# Endemism and diversity of small mammals along two neighboring Bornean mountains

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Mountains offer replicated units with large biotic and abiotic gradients in a reduced spatial scale. This transforms them into well-suited scenarios to evaluate biogeographic theories. Mountain biogeography is a hot topic of research and many theories have been proposed to describe the changes in biodiversity with elevation. Geometric constraints, which predict the highest diversity to occur in mid-elevations, have been a focal part of this discussion. Despite this, there is no general theory to explain these patterns, probably because of the interaction among different predictors with the local effects of historical factors. We characterize the diversity of small non-volant mammals across the elevational gradient on Mount (Mt.) Kinabalu (4,095 m) and Mt. Tambuyukon (2,579 m), two neighboring mountains in Borneo, Malaysia. We documented a decrease in species richness with elevation which deviates from expectations of the geometric constraints and suggests that spatial factors (eg. larger diversity in larger areas) are important. The lowland small mammal community was replaced in higher elevations (from above ~1900 m) with montane communities consisting mainly of high elevation Borneo endemics. The positive correlation we find between elevation and endemism is concordant with a hypothesis that predicts higher endemism with topographical isolation. This supports lineage history and geographic history could be important drivers of species diversity in this region.

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20   **Abstract**

21   Mountains offer replicated units with large biotic and abiotic gradients in a reduced spatial scale.

22   This transforms them into well-suited scenarios to evaluate biogeographic theories. Mountain

23   biogeography is a hot topic of research and many theories have been proposed to describe the

24   changes in biodiversity with elevation. Geometric constraints, which predict the highest diversity

25   to occur in mid-elevations, have been a focal part of this discussion. Despite this, there is no

26   general theory to explain these patterns, probably because of the interaction among different

27   predictors with the local effects of historical factors. We characterize the diversity of small non-

28   volant mammals across the elevational gradient on Mount (Mt.) Kinabalu (4,095 m) and Mt.

29   Tambuyukon (2,579 m), two neighboring mountains in Borneo, Malaysia. We documented a

30   decrease in species richness with elevation which deviates from expectations of the geometric

31   constraints and suggests that spatial factors (eg. larger diversity in larger areas) are important.

32   The lowland small mammal community was replaced in higher elevations (from above ~1900 m)

33   with montane communities consisting mainly of high elevation Borneo endemics. The positive

34   correlation we find between elevation and endemism is concordant with a hypothesis that

35   predicts higher endemism with topographical isolation. This supports lineage history and

36   geographic history could be important drivers of species diversity in this region.

37   **Keywords**: Mt. Kinabalu, Mt. Tambuyukon, Shannon index, Sundaland, elevational gradient

## Introduction

40 Understanding the mechanisms that are responsible for shapping patterns of biodiversity across

41 geography has been an important driver of biological research (eg. Wallace, 1869; Heaney, 1986;

42 Rosenzweig, 1995; Lomolino et al., 2010). Mountains are valuable natural experiments that

43 allow researchers to test biogeoraphical hypotheses for these reasons: (1) they have limited

44 confounding variation across historical and ecological conditions, (2) they are discrete units to

45 study and (3) they offer replicated gradients for factors (climatic, spatial, ecological) that have

46 been central for research in biogeography (Brown, 2001). Numerous studies have sought to

47 explain the change of alpha diversity across elevation for diverse taxonomic groups (eg. Rahbek,

48 1995; Patterson & Stotz, 1998; Heaney, 2001; Chen et al., 2006; Kluge, Kessler & Dunn, 2006).

49 Previous research on diversity gradients on mountains has focused on the relationship between

50 diversity gradients on mountains with temperature and precipitation, primary productivity, area,

51 isolation, and geometric constraints. However, the effects of abiotic predictors on mountains are

52 inconsistent across studies (eg. Rahbek, 1995; Patterson & Stotz, 1998; Heaney, 2001; Chen et

53 al., 2006; Kluge, Kessler & Dunn, 2006), and to date, no uniform theory explains mammalian

54 diversity gradients on mountains (Brown, 2001; Lomolino, 2001; Heaney, 2001; Stevens, Rowe

55 & Badgley, 2019).

56 Geometric constraints stand out from the former predictors as the most recurrent

57 explanation for diversity gradients on mountains across many systems (Rahbek, 1995; Fu et al.,

58 2006; Kluge, Kessler & Dunn, 2006; Rowe, 2009). Geometric constraints predict that the overlap

59 of species' ranges on a constrained area causes species richness to be higher at the center of this

60 area (Colwell & Lees, 2000). Translated to mountains, geometric constraints predict a higher

61 diversity at mid-elevations (mid-elevation bulge) caused by the overlap of species ranges with

62     midpoints at different elevations. This phenomenon is often referred to as Mid-Domain Effect

63     (MDE). In mammals, a MDE has been reported across different mountain ranges, but it is not a

64     global pattern (Rickart, 2001; Heaney, 2001; Nor, 2001; Li, Song & Zeng, 2003; McCain, 2004,

65     2005; Rowe, 2009; Rowe, Heaney & Rickart, 2015; Hu et al., 2017).

66         The history of lineage and place can profoundly influence current patterns of diversity on

67     mountains (Brown, 2001; Lomolino, 2001; Stevens, Rowe & Badgley, 2019). These effects of

68     history vary from mountain system and taxa, which has hampered the consolidation of a theory

69     to explain species richness on mountain gradients (Brown, 2001). On mountaintops, (1) more

70     geographical isolation should favor speciation and restrict processes of dispersal and

71     colonization, and (2) species richness should decline as a consequence of higher extinction

72     caused by generally smaller areas associated with higher elevation bands (Brown, 2001;

73     Lomolino, 2001). This, in turn, should lead to fewer species but higher endemism on

74     mountaintops. A recent worldwide review on plant endemism on mountains by Steinbauer et al.

75     (2016) found a clear correlation of peak isolation with increased endemism in mountaintops.

76     They suggested the coupling of historical climate changes with topography as a "pump" for

77     montane endemism (Steinbauer et al., 2016). For mammals, there is growing evidence that

78     endemism increases with elevation (Sánchez-Cordero, 2001; Heaney, 2001; Swenson et al.,

79     2012; Chen et al., 2017), but this data is often descriptive and lacks statistical testing.

80         Here we surveyed non-volant small mammals across elevational gradients on two tropical

81     mountains from the same range, Mt. Kinabalu and Mt. Tambuyukon, in northern Borneo. Mt.

