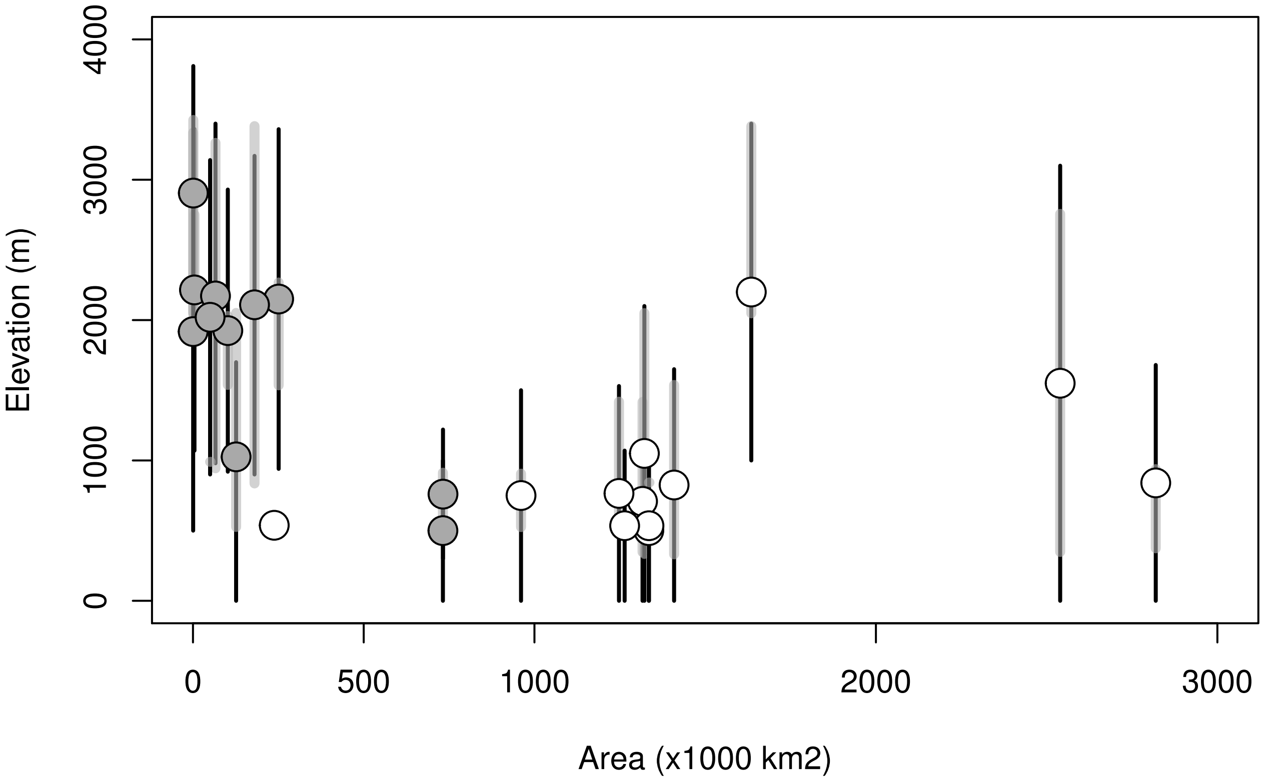
Elevation (m)
0
1000
2000
3000
4000
0
500
1000
2000
3000
Area (x1000 km2)

Figure 6(on next page)

Similarity between the small mammal communitites from different elevations.

Dendrogram of species composition for both Mt. Kinabalu (grey text and triangle symbols) and Mt. Tambuyukon (black font and square symbols) based on Jaccard's similarity.

