**ORIGINAL ARTICLE**

# Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo

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**ABSTRACT**

**Aim** We quantify the elevational patterns of species richness for all vascular plants and some functional and taxonomic groups on a regional scale on a tropical mountain and discuss some possible causes for the observed patterns.

**Location** Mount Kinabalu, Sabah, Borneo.

**Methods** A data base containing elevational information on more than 28,000 specimens was analysed for vascular plant distribution, taking into account sampling effort. The total species richness pattern was estimated per 300-m elevational interval by rarefaction analyses. The same methods were also applied to quantify species richness patterns of trees, epiphytes, and ferns.

**Results** Total species richness has a humped relationship with elevation, and a maximum species richness in the interval between 900 and 1200 m. For ferns and epiphytes the maximum species richness is found at slightly higher elevations, whereas tree species did not have a statistically significant peak in richness above the lowest interval analysed.

**Main conclusions** For the first time a rigorous estimate of an elevational pattern in species richness of the whole vascular plant flora of a tropical mountain has been quantified. The pattern observed depends on the group studied. We discuss the differences between the groups and compare the results with previous studies of elevational patterns of species richness from other tropical areas. We also discuss the methods used to quantify the richness pattern and conclude that rarefaction gives an appropriate estimate of the species richness pattern.

**Keywords**

Altitudinal gradient, Borneo, macroecology, Mount Kinabalu, rarefaction, sampling effort, species diversity, species richness gradient, tropical mountains.

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## INTRODUCTION

Mount Kinabalu in Sabah, Borneo probably has one of the richest floras in the world, with *c.* 5000 species of vascular plants documented from an area of 1200 km[2] (Beaman, 2005). Kinabalu is also the highest mountain in Southeast Asia. Elevational gradients offer a fascinating challenge for understanding broad-scale patterns of species distributions and patterns of diversity. Owing to the short geographical distances and large climatic differences, elevational gradients are ideal for studying broad-scale patterns in diversity. Studies of species diversity along elevational gradients have become increasingly popular during the last decade, and our knowledge about elevational diversity patterns is accumulating rapidly (Rahbek,

1995, 2005). Relatively few studies have, however, been made on vascular plants in species-rich areas such as Mount Kinabalu. Most studies from tropical areas have been made at a local scale, based on field sampling of transects and often only on a subset of the total flora (Kitayama, 1992, 1996; Lieberman *et al.*, 1996; Kessler, 2001; Bachman *et al.*, 2004). Indeed, studies of elevational patterns considering the pattern of the whole vascular plant flora along the entire elevational gradient on a tropical mountain, and where sampling effort is standardized are rare. Rahbek (1995) reviewed the then available elevational studies and found 12 regional studies of plants from the Tropics; none of these had attempted to standardize for sampling effort. The situation 10 years later is probably similar, and we do not know of any studies that have

quantified the elevational pattern of the whole vascular flora on a tropical mountain and accounted for sampling effort. There are many problems in the estimation of species richness in tropical areas, because the flora and fauna are often poorly described and high diversity complicates species identification (Prance *et al.*, 2000; Phillips *et al.*, 2004). Despite the difficulties of working in remote settings, high-quality data are increasingly available from projects where taxonomic experts have investigated the flora of a region. Such a project has now been completed for Mount Kinabalu. An account of this flora has been published in five volumes (Parris *et al.*, 1992; Wood *et al.*, 1993; Beaman & Beaman, 1998; Beaman *et al.*, 2001; Beaman & Anderson, 2004), and a data base of this flora has been prepared with information on all specimens examined, including elevational data. This detailed information at the specimen level, with careful species identification, provides a unique opportunity for the elevational pattern on Mount Kinabalu to be quantified in a rigorous way. Such studies have recently been called for to achieve progress in quantifying and understanding broad-scale patterns of diversity (Gotelli, 2004).

Elevational patterns of parts of the vascular plant species richness on Mount Kinabalu have been quantified previously (Kitayama, 1992, 1996; Aiba & Kitayama, 1999; Kessler *et al.*, 2001). Kitayama (1992, 1996) and Aiba & Kitayama (1999) used field sampling along transects to quantify the elevational pattern of tree species richness. They found that richness decreased exponentially with elevation. Kessler *et al.* (2001) sampled plots of 400 m$^2$ and counted the number of ferns in these plots. The results indicated a mid-elevational peak, but the variance in richness between plots was large and no statistics were applied.