82     Kinabalu (4,095 m) is the tallest mountain in Sundaland, a tropical hotspot of biodiversity

83     (Myers et al., 2000). A number of taxa have been surveyed across large elevational transects on

84     this mountain: moths (Beck & Chey, 2008), ants (Brühl, Mohamed & Linsenmair, 1999; Malsch

85   et al., 2008), plants (Kitayama, 1992; Aiba & Kitayama, 1999; Aiba, Takyu & Kitayama, 2005;

86   Grytnes & Beaman, 2006; Grytnes et al., 2008), oribatid mites (Hasegawa, Ito & Kitayama,

87   2006), snails (Liew, Schilthuizen & bin Lakim, 2010) and small mammals (Nor, 2001). These

88   studies have recovered either a decline in diversity with elevation, which seems to fit a global

89   pattern (Rahbek, 1995) or a mid-domain effect (MDE). To date, Nor's (2001) survey is the most

90   comprehensive dataset of non-volant small mammals on Mt. Kinabalu. It describes a clear MDE,

91   although the number of species he reports in the lowest elevation was unexpectedly low (only

92   five species), compared to the maximum of approximately 35 non-volant small mammals that are

93   known to be distributed in the lowland forests of Borneo (Nor, 2001; Payne et al., 2007). Thus,

94   there could be a strong bias in the interpretations caused by incomplete sampling of the lowest

95   elevation (Rahbek, 1995; Lomolino, 2001). Furthermore, Mt. Kinabalu is a hotspot of endemism

96   for many mountain lineages (Payne et al., 2007; van der Ent, 2013; Merckx et al., 2015). The

97   montane conditions in the upper slopes of Mt. Kinabalu are unique in Sundaland. Similar

98   conditions are only partially found on a handful of other peaks in Borneo (ie. upper montane

99   forest in Mt. Tambuyukon, 2,579 m, Wood & van der Ent, 2012; Mt. Trusmadi, 2,642 m,

100  Kitayama et al., 1993; Mt. Murud, 2,423 m, Beaman & Anderson, 1997; and Mt. Mulu, 2,376 m,

101  Collins, 1980) and on several peaks in Sumatra (Laumonier, 1997).

102       This study aimed to describe the effects of (1) the MDE on alpha diversity (species

103  richness) and (2) mountain endemics on beta diversity (change in the composition of the

104  community), for small non-volant mammals along the elevational gradient on Mt. Kinabalu and

105  Mt. Tambuyukon. We hypothesized that alpha diversity should decrease with elevation

106  coinciding with less available area and less complex habitat heterogeneity, while greater

107  endemism on higher elevational bands should correlate with the particular isolation of Mt.

108   Kinabalu in Sundaland. For this purpose, we characterized the small mammal diversity along the

109   elevational gradient on Mt. Kinabalu and Mt. Tambuyukon. The raw data is fully accessible and

110   all analyses and figures are reproducible (DOI: 10.5281/zenodo.3341178).

111   **Materials & Methods**

112   *Study sites*

113   Mt. Kinabalu and Mt. Tambuyukon are two neighboring peaks inside Kinabalu National Park in

114   the Malaysian state of Sabah, Borneo (Figure 1). This park covers 764 square kilometers. Mt.

115   Kinabalu is the tallest peak in Borneo at 4,095 m and is home to thousands of endemic plant and

116   animal species (Payne et al., 2007; van der Ent, 2013). Mt. Tambuyukon (the 3rd highest peak in

117   Borneo, 2,579 m; Figure 1), despite being only 18 km away, is far less scientifically explored.

118   The vegetation zones as described by Kitayama (1992) for Mt. Kinabalu have been used for

119   simplicity as well as for consistency with previous elevational surveys (Nor, 2001): lowland

120   (>1,200 m), lower montane (1,200-2,000 m), upper montane (2,000-2,800 m) and subalpine

121   (2,800 -3,400 m).

122         The lowland dipterocarp forest dominates both mountains from the lowest elevations up

123   to 1,200 m. Above this elevation begins the lower montane oak forest of 10-25 m trees up to

124   around 1,800-1,900 m on both Mt. Kinabalu and Mt. Tambuyukon. On Mt. Tambuyukon at

125   1,440 m there is a sharp break to an ultramafic outcrop and the vegetation changes to a low

126   productivity forest with shorter trees. The mossy or cloud forest begins at around 2,000 m on

127   both mountains. This zone is usually immersed in clouds, moss covers most surfaces, and pitcher

128   plants (genus *Nepenthes*), epiphytes, orchids, and climbing bamboos are abundant. At 2,350 m

129   on Mt. Tambuyukon and 2,600 m on Mt. Kinabalu there is a fast transition to an open stunted

130   forest dominated by *Dacrydium* and *Leptospermum* species. At these elevations, the vegetation

131 develops a sclerophyllous and microphyllous syndrome. At 2,800 m the subalpine vegetation

132 appears on Mt. Kinabalu, which is absent on Mt. Tambuyukon.

133 *Field survey*

134 Surveys were conducted in two consecutive field seasons along elevational gradients following

135 climbing trails along Mt. Tambuyukon and Mt. Kinabalu. We targeted small non-volant

136 mammals and further included opportunistic observations and data from trail cameras. Species

137 identification was performed according to Payne *et al*. (2007). During the first field season, we

138 surveyed Mt. Tambuyukon in June-August 2012. Surveys for the second field season were

139 conducted on select locations on Mt. Tambuyukon (to fill gaps in the first season sampling) and

140 along the full elevational gradient of Mt. Kinabalu in February-April 2013.

141 We set traps from ~331 - 2,509 m on Mt. Tambuyukon, and from 503 - 3,466 m on Mt.

142 Kinabalu (Dataset S1). The taxa we expected in the small mammal trap surveys included

143 members of the families Soricidae (shrews), Erinaceidae (gymnures), Tupaiidae (treeshrews),

144 and rodents in the families Muridae (mice and rats) and Sciuridae (squirrels). Trapping was

145 conducted following ethical standards according to the guidelines of the American Society of

146 Mammalogists (Sikes et al., 2011). Animal care and use committees approved the protocols

147 (Smithsonian Institution, National Museum of Natural History, Proposal Number 2012-04 and

148 Estación Biológica de Doñana Proposal Number CGL2010-21524). Field research was approved

149 by Sabah Parks (TS/PTD/5/4 Jld. 45 (33) and TS/PTD/5/4 Jld. 47 (25)), the Economic Planning

150 Unit (100-24/1/299) and the Sabah Biodiversity Council (JKM/MBS.1000-2/2(104)).

151 Line transects were set at approximately every 400 - 600 m in elevation. On Mt.

152 Tambuyukon, transects were placed along the mountaineering trail markers (placed every 1

153 kilometer along the trail) as follows: from Monggis substation to km 1 at 500 m, 900 m (km 7.5),

154    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.

155    Kinabalu the 500 and 900 m transects were located at Poring Hot Springs from the entrance and

156    along the trail to the Langanan Waterfall. The next elevation transect for Mt. Kinabalu was set at

157    ~1,500 m at the Park Headquarters, ~2,200 m along the Timpohon mountaineering trail (km 2,

158    Kamborangoh), 2,700 m (km 4, Layang-Layang), and 3,200 m (around Waras, Pendant hut, and

159    Panar Laban). For reporting results and data analysis, we hereafter refer to these locations as

160    "trapping locations". Each trapping location gathered the trap data from transects which could

161    span a distance of over 100 m up- or downhill (raw data in Dataset S1).