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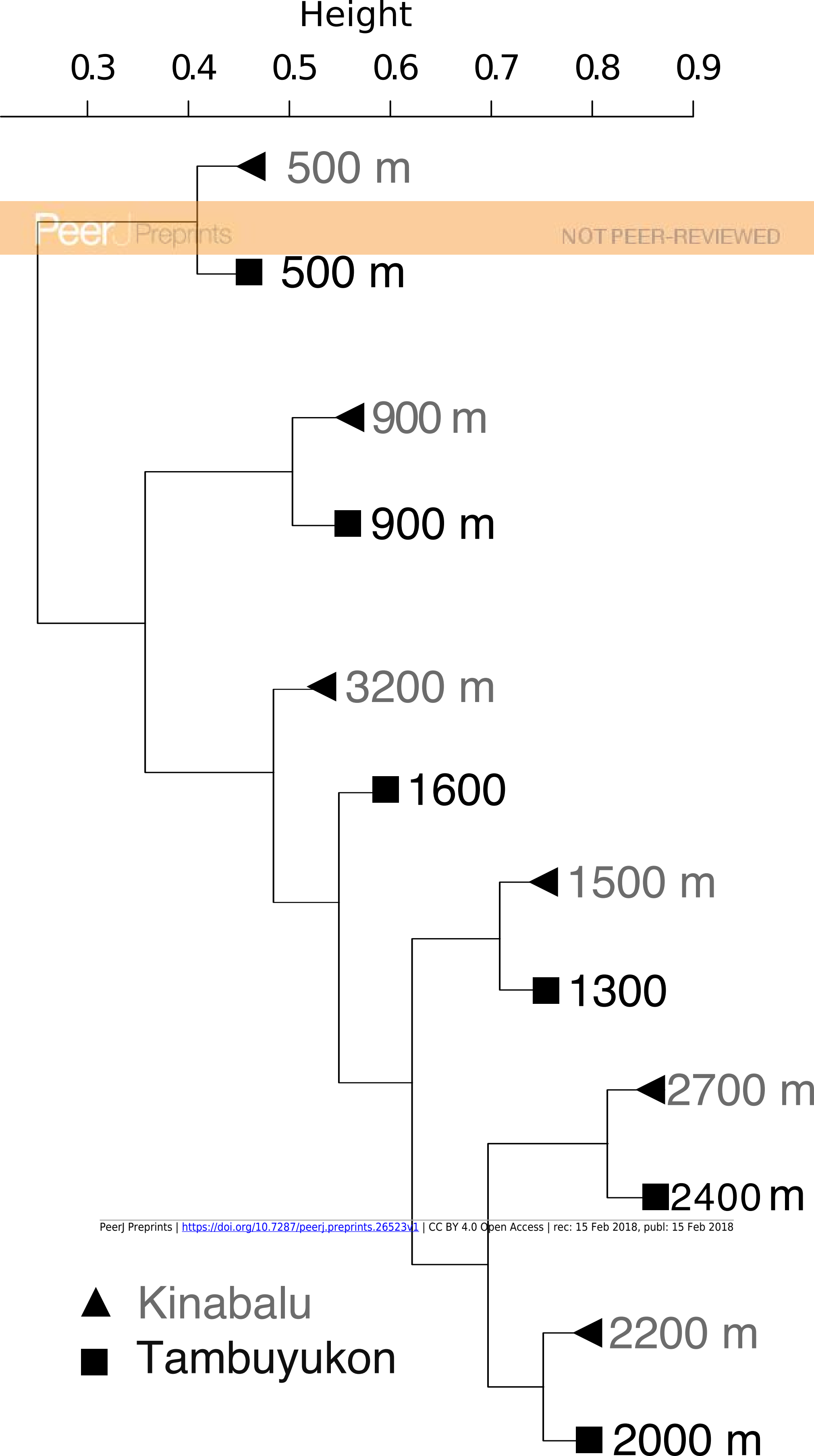
Height
0.3
0.4
0.5
0.6
0.7
0.8
0.9
500 m
500 m
900 m
900 m
3200 m
1600
1500 m
1300
2700 m
2400 m
2200 m
2000 m
Kinabalu
Tambuyukon