The aim of this study is to quantify the elevational species richness pattern of all vascular plants on Mount Kinabalu. To make the present study comparable with previous studies on Mount Kinabalu we look at elevational patterns of subsets of the flora. In addition to looking at trees and ferns, we also look at epiphytic species because these are thought to constitute a large component of the diversity in tropical wet forests (Gentry & Dodson, 1987; Wolf & Flamenco-S, 2003).

## STUDY AREA

Mount Kinabalu is centred at approximately 6°05′ N, 116°35′ E. Extending to 4094 m above sea level, Kinabalu is the highest mountain in Southeast Asia. The geology of the area is complex (Collenette, 1958; Jacobson, 1978). The lower slopes of the mountain have thick layers of late Cretaceous to Tertiary sandstones and shales of the Trusmadi and Crocker Formations. The core of the mountain is a pluton of mainly hornblende and (granitic) adamellite diapirically emplaced into the complex of older rocks, and is part of a large batholith underlying the area. The central part of the batholith was uplifted during the Pleistocene and constitutes much of the present mountain, one of the youngest major mountains in the world. It may still be rising at a rate of about 5 mm a year

(Tain Choi, 1996). Pleistocene glaciation produced the present ice-carved topography of the summit area. Intrusive ultramafic rocks were uplifted with the core and appear rather like a collar around the mountain at lower and middle elevations. During the Pleistocene, the summit supported an ice cap of about 5 km$^2$ in extent. Deglaciation of the summit occurred *c.* 9200 years ago (Jacobson, 1978).

The mountain has a humid tropical climate, and the mean annual temperature at sea level is 27.5 °C, with a lapse rate of 0.55 °C per 100 m (Kitayama, 1992; Kitayama *et al.*, 1999). Precipitation shows a much more erratic pattern, and no statistically significant simple trends have been found with elevation (Kitayama, 1992; Kitayama & Aiba, 2002). As a result of the cloud zone, however, a steeply increasing moisture gradient is found between 1500 and 2000 m, where the latter elevational level corresponds to the lower cloud level (Kitayama, 1992).

## METHODS

The first scientific collections of the flora of Mount Kinabalu were made in 1851 by Hugh Low (Beaman & Anderson, 2004). Comprehensive works on the Kinabalu flora are Stapf's (1894) monumental account, *On the Flora of Mount Kinabalu, in North Borneo* and Gibbs's (1914) work, *A Contribution to the Flora and Plant Formations of Mount Kinabalu and the Highlands of British North Borneo*. The recent enumeration of the flora is based on inspection of more than 42,000 unique specimens representing around 5000 taxa. A data base of these collections has been developed by Beaman and colleagues [see Beaman (2005) for a description of the data base]. After removing duplicate specimens and specimens that are undetermined (indet. or cf. in the data base; 1589 specimens) 40,264 specimens remain in the data base. Specimens that wait further examination before being given a species name but that are clearly different from any of the other species [aff. (755 specimens) and sp. (981 specimens) in the data base] are included in our analyses. For 29,123 of these collections elevational data have been recorded. For 5339 specimens elevation was given as a range and the range was generally meant to indicate the uncertainty of the collector about the exact elevation. We did not want to discard such a large amount of data so we randomly assigned an elevation within the given range for these species. Specimens with a range larger than 500 m were not included, resulting in our discarding 665 specimens. The remaining number of specimens, used to quantify the elevational patterns, was thus 28,458.