162           We set traps at approximately 5 - 10 m intervals for a total of around 40 traps per

163    transect. Trapping locations are shown in Figure 1. Collapsible Tomahawk live traps (40 cm

164    long), collapsible Sherman traps (two sizes used: 30 cm and 37 cm long), and local mesh-wire

165    box traps were used. We considered traps as 'close to the ground' if set below approximately 3 m

166    off the ground. Most of these traps were directly set on the ground, while a small proportion was

167    set on branches or vines at the reach of the hand. We considered the 3-m threshold as reasonable

168    to describe the terrestrial small mammal community given the arboreal habits of many small

169    terrestrial Bornean mammals (Wells et al., 2004) and the high-complexity of the vegetation in

170    most transects. Any trap above that was considered 'arboreal'. A bait mixture (of varying

171    composition) consisting of bananas, coconuts, sweet potatoes, palm fruit and oil, vanilla extract,

172    and dried fish was placed in each trap. A small number of pitfall traps were distributed from 500

173    - 2,000 m on Mt. Tambuyukon (number and distribution were limited by the substrate) (Table 1).

174           Each trapping location had a total of 2 - 4 transects. The highest elevation had a lower

175    number of trap nights due to the smaller area available for placement of traps. Coordinates for

176    trapping locations were recorded using Garmin eTrex® series and Garmin GPSmap 60CSx. The

177    minimum number of trap nights was based on the saturation rates obtained from Nor (2001) at

178    approximately 300 trap nights. For every sampling location (elevation within mountain) the

179    cumulative trap-nights and species richness were calculated by adding the cumulative number of

180    species caught and trap-nights for each trap for each successive day from the date the trap was

181    set.

182          We set up 4 camera traps (Reconyx RapidFire RC55™ cameras, and ScoutGuard HCO™

183    cameras) along the mountaineering trail on Mt. Tambuyukon. Camera 1 was placed at 500 m, at

184    the first-kilometer marker for the hiking trail. Cameras 2 and 3 were placed along the Kepuakan

185    River near km 8 and at approximately 900 m. Camera 4 was placed at approximately 1,300 m

186    near km 10.5. No cameras were deployed along the Mt. Kinabalu trail due to a large number of

187    day hikers and mountain climbers.

188          Additionally, while on Mt. Tambuyukon we opportunistically recorded mammal

189    observations while walking to, from and along our trap lines, while setting cameras, or while in

190    our campsite.

191    *Alpha diversity*

192          *Diversity index*. We computed diversity indices for each trapping location. The

193    Community Ecology Package 'vegan' 2.5-5 (Dixon, 2003) in R  3.5.1 (R Development Core

194    Team, 2018) was used to calculate the Shannon diversity (H') and Simpson's diversity. Pielou's

195    evenness (J') was calculated as J' = H' / $H_{max}$, and species richness (S) as the number of species.

196    We used the LOWESS smoother (*stats::lowess* function, in R) to visualize the change of these

197    indexes with elevation. The pattern of species richness across elevation in each mountain was

198    contrasted against the mid-domain effect using 'rangemodelR' 1.0.4 (Marathe, 2019) in R, as in

199    Wang & Fang, 2012. We used the function *range.shuffle* which returns the pattern of species

200  diversity under the mid-domain effect. The following arguments were used for computations: 50

201  m as the interval to discretize species ranges and midpoints into elevational bands, soft

202  boundaries, and 5,000 repetitions.

203      *Predictors of species richness*. The relation between species richness and two predictors,

204  (1) elevation and (2) expectations under the MDE, were assessed in separate linear models with

205  mixed-effects (Laird & Ware, 1982) using *lme* function from 'nlme' package 3.1-137 (Pinheiro

206  et al., 2018) in R. Model building and the evaluation of their fit was carried following the

207  recommendations in Harrison et al. (2018). In both models, we corrected for spatial

208  autocorrelation by including a term to account for the correlation structure built with

209  *nlme::corSpatial* function in R. This object contained the centroids of coordinates from all

210  animals trapped at a given location. Mountain was included as a random intercept. The fit of

211  these models was compared using likelihood ratio tests (King, 2010) against a null model that

212  excluded the fixed effect (Nickerson, 2000; Pinheiro & Bates, 2006; Harrison et al., 2018).

213      *Endemism*. We quantified endemism at each trapping location as the proportion of

214  endemic species. This measure is robust to sampling bias and it is not overridden by local

215  diversity (Steinbauer et al., 2016). We defined endemic as only found in Borneo. Shrews were

216  excluded as we were not able to identify them to the species level. To visualize the change of

217  proportion of endemics with elevation we created a confidence envelope by resampling 1,000

218  times the species present at each trapping location. This same approach was used to visualize the

219  proportion of captures that belonged to endemic species across elevation. We evaluated the

220  contribution of elevation (predictor) to explaining the proportion of endemism (dependent

221  variable 1) and the proportion of captures (dependent variable 2) that corresponded to endemic

222  species. We used generalized models with mixed effects using a binomial family with logit link.

223    Mountain was added as a random intercept. Model fitting was done using *glmer* function from

224    'lme4' package 1.1-21 (Bates et al., 2015) in R. The fit of these models was compared using

225    likelihood ratio tests against a null model that excluded the fixed effect (Nickerson, 2000;

226    Pinheiro & Bates, 2006).

227    *Beta diversity*

228        We calculated beta diversity for each mountain using a Sorensen-based dissimilarity

229    index ($\beta_{SOR}$) with its turnover ($\beta_{SIM}$) and nestedness ($\beta_{NES}$) components (Baselga, 2010). For

230    calculations we used function *beta.multi*, from package 'betapart' 1.3 (Baselga & Orme, 2012) in

231    R. These calculations were also done pairwise between all trapping locations within the same

232    mountain using the function *betapart::beta.pair*. These distances were used for a cluster analysis

233    using neighbor-joining with (Saitou & Nei, 1987) using *ape::nj* function in R to evaluate the

234    community similarity between mountains and elevations.

235        We estimated the contribution of endemics to $\beta_{SIM}$ and $\beta_{NES}$ components of beta

236    diversity. For each mountain, we removed endemic species from the dataset and recalculated

237    $\beta_{SIM}$ and $\beta_{NES}$ (hereafter referred to as $\beta_{SIM\text{-}end}$ and $\beta_{NES\text{-}end}$). We created subsets of the data to

238    which these measures could be directly compared by randomly sub-sampling 5,000 times

239    without replacement, several species from the complete dataset equal to the non-endemics

240    present in that mountain. P-values were determined from the distributions of the permutated

241    values.

242    **Results**

243    *Field survey*

244    The overall trapping success increased towards high elevation on both mountains. On Mt.

245    Tambuyukon, we trapped a total of 295 different individuals (not including recaptured animals)

246    from 21 different species (Dataset S1, Table S1) over 5,957 trap nights, for a total of 5.0% trap

247    success (not including arboreal or pitfall trapping; Table 1). Trap success at each elevation

248    ranged from 2.1% at 1,600 m to 9.6% at 2,400 m. One non-target capture of a carnivore, a

249    Kinabalu ferret-badger (*Melogale everetti*), was recorded. The trap success calculations were

250    done excluding pitfall traps and arboreal traps (due to inconsistent placement of traps). The use

251    of pitfall and arboreal traps was limited by the time necessary to set and check arboreal traps,

252    difficulty finding appropriate places to set pitfall traps and the high number of tourists on Mt.

253    Kinabalu, which limited the sites we could set traps to those out of sight of the trails. The

254    accumulation of species across trap nights varied across elevations, and appeared near saturation

255    in all trapping locations (Figure S1). A species of shrew, *Suncus sp.*, was collected in a pitfall

256    trap, and a gray tree rat (*Lenothrix canus*) in an arboreal trap, bringing the total number of

257    species to 23.

258            On Mt. Kinabalu, we trapped a total of 20 species from 209 different individuals (Dataset

259    S1; Table S1) over 2,022 trap nights, for an average trap success of 10.3% (Table 1). The trap

260    success across elevations was much higher on Mt. Kinabalu, ranging from 5.6% (at 900 m), to

261    15.4% (at 2,700 m) (Table 1). This overall higher capture rate resulted in species saturation with

262    a lower number of trap nights on Mt. Kinabalu than on Mt. Tambuyukon (Figure S1).

263   *Species distribution*

264   The mountain treeshrew, *Tupaia montana,* was the most frequently caught species (35.7 % of all

265   catches) and it had a wide elevational distribution from 836 - 3,382 m. The Bornean mountain

266   ground squirrel (*Sundasciurus everetti,* formerly *Dremomys everetti*; Hawkins et al. 2016), the

267   long-tailed giant rat (*Leopoldamys sabanus*), and Whitehead's spiny rat (*Maxomys whiteheadi*)

268   also had large elevational distributions on both mountains (Figure 2). The lowland (< 1,000 m)

269   terrestrial small mammal community was the most diverse with 19 species trapped. We captured

270   16 species in the community associated with montane forest between 1,000 - 2,400 m and only 7

271   species at 2,400 m and above (Figure 2).

272         We captured a single shrew (*Suncus sp.*) after a trapping effort of 176 pitfall trap nights.

273   A less intensive arboreal trapping effort of 76 trap nights yielded seven individuals from six

274   small mammal species: *Tupaia montana* (n = 2), *Lenothrix canus* (n = 1), *Callosciurus prevostii*

275   (n = 1), *Sundasciurus jentinki* (n = 1), *Sundamys muelleri* (n = 1) and *Tupaia minor* (n = 1).

276   Despite the smaller effort of arboreal trap nights, we still captured two species that were not

277   trapped elsewhere (*Lenothrix canus* and *Sundasciurus jentinki*). We used a threshold of three

278   meters off the ground to consider a trap arboreal. However, we also caught arboreal species in

279   ground traps or traps close to the ground (< 3m), including *Chiropodomys pusillus*, *Callosciurus*

280   *prevostii* and *Tupaia minor*.

281         We set 4 trail cameras on Mt. Tambuyukon to document larger mammals not targeted by

282   our traps. They documented an additional 8 species of mammals (Table 2; Figure S2). The

283   number of species captured by the cameras varied from one to five, with the camera at 500 m

284   exhibiting the most diversity, both in number of species and number of independent visits (Table

285   2). They documented four species that were not documented in any other way.

286    On Mt. Tambuyukon, several species were detected only through direct observation

287    (Table 3). Of these sightings many were documented only a single time, including the orangutan

288    (*Pongo pygmaeus*), the Bornean giant tufted ground squirrel (*Reithrosciurus macrotis*),

289    Whitehead's squirrel (*Exilisciurus whiteheadii*), and the bearded pig (*Sus barbatus*). The

290    Bornean gibbon (*Hylobates muelleri*) was heard singing on an almost daily basis, but only

291    directly observed a single time. The sambar deer (*Rusa unicolor*) was heard vocalizing once at

292    1,400 m. Only one observation was made of a carnivore, the Malay civet (*Viverra tangalunga*),

293    which was observed during a late night-walk. The visual observations increased the diversity of

294    species documented, especially for primates and tree squirrels.

295    *Alpha diversity*

296    Both mountains showed a similar pattern for alpha diversity indices across elevations (Figure 3;

297    Table S2). Species richness and Shannon diversity were maximum in low elevations and

298    decreased gradually towards high elevations. However, evenness was lowest at middle elevations

299    (U-shaped) (Figure 3). The high dominance of some species at middle elevations (e.g. mountain

300    treeshrew) leads the Shannon diversity to sink at around 1,500 m in both mountains. However,

301    Shannon diversity increases again towards the highest elevations due to the more even

302    occurrence of the species in the small mammal communities at these elevations, despite the

303    lower species richness (Figure 3). The species richness we report in low elevations for both

304    mountains are above the upper 97.5% quantile of the expected richness expected under the

305    hypothesis of the mid-domain effect (Figure 3A).

306        We detected a significant negative relationship between species richness and elevation (

307    $\chi^2_1 = 8.81$, p = 0.003). However, species richness was not correlated with expected species

308    richness under the MDE ($\chi^2_1 = 0.54$, p = 0.46) (Figure 3).

309    Elevation was positively correlated with higher proportion of endemic species ($\chi^2 = 7.96$,

310    df = 1, p = 0.005) and a greater proportion endemic species captured ($\chi^2 = 10.7$, df = 1, p =

311    0.001) (Figure 4).

*Beta diversity*

313    Variation in the species composition assemblages, or beta diversity, was very similar for

314    both mountains ($\beta_{SOR} = 0.77$ on Mt. Kinabalu and $\beta_{SOR} = 0.74$ on Mt. Tambuyukon). Most of this

315    beta diversity derived from the turnover component ($\beta_{SIM} = 0.73$ for Mt. Kinabalu and 0.65 for

316    Mt. Tambuyukon). The nestedness component was very low on both mountains ($\beta_{NES} = 0.04$ for

317    Mt. Kinabalu and 0.09 for Mt. Tambuyukon) (Figure 5). This indicates that the assemblages at

318    different elevations are not the product of species loss from the richest assemblages. Instead, they

319    are singular assemblages with different species compositions. We found large dissimilarities in

320    the turnover component between pairwise locations within each mountain ($\beta_{sim}$) associated with

321    < ~1900 m vs > ~ 1900 m locations, compared to lower values within lowland or highland

322    locations (Tables S3). When removing endemic species from the dataset, $\beta_{NES-end}$ increased and

323    $\beta_{SIM-end}$ decreased on both mountains (Figure 5). The permutations indicated that this decrease in

324    the turnover component ($\beta_{SIM-end}$) was significant in Tambuyukon ($\beta_{SIM-end} = 0.36$, $p = 0.002$), but

325    not in Kinabalu ($\beta_{SIM-end} = 0.68$, $p = 0.36$), and that the increase in nestedness ($\beta_{NES-end}$) was

326    significant for Mt. Tambuyukon ($\beta_{NES-end} = 0.38$, $p = 0.001$), but only marginally significant for

327    Mt. Kinabalu ($\beta_{NES-end} = 0.14$, $p = 0.05$) (Figure 5).

328    The clustering analysis grouped trapping locations in 2 main groups, above and below

329    ~1,400 m (Figure S3). Within the high elevation group, all locations above ~ 1,900 m clustered

330    together.