When plotting the frequencies of specimens along the elevational gradient at 100-m intervals a peak was observed for each 300 m (Fig. 1). This is because of the tendency of collectors to use round numbers and because many numbers originally were given in feet (i.e. a peak for each 1000 feet). Using 300-m intervals produces a much smoother curve when plotting the frequencies of specimens along elevation (Fig. 1). We therefore use a 300-m interval when estimating species richness.
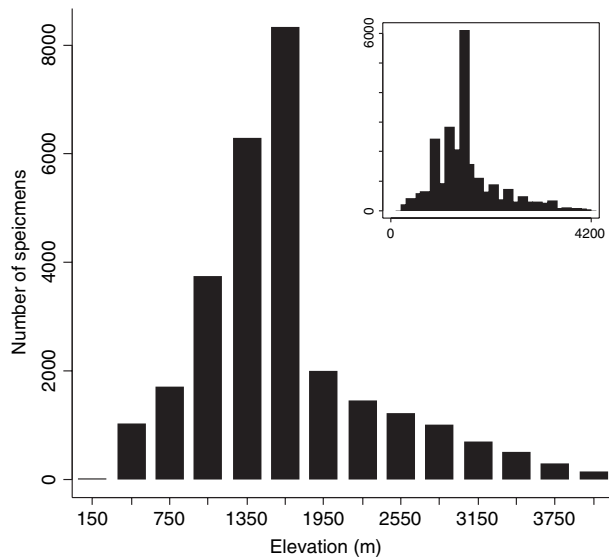
**Figure 1** Number of specimens of vascular plants per 300-m elevational interval on Mount Kinabalu that are found in the data base. Total number of specimens is 28,458. The mid-point of each interval is set along the *x*-axis. The inset figure shows the number of specimens per 100-m elevational interval. Observe the peak in the number of specimens for each 300 m.

When counting species richness per elevational interval the gradient is divided into segments of 300 vertical m. The first segment is from 1 to 300 m (300 m is included). The next segment is then from 301 m up to and including 600 m, and so on until the last interval, which goes from 3901 m up to the summit. In the lowest interval, from 1 to 300 m, only 18 specimens have been recorded and assigned an elevation. Paucity of data for the lowest elevational band means that our analysis begins at 301 m elevation.

As observed from Fig. 1, the differences in sampling at the different elevational intervals are large. A direct comparison of species richness would therefore be meaningless. We want only to quantify the relative species richness of each elevational interval, i.e. the elevational richness pattern, and we therefore use rarefaction methods to estimate the pattern (Fisher, 1999; Brehm *et al.*, 2003; Wolf & Flamenco-S, 2003). The rarefaction methodology makes it possible to compare samples that have different numbers of specimens sampled by randomly drawing an equal number of specimens from the samples and counting the number of species drawn from each sample (Gotelli & Colwell, 2001; Magurran, 2004). Using rarefaction we depict the species richness pattern in three different ways. First, rarefaction curves for the different elevational intervals are shown. Second, we show the pattern of estimated species richness when drawing an appropriate number of specimens from each elevational interval. The number of specimens drawn is a trade-off between how fine-tuned a pattern we are able to detect, and, because some intervals have few specimens, how many intervals we can include in our analyses. Third, we compare elevational intervals pair-wise by estimating by

rarefaction the species richness of the interval with most specimens down to the same number of specimens as the interval with fewest specimens. For the latter approach we also found a 95% confidence interval. If the observed species richness of the interval with fewest specimens was outside this interval we considered the difference statistically significant. Rarefactions were calculated using ecosim 7.68 (Gotelli & Entsminger, 2004). For the first two analyses the average of 100 simulations gave stable results and was therefore considered sufficient. To obtain reliable estimates of the confidence interval for rarefied species richness in the third analysis we used 1000 simulations, and in the few cases where the confidence interval of the rarefied value was exactly equal to the observed value from the other interval we redid the analysis with 10,000 simulations.

If rarefaction is to give a correct relative estimate of species richness it needs to be assumed that the original collections were made randomly. This is probably not true for any data based on herbarium material, because conspicuous and beautiful species tend to be over-represented, and rare species tend to be more commonly collected than would be expected if the sampling effort were completely random. However, we assume that this bias is approximately similar for all the elevational intervals and therefore will consider the patterns that appear to be reliable estimates of the 'true patterns'.

The various subsets of the flora were defined with the aid of information on the species found in the data base. The same information can be found in the volumes of the *Plants of Mount Kinabalu* (Parris *et al.*, 1992; Wood *et al.*, 1993; Beaman & Beaman, 1998; Beaman *et al.*, 2001; Beaman & Anderson, 2004). The previous studies on tree species richness from Mount Kinabalu have focussed on specimens and defined as trees all specimens with a certain minimum diameter at breast height (Kitayama, 1992; Aiba & Kitayama, 1999). Since we do not have this information at the specimen level we have to base the information at the species level. All species that have the potential to be trees are defined as trees in the present study. Likewise, specimens that belong to a species that is often epiphytic are defined as epiphytes in this study (including the ferns). Species that are noted to be rarely or sometimes found as epiphytes are not included in this category. The third subgroup is the ferns, in which we have included fern allies.

When establishing an elevational pattern in richness we acknowledge that elevation itself is not causing any change in species richness (Hawkins & Diniz-Filho, 2004). Unfortunately, it is difficult to correlate climate or environmental data directly with the species richness because such data are limited. We therefore only quantify the relationship between species richness and elevation, and discuss the importance of the various climatic and environmental variables subsequently. Information on climate is primarily taken from Kitayama (1992) and Kitayama *et al.* (1999). Area per 300-m elevational interval is estimated from information found in the Global Land Cover Facility, http://www.landcover.org (USGS, 2004).

## RESULTS

The 28,458 specimens with elevational information represent 3854 species. The species rarefaction curves for each elevational interval are shown in Fig. 2. For none of the rarefaction curves is there any sign of complete sampling, indicating that, even in the elevational interval that has been sampled most intensively (between 1500 and 1800 m), there are still species to be discovered. The rarefaction curves in Fig. 2 show that the intervals between 300 and 1500 m have approximately the same species richness, and that after that a continuous decrease is found. For easier comparison of the species richness pattern, Fig. 3 depicts the rarefied species richness for 250 and 1000 specimens. Estimated species richness based on rarefaction to 250 specimens confirms the impression from the rarefaction curves that species richness is relatively constant from 300 to 1500 m and thereafter decreases all the way towards the summit. Estimated species richness based on 1000 specimens gives a better resolution of what happens at lower elevations, but because many of the intervals at higher elevations have too few specimens, the pattern towards the summit is not seen here. This indicates that the interval from 900 to 1200 m is the most species-rich and that a slight decrease in species richness is found towards the two lowermost intervals. A pair-wise comparison of all intervals, rarefying the number of specimens in the interval with most species down to the same number of specimens as the one with fewest individuals, is shown in Table 1. All comparisons above 1200 m clearly show that species richness is significantly smaller for all interval steps
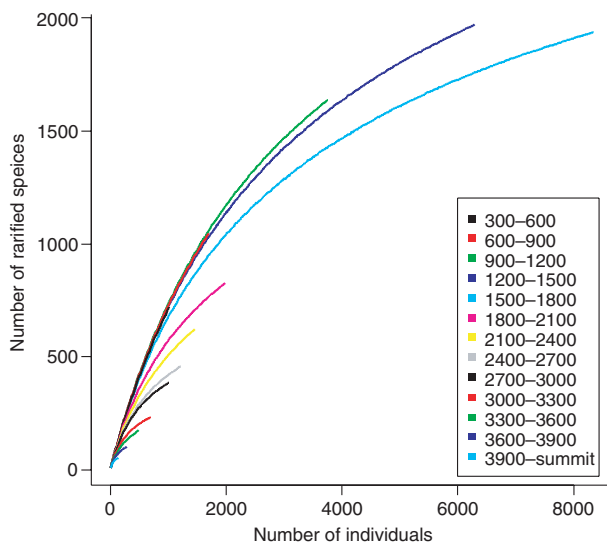


**Figure 3** Estimated species richness of vascular plants per 300-m interval by rarefaction of specimens down to 250 specimens (filled squares) and 1000 specimens (open circles). The estimates are averages of 100 rarefactions for each elevational interval. The intervals with no estimates had fewer than 250 or 1000 specimens, respectively, so estimates for these intervals could not be obtained.

taken towards higher elevations. Below 1200 m the picture is more complex. Rarefied species richness of the interval from 600 to 900 m is higher, but not significantly higher, than that of the lowermost interval analysed (from 300 to 600 m). Rarefied species richness in the interval from 900 to 1200 m is not significantly different from species richness in the interval from 600 to 900 m but it is significantly higher than what is found for the lowermost interval. This means that the rarefaction analyses demonstrate that there is a statistically significant humped elevational pattern of species richness on Mount Kinabalu, although the hump is very weak, and we are not able to say if the peak is in the interval between 600 and 900 m or in the interval between 900 and 1200 m.