331    **Discussion**

332    We report an extensive survey of non-volant small mammals within Kinabalu National Park,

333    Borneo. A sampling effort of 8,231 trap-nights in Mt. Kinabalu (n = 2,044) and its neighbor peak

334    Mt. Tambuyukon (n = 6,187) yielded a total of 512 individual records (Mt. Kinabalu, n = 213;

335    Mt. Tambuyukon, n = 299) from 27 species (Mt. Kinabalu, n = 20; Mt. Tambuyukon, n = 23)

336    (Table 1; Figure 2). Records from camera traps and direct observations increased the total

337    number of species recorded for Mt. Tambuyukon by 18 to a total of 44 (Table 3).

338           Mt. Kinabalu is a biodiversity hotspot for many taxa (van der Ent 2013). Its mammal

339    fauna has been studied for over a century (eg. Oldfield, 1889; Whitehead, 1893; Emmons, 2000;

340    Nor, 2001) and it is known to host 61 species of non-volant small mammals (Nor, 2001; Payne et

341    al., 2007). We further explored for the first time the non-volant small mammal diversity along

342    the complete elevational gradient in Mt. Tambuyukon (2,579 m), the third-highest peak in

343    Borneo and only 18 km away from Mt. Kinabalu. Some important sightings on Mt. Tambuyukon

344    included the orangutan (*Pongo pygmaeus*), which has an estimated population of only 50

345    individuals within Kinabalu Park boundaries (Ancrenaz et al., 2005). The Kinabalu ferret-badger

346    (*Melogale everetti*) was a significant finding since it is the first official record of this species on

347    Mt. Tambuyukon (Payne et al., 2007; Wilting et al., 2016). We trapped this species at 2,051 m

348    on Mt. Tambuyukon and 3,336 m on Mt. Kinabalu. We identified a population of the summit rat

349    (*Rattus baluensis*) on Mt. Tambuyukon, previously only known from Mt. Kinabalu. This species

350    was common at high elevations and has its lower distribution limit at around 2,000 m. A

351    population genetic analysis of the summit rats from Mt. Kinabalu and Mt. Tambuyukon

352    demonstrated that they are currently genetically isolated (Camacho-Sanchez *et al.* 2018). We

353    also make the first records of the mountain species *Maxomys alticola*, *Melogale everetti*,

354    *Hylomys suillus* and *Niviventer rapit* on Mt. Tambuyukon.

355    *Alpha diversity*

356    Species richness peaked at low elevations on both mountains coinciding with the lowland

357    dipterocarp forest. Then, it decreased gradually towards the highest elevations where it was

358    lowest (Figure 3). This pattern deviates from the expectations of the MDE (Figure 3), and the

359    MDE reported by Nor (2001) in a previous small mammal survey on Mt. Kinabalu with a very

360    similar survey scheme to ours. Colwell & Lees (2000) suggested that a MDE should constitute

361    the null hypothesis over which deviations should be interpreted. However, this point of view is

362    not universal (Rahbek, 1995; McCain, 2007, 2009). Incomplete sampling of the low elevations

363    happens regularly and can artificially create a MDE (Rahbek, 1995; Lomolino, 2001), which

364    may explain the difference between Nor (2001) and our results for the same mountain. Our

365    surveys detected 12 more species as compared to Nor (2001), including a climbing mouse,

366    *Chiropodomys pusillus*, a tree rat *Lenothrix canus*, Prevost's squirrel, *Callosciurus prevostii*,

367    Jentink's squirrel, *Sundasciurus jentinki*, the rats *Maxomys rajah*, *M. alticola* and *Sundamys*

368    *muelleri*, the non-native species *Rattus exulans* and *R. tiomanicus*, two species of treeshrews

369    *Tupaia longipes* and *T. minor*, and two species of shrews, one trapped in a small Sherman trap,

370    *Crocidura* sp.*,* and one in a pitfall trap, *Suncus sp.*. The effects of an incomplete sampling should

371    be more acute in lowland elevations where there is more habitat heterogeneity (Rosenzweig,

372    1992, 1995) and species might tend to occupy smaller ranges (Rosenzweig, 1995; Brown, 2014).

373    However, we report the highest alpha diversity in the lowest elevations, which supports that our

374    sampling scheme was not affected by this low-elevation sampling bias. Another observation

375    supporting the comprehensiveness of our sampling is that we documented species in all sites

376    between the lowest and highest occurrences, except for *M. whiteheadi* on Mt. Kinabalu, and *M.*

377    *ochraceiventer* and *N. rapit* on Mt. Tambuyukon.

378         Conversely, the gradual decrease of species richness we recorded was explained by

379    elevation alone. Even in the presence of a MDE, a gradual decrease of species richness with

380    elevation seems to be a general pattern in mountain gradients (Rahbek, 1995). There are multiple

381    factors that are correlated with elevation which have been proposed to explain diversity across

382    mountains gradients, but disentangling their effects is difficult given the multicollinearity

383    (Heaney, 2001; Fu et al., 2006; Kluge, Kessler & Dunn, 2006). The strong correlation of alpha

384    diversity with elevation enables further discussion. Diversity has been proposed to peak with

385    precipitation (Heaney, 2001), but on Mt. Kinabalu the peak of precipitation, at around 2,000 m

386    (Kitayama, 1992), did not match the diversity peak. Productivity (Aiba, Takyu & Kitayama,

387    2005) and temperature (Kitayama, 1992) are negatively correlated with elevation in Kinabalu,

388    and could potentially explain the diversity pattern. Nevertheless, it has been suggested that

389    examining resource availability for this taxonomic group is more appropriate than simply

390    looking at productivity (Brown, 2001; Heaney, 2001). However, this is a difficult variable to

391    measure that was not incorporated in our original survey experimental design. A more plausible

392    explanation for the change in diversity is area and habitat complexity. Available area (Camacho-

393    Sanchez et al., 2018) and complexity of the forest (Kitayama, 1992) decrease with elevation on

394    Mt. Kinabalu. The peak in diversity we find in low elevations is consistent with the spatial

395    hypothesis which states that (1) at the regional level, larger areas (such as the lower elevations in

396    mountains) have lower rates of extinction over speciation (Rosenzweig, 1992) and (2) that larger

397    areas have more types of different habitats, so greater species diversity should be observed in

398    larger areas (Rosenzweig, 1995). Perhaps, the relationship between area and diversity on

399  elevational gradients along large mountains falls somewhere between these processes (McCain,

400  2007).

401  *Beta diversity*

402      The composition of the small mammal assemblage changed across elevation in a similar

403  way between mountains. Indeed, all trapping locations in high elevations (above ~1,900 m) were

404  very similar in composition (Figure S3). Mid-mountain locations showed intermediate

405  compositions whereas the 500 m and 900 m locations on both mountains also clustered together.