Dividing the species up into different life-forms reveals some interesting patterns. Tree species richness has a pattern rather similar to the total species richness, but here the maximum species richness is found to be slightly below that found for total species richness, as the interval from 600 to 900 m has the highest estimated richness (Fig. 4). This interval cannot, however, be separated from the lowermost elevational interval analysed (Table 2). Above the 600 to 900 m band there is a statistically significant decrease in species richness all the way to the summit. This means that we are not able to demonstrate statistically that there is a humped pattern in tree species richness along the elevational gradient on Mount Kinabalu. In the topmost interval there are 13 specimens representing eight species. Note that these specimens are not necessarily trees but belong to species that have the potential to become trees.

For the epiphytes the pattern is clearly humped (Fig. 4). The interval from 1200 to 1500 m has a significantly higher rarefied species richness than the lowermost interval (Table 3). Com-



**Figure 2** Rarefaction curves for vascular plants on Mount Kinabalu. The legend refers to the elevational interval (in metres) for the different curves. The uppermost and lowermost elevational intervals had too few specimens to show visible lines. The curves are the average result of randomly sampling the specimens 100 times for each elevational interval. Note that the intervals between 300 and 1500 m have very similar curves and are therefore difficult to separate on this figure.
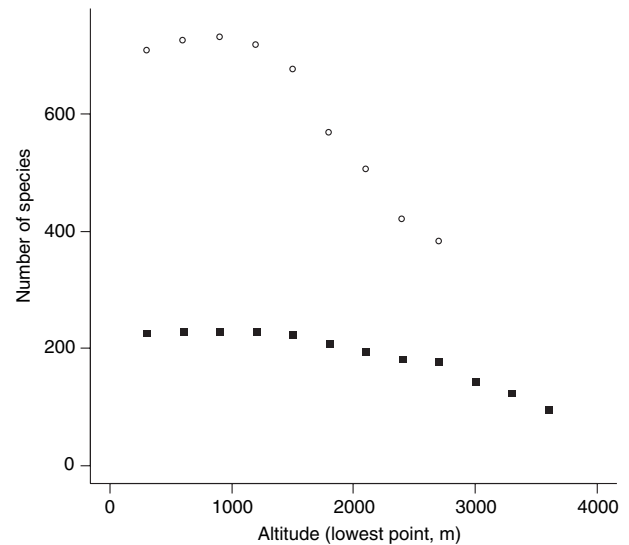
**Table 1** Summary of the pair-wise comparison of the species richness for all vascular plants. The total number of specimens in each elevational interval is shown in column 2. The total number of species observed in each elevational interval is shown in column 3. The subsequent columns show the rarefied species richness estimate based on the specimens in the interval indicated in the column label. For example, a rarefaction of the 1709 specimens in the interval from 600 to 900 m down to 1020 specimens (corresponding to the number of specimens found in the interval from 300 to 600 m) results in an estimated 736 species. This number is based on the average of 1000 rarefaction rounds. The observed number of specimens in the 300–600 m interval is 719 species, meaning that richness is estimated to be higher in the interval from 600 to 900 m when the same number of specimens are sampled but the difference is not statistically significant. Only intervals with more than 20 specimens have been included in the analyses