406  This montane fauna transition was already identified by Nor (2001) to be at around 1,800 m, and

407  it matches approximately the vegetation limit between the lower and upper montane forests on

408  Mt. Kinabalu (Kitayama 1992). The influence of this shift is reflected in the overall high

409  turnover component of beta diversity ($\beta_{SIM}$) for both mountains (Figure 5). The pairwise turnover

410  components ($\beta_{sim}$) were highest between lowland - highland locations (Tables S3). This indicates

411  the lowland and highland communities are composed of different species, rather than the

412  community with the lowest richness (highland) being a subset of the species present on the

413  richest one (lowland). This pattern has already been described for other small mammals across

414  several mountain systems (Mena & Vázquez-Domínguez, 2005). Unfortunately, there is no

415  consistent data collection from other tall mountains in Sundaland to discuss a common mountain

416  biogeography pattern in this region. Historical expeditions to Sumatra also point to a similar shift

417  in vegetation structure and different mammal assemblages at high elevations above 2,000 m

418  (Robinson & Kloss, 1918, 1919; Miller, 1942).

419  *Pattern of endemism*

420      Beyond the net alpha and beta diversity we describe, we place special attention on the

421  nature of the species that could be driving these diversity patterns. Our models predicted that the

422   proportion of Bornean endemism as well as the proportion of endemic species captured increased

423   with elevation (Figure 4). At the same time, we found that the high-elevation endemics were

424   responsible for the high turnover component in beta diversity in both mountains (Figure 5). The

425   species that had the greatest contribution to this high-elevation endemism were *Rattus baluensis,*

426   *Tupaia montana*, *Sundasciurus everetti* and *Maxomys alticola* (Table S1). These species are

427   restricted to mountain areas in northern or central-northern Borneo, and were present in high

428   abundance and evenness from 2,000 m (Table S1). Nor (2001) reported high trapping success on

429   Mt. Kinabalu, associated with higher abundance at these elevations, but he did not record

430   *Maxomys alticola*. Heaney (2001) also recorded the highest abundances in the top elevations in

431   the Philippines, and a peak of endemics at higher elevations. Three additional trapped species are

432   mountain endemics (*Melogale everetti, Sundasciurus jentinki* and *Niviventer rapit*) but

433   contributed less to our analysis because of their lower densities or detectability. This pattern of

434   high-elevation endemics could be even more pronounced as the distribution and taxonomy of the

435   highland mammals also found on other islands in Sundaland are further updated and revised (i.e.

436   *Hylomys suillus* and *Sundamys infraluteus*; Camacho Sánchez, 2017). A majority of the lowland

437   species are widespread, and also distributed across other Sundaland landmasses such as Sumatra

438   and the Malay Peninsula (Corbet & Hill, 1992).

439        The pattern of mountain endemics on Mt. Kinabalu has previously been described for

440   other taxa (Merckx et al., 2015). For mammals, this has also been observed by Heaney (2001),

441   Sanchez-Cordero (2001), Swenson et al. (2012) and Chen et al. (2017) on other mountains. Mt

442   Kinabalu is unique in Sunland due to its high elevation (4,095 m) and the scarcity of nearby

443   peaks above 2,000 m. Higher isolation on mountain peaks boosts mountain endemism worldwide

444   (Steinbauer et al., 2016), which could explain the greater endemism in the higher elevations in

445    the Kinabalu range. For instance, a pattern of mountain endemism linked to divergence in

446    allopatry induced by isolation from the combination of topography with past climate changes has

447    been described in Bornean birds (Sheldon, Lim & Moyle, 2015; Moyle et al., 2017; Manthey et

448    al., 2017). A similar pattern of high mountain endemism driven by intra-island speciation has

449    been reported for shrews in Sumatra and Java (Esselstyn et al., 2013; Demos et al., 2016).

450    Presumably, the high degree of isolation of the habitats on the higher slopes of Mt. Kinabalu help

451    to maintain a highly endemic community. This could be due to reduced dispersal and

452    colonization to/from nearby similar areas as proposed by Steinbauer et al. (2016).

453    **Conclusions**

454    We found a decline in small mammal diversity from low to high elevations on both Mt. Kinabalu

455    and Mt. Tambuyukon. This pattern differs from the MDE previously described for Mt. Kinabalu

456    and other mountains worldwide. The decrease in diversity with elevation is concordant with the

457    spatial hypothesis predicting higher diversity in lowlands driven by historically larger areas with

458    less extinction and more habitat heterogeneity. However, we cannot exclude other climatic or

459    ecological hypothesis. Endemic species were in higher proportion and more abundant in higher

460    elevations and they drove the turnover component of beta diversity. The high number of

461    mountain endemics point to historical factors as important drivers of the biogeography in this

462    region.

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699    **Supplementary Information**

700    Dataset S1: Data on animals sampled and trapping effort.
701    Table S1: Summary table of species per elevation.
702    Figure S1: Trap-night accumulation curves
703    Figure S2: Photographs from camera traps.
704    Table S2: Diversity indices.
705    Figure S3: Cluster analysis.
706    Tables S3: Pairwise beta diversity.

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% |

Results of camera trap survey.

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

1 Table 2: Results of camera trap surveys on Mt. Tambuyukon, with relative abundance calculated

2 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 |

All species recorded on Mt. Tambuyukon.

All species recorded on Mt. Tambuyukon.