| Elevational interval (m) | Number of specimens | Number of species observed | Number of rarefied species based on the specimens in the interval (m) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 300–600 | 600–900 | 900–1200 | 1200–1500 | 1500–1800 | 1800–2100 | 2100–2400 | 2400–2700 | 2700–3000 | 3000–3300 | 3300–3600 | 3600–3900 |
| 300–600 | 1020 | 719 | | 736 | 744* | 729 | 684* | 578* | 512* | 424* | | | | |
| 600–900 | 1709 | 1050 | | | 1062 | 1033 | 951* | 767* | | | | | | |
| 900–1200 | 3754 | 1636 | | | | 1588* | 1427* | | | | | | | |
| 1200–1500 | 6306 | 1971 | | | | | 1759* | | | | | | | |
| 1500–1800 | 8343 | 1937 | | | | | | | | | | | | |
| 1800–2100 | 1996 | 828 | | | 1169* | 1136* | 1040* | | | | | | | |
| 2100–2400 | 1460 | 622 | | 947* | 958* | 934* | 865* | 708* | | | | | | |
| 2400–2700 | 1210 | 457 | | 833* | 842* | 823* | 767* | 638* | 563* | | | | | |
| 2700–3000 | 1015 | 385 | 716* | 734* | 741* | 726* | 682* | 576* | 511* | 423* | | | | |
| 3000–3300 | 698 | 234 | 539* | 550* | 555* | 547* | 520* | 454* | 407* | 350* | 327* | | | |
| 3300–3600 | 493 | 173 | 406* | 414* | 416* | 412* | 396* | 355* | 323* | 287* | 273* | 202* | | |
| 3600–3900 | 291 | 101 | 257* | 261* | 262* | 261* | 254* | 236* | 219* | 203* | 197* | 155* | 133* | |
| 3900–summit | 145 | 54 | 136* | 137* | 137* | 137* | 135* | 130* | 124* | 119* | 117* | 100* | 88.5* | 74.5* |

*The 95% confidence interval of the rarefied species richness does not include the observed species richness.
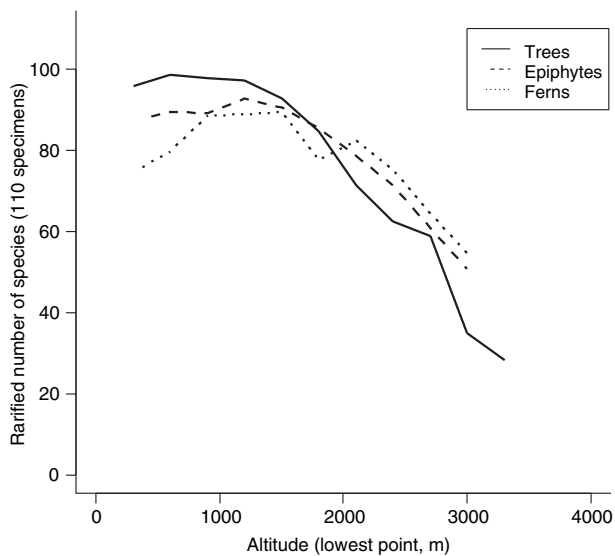
**Figure 4** Estimated species richness of trees, ferns, and epiphytes per 300-m interval by rarefaction of specimens down to 110 specimens, which corresponds to the lowest number of specimens in the interval between 300 and 600 m for ferns. The two other groups and all other intervals are therefore rarefied down to this number of specimens for comparability. The intervals with no estimates had fewer than 110 specimens for the respective group, so estimates for these intervals could not be obtained.

paring the interval from 1200 to 1500 m with the two intervals below gave the same value for the lower confidence interval as the observed value for both of the other two intervals (177 species for 600–900 m and 317 species for 900–1200 m). This means that these intervals are close to being significantly different. Redoing the analyses with 10,000 simulations gave a significant difference between the 900–1200 m interval and the 1200–1500 m interval, but the same result for the comparison with the 600–900 m interval. This occurs even though Fig. 4 shows that the interval from 600 to 900 m probably has lower species richness than the interval from 900 to 1200 m. The reason for this discrepancy is the lower sampling size in the interval from 600 to 900 m, which increases the uncertainty in the rarefied estimate. Above 1500 m there is a statistically significant decrease in rarefied species richness with each elevational step, apart from the step between the two highest intervals analysed. At this step the richness does decrease but it is not statistically significant (although it is close to being significant). Redoing the analysis with 10,000 rarefactions did not alter this conclusion (Table 4).

A humped pattern is also observed for the ferns. The three intervals between 900 and 1500 m have significantly higher richness than any other intervals. At the same time there is no significant difference between these three intervals as judged by the rarefaction analyses. Both above and below these three intervals the species richness decreases. A statistical comparison of the two lowermost intervals has not been made because they have the same number of specimens, but the lowermost interval has fewer species than the interval above, indicating a

steady decrease from the three intervals with most species. The interval from 1500 to 1800 m reveals an irregularity in the continuous decrease above 1500 m. The reason for this is probably related to sampling, but when looking at the 222 specimens found in this interval we were not able to identify any more specific cause for this irregularity.

## DISCUSSION

This is the first study to quantify the regional elevational species richness pattern of the whole vascular plant flora on a tropical mountain while accounting for sampling effort. More than 28,000 unique herbarium specimens identified by specialists form an exceptionally high-quality data set for the study of regional elevational species richness patterns in the Tropics.

Rarefaction analyses are employed to correct for sampling effort, and, despite the fact that the data are not derived from random collection (random sampling being ideal for rarefaction analyses – Gotelli & Colwell, 2001; Magurran, 2004), the data are internally consistent. Although the lack of randomness puts some restrictions on how the data can be treated for macroecological analyses, we believe that these data, and herbarium data in general, are suitable for quantifying elevational patterns in species richness. Actually, the data used here are probably more random with respect to elevation than those of many other data sets, because the collectors' knowledge about prior collections is in most cases limited. An alternative way of treating such data would be to interpolate the species as present at all intervals between the observed extreme elevations. Such treatment has been demonstrated to create artificially humped patterns (Grytnes & Vetaas, 2002). Extrapolation of species richness by, for example, Chao estimators or abundance-based coverage estimator (ACE) has been applied in some studies (Brehm et al., 2003; Wolf & Flamenco-S, 2003). Extrapolations were also tried here, but we abandoned the approach because the estimates turned out to be very dependent on the number of individuals included. The reason for the failure of these methods is probably related to the high species diversity of the area and to the fact that the sampling size is not large enough for such a high-diversity area to give reliable estimates (Colwell & Coddington, 1994). As the aim of this paper was primarily to quantify species richness patterns, i.e. the relative number of species in each elevational interval and not the absolute number, we found that rarefaction gave sensible estimates of the patterns. Consequently, we consider rarefaction to be the best way to quantify regional richness patterns in species-rich and underexplored areas, i.e. in most of the Tropics.

We found that species richness along an elevational gradient on Mount Kinabalu, from 300 to c. 4000 m, shows a weak hump. Maximum species richness is observed in the interval from 900 to 1200 m. A moderate decrease in species richness is found in the two elevational intervals below 900 m, but a steeper, progressive, decrease in species richness is found in the intervals above 1200 m. Relatively few studies have looked at

**Table 2** Summary of the pair-wise comparison of the species richness for tree species. The total number of specimens in each elevational interval is shown in column 2. The total number of species observed in each elevational interval is shown in column 3. The subsequent columns show the rarefied species richness estimate based on the specimens in the interval indicated in the column label. See Table 1 for further explanations. Only intervals with more than 20 specimens have been included in the analyses

| Elevational interval (m) | Number of specimens | Number of species observed | Number of rarefied species based on the specimens in the interval (m) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 300–600 | 600–900 | 900–1200 | 1200–1500 | 1500–1800 | 1800–2100 | 2100–2400 | 2400–2700 | 2700–3000 | 3000–3300 | 3300–3600 |
| 300–600 | 361 | 250 | | 261 | 255 | 248 | 228* | 191* | 145* | | | | |
| 600–900 | 757 | 427 | | | 408* | 393* | 348* | | | | | | |
| 900–1200 | 1201 | 515 | | | | 495* | 431* | | | | | | |
| 1200–1500 | 2495 | 658 | | | | | 561* | | | | | | |
| 1500–1800 | 2859 | 584 | | | | | | | | | | | |
| 1800–2100 | 558 | 241 | | 354* | 341* | 329* | 296* | | | | | | |
| 2100–2400 | 406 | 154 | | 285* | 277* | 269* | 246* | 204* | | | | | |
| 2400–2700 | 328 | 110 | 233* | 244* | 238* | 232* | 214* | 181* | 138* | | | | |
| 2700–3000 | 218 | 81 | 170* | 177* | 174* | 171* | 160* | 140* | 110* | 90.9* | | | |
| 3000–3300 | 148 | 40 | 124* | 128* | 127* | 125* | 119* | 106* | 86.9* | 74.1* | 68.5* | | |
| 3300–3600 | 119 | 29 | 103* | 106* | 105* | 103* | 99.3* | 90.5* | 75.3* | 65.5* | 61.6* | 36.5* | |
| 3600–3900 | 42 | 13 | 39* | 40.3* | 40.1* | 39.9* | 39.3* | 37.7* | 34.7* | 32.4* | 31.5* | 22.0* | 18.6* |

*The 95% confidence interval of the rarefied species richness does not include the observed species richness.