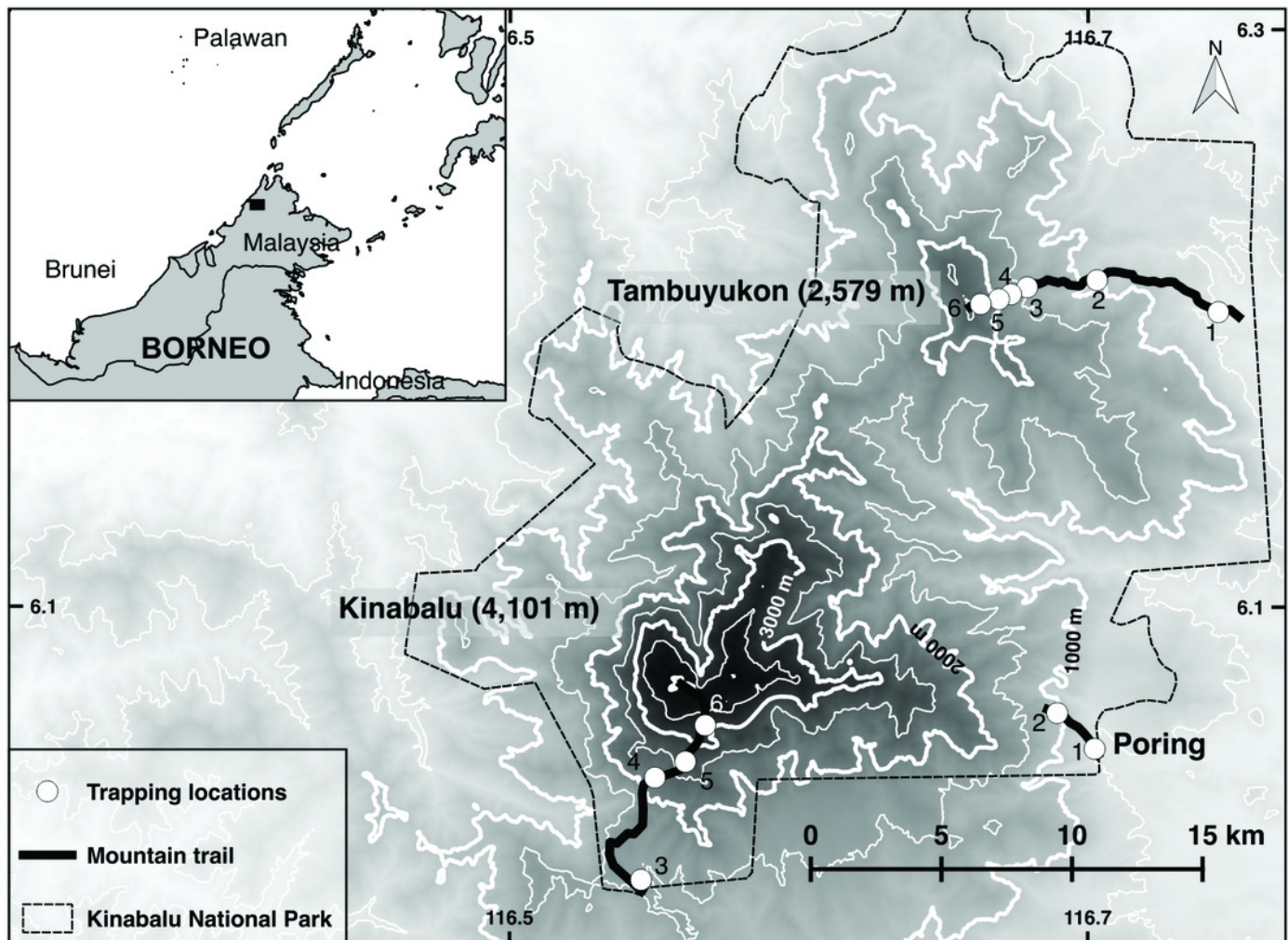
1 Table 3: All species recorded on Mt. Tambuyukon.

| 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 |

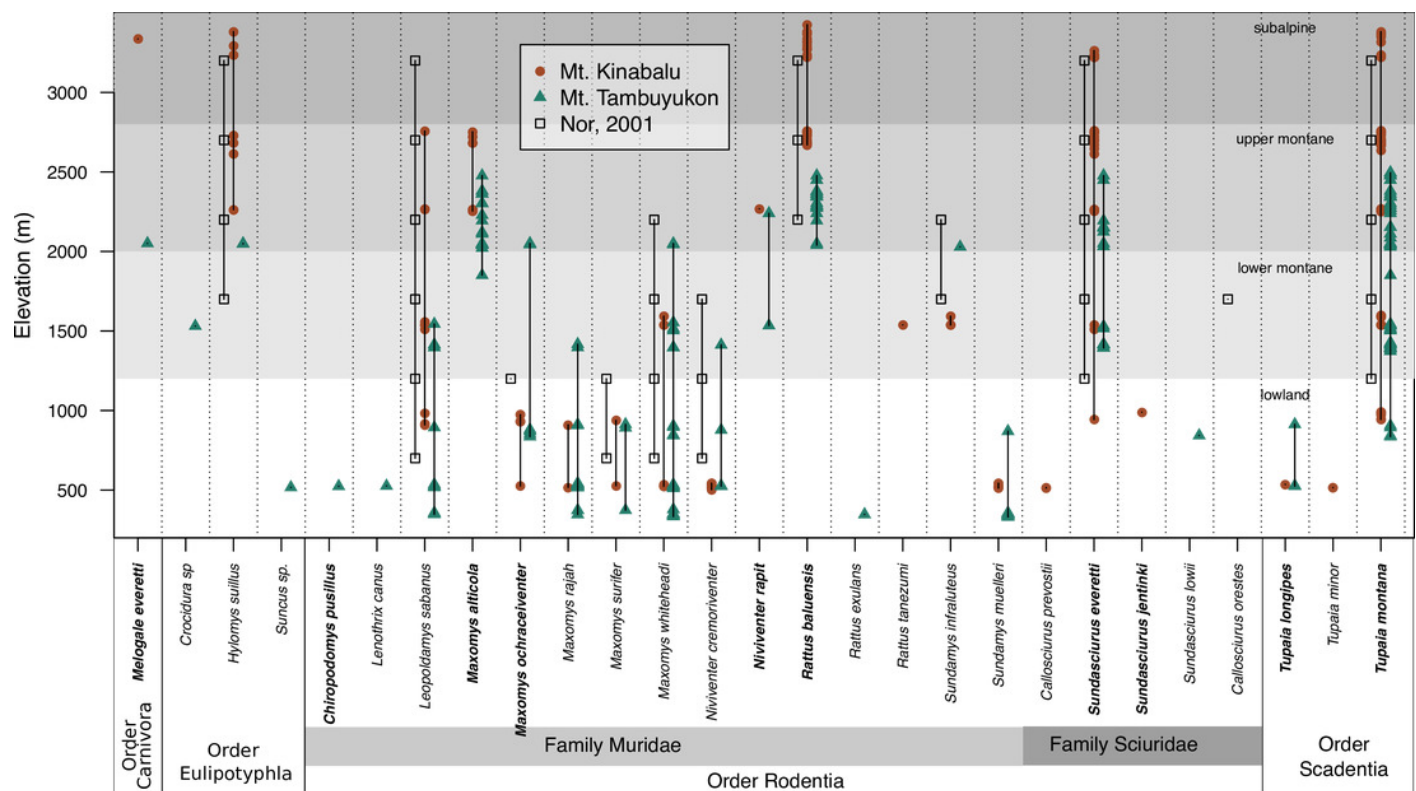
| 32 | Sciuridae | Whitehead's Squirrel | *Exilisciurus whiteheadi* | observation |
|---|---|---|---|---|
| 33 | Sciuridae | Giant Bornean Tufted Ground Squirrel | *Reithrosciurus macrotis* | observation |
| 34 | Soricidae | Shrew | *Crocidura* sp. | live trap |
| 35 | Soricidae | Shrew | *Suncus sp.* | 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 |

# Figure 1

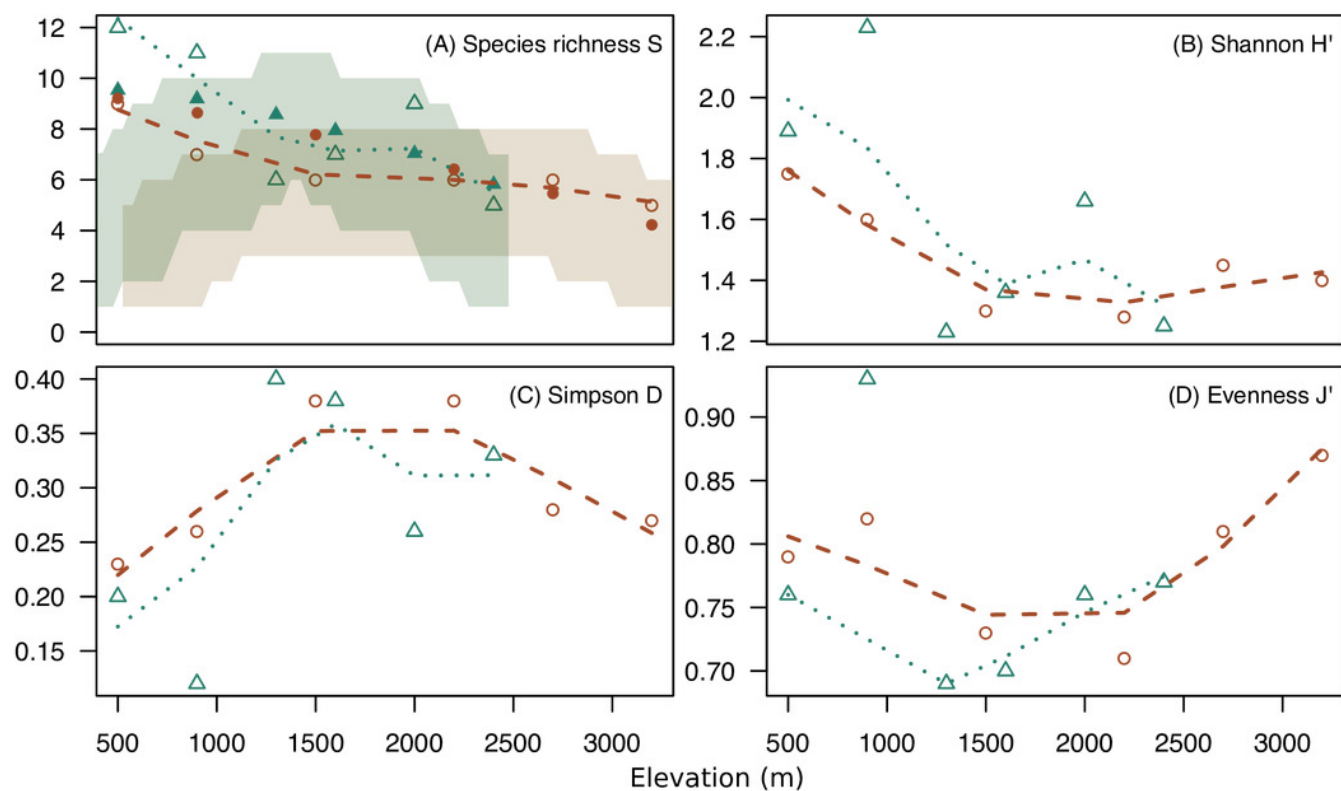
Trapping locations

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

# Figure 2

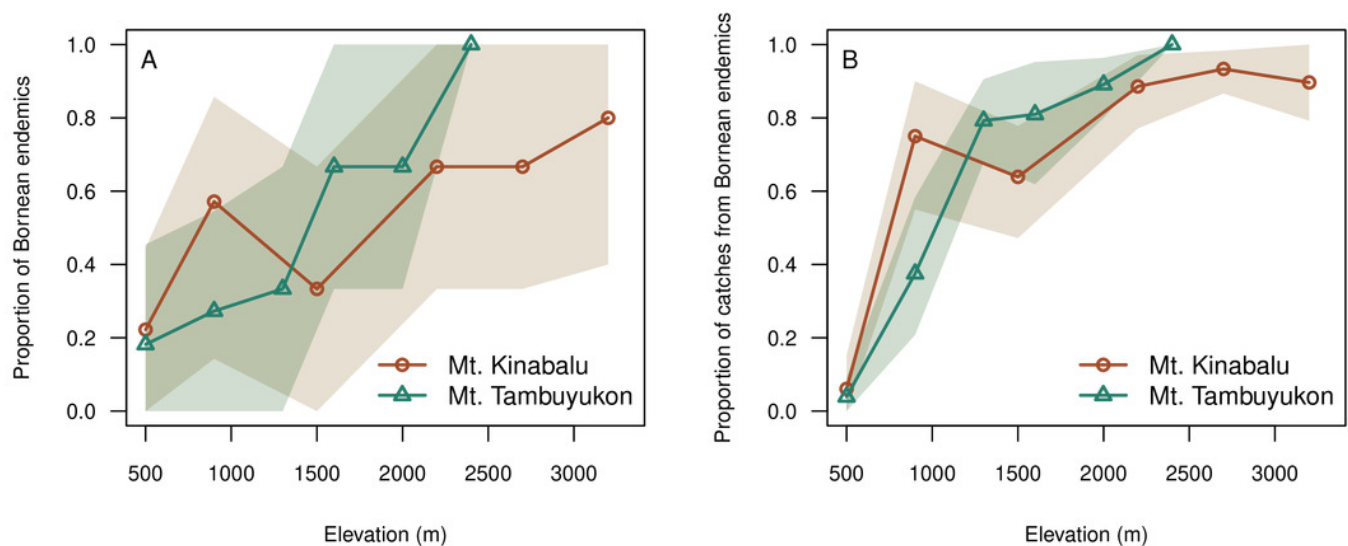
Species distribution across elevations.

Species distribution across elevations. Our two field surveys are represented by circles (Mt. Kinabalu), and triangles (Mt. Tambuyukon), together with a previous small mammal survey on Mt. Kinabalu (open squares; Nor, 2001). Endemic species are bolded. We have represented the vegetation levels as described in Kitayama (1992) for Mt. Kinabalu in greyscale in the background.

# Figure 3

Diversity indices across elevations.

Diversity indices across elevations for Mt. Kinabalu (circles) and Mt. Tambuyukon (triangles) with loess regressions (Mt. Kinabalu, dashed line; Mt. Tambuyukon, pointed line). Shaded areas represent the 2.5% and 97.5% percentiles of the species richness for expectations under the MDE (Mt. Kinabalu, brown; Mt. Tambuyukon, green). Closed symbols in panel A are the fitted values of species richness corrected for autocorrelation.

# Figure 4

Endemism with elevation

Proportion of Bornean endemics (A) and proportion of catches belonging to Bornean endemics (B) across elevation. A confidence envelope for the observed values is represented as a shaded area from 1000 bootstrap replicates.

# Figure 5

Beta diversity with and without endemics

Sorensen dissimilarity ($B_{SOR}$) decomposed in it nestedness ($B_{SNE}$) and turnover ($B_{SIM}$) components, for Mt. Kinabalu and Mt. Tambuyukon (left/right depiction in set of data points, respectively). Solid horizontal lines represent the observed values, while the dotted horizontal lines are the estimated beta diversity measures after removing endemic species from the matrix ($B_{SIM-end}$, $B_{SNE-end}$ and $B_{SOR-end}$). The random expectations for $B_{SIM-end}$, $B_{SNE-end}$ and $B_{SOR-end}$ are represented from the dotted cloud with 5,000 permuted values (see main text), together with their corresponding 2.5% and 97.5% percentiles (vertical grey bar).