**Table 3** Summary of the pair-wise comparison of the species richness for epiphytic species. The total number of specimens in each elevational interval is shown in column 2. The total number of species observed in each elevational interval is shown in column 3. The subsequent columns show the rarefied species richness estimate based on the specimens in the interval indicated in the column label. See Table 1 for further explanations. Only intervals with more than 20 specimens have been included in the analyses

| Elevational interval (m) | Number of specimens | Number of species observed | Number of rarefied species based on the specimens in the interval (m) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 300–600 | 600–900 | 900–1200 | 1200–1500 | 1500–1800 | 1800–2100 | 2100–2400 | 2400–2700 | 2700–3000 | 3000–3300 | 3300–3600 |
| 300–600 | 224 | 146 | | 154* | 155 | 164* | 157 | 141 | 128* | 107* | 85.3* | | |
| 600–900 | 272 | 177 | | | 178 | 188 | 180 | 159* | 143* | 117* | 91.4* | | |
| 900–1200 | 688 | 317 | | | | 330* | 307 | | | | | | |
| 1200–1500 | 1246 | 433 | | | | | 397* | | | | | | |
| 1500–1800 | 2070 | 473 | | | | | | | | | | | |
| 1800–2100 | 619 | 244 | | | | 313* | 291* | | | | | | |
| 2100–2400 | 443 | 184 | | | 246* | 259* | 243* | 209* | | | | | |
| 2400–2700 | 297 | 121 | | | 190* | 200* | 191* | 168* | 150* | | | | |
| 2700–3000 | 297 | 94 | | | 190* | 200* | 190* | 168* | 150* | | | | |
| 3000–3300 | 185 | 64 | 128* | 134* | 135* | 142* | 137* | 124* | 114* | 97* | 79* | | |
| 3300–3600 | 57 | 31 | 50.2* | 50.8* | 50.7* | 52* | 51.4* | 49.2* | 47.6* | 44.2* | 40.2* | 35.3* | |
| 3600–3900 | 26 | 15 | 24.5* | 24.6* | 24.7* | 25* | 24.8* | 24.3* | 23.9* | 23* | 21.9* | 20.2* | 17.7 |

*The 95% confidence interval of the rarefied species richness does not include the observed species richness. Note that some pair-wise comparisons are not made because intervals have same number of specimens.

**Table 4** Summary of the pair-wise comparison of the species richness for fern species. The total number of specimens in each elevational interval is shown in column 2. The total number of species observed in each elevational interval is shown in column 3. The subsequent columns show the rarefied species richness estimate based on the specimens in the interval indicated in the column label. See Table 1 for further explanations. Only intervals with more than 20 specimens have been included in the analyses

| Elevational interval (m) | Number of specimens | Number of species observed | Number of rarefied species based on the specimens in the interval (m) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 300–600 | 600–900 | 900–1200 | 1200–1500 | 1500–1800 | 1800–2100 | 2100–2400 | 2400–2700 | 2700–3000 | 3000–3300 | 3300–3600 |
| 300–600 | 119 | 79 | | | 94.9* | 95* | 95.3* | 82.1 | 87.3* | 79.3 | 67.7* | 56.9* | |
| 600–900 | 119 | 84 | | | 94.6* | 94.6* | 95.5* | 82.2 | 87.3 | 79.4 | 67.7* | 57* | |
| 900–1200 | 330 | 189 | | | | 194 | 194 | | | | | | |
| 1200–1500 | 661 | 278 | | | | | 276 | | | | | | |
| 1500–1800 | 846 | 304 | | | | | | | | | | | |
| 1800–2100 | 222 | 120 | | | 149* | 150* | 151* | | 131* | 113* | 92.4* | | |
| 2100–2400 | 276 | 149 | | | 170* | 173* | 175* | | | | 101* | | |
| 2400–2700 | 231 | 115 | | | 153* | 155* | 156* | | 135* | | 94.1* | | |
| 2700–3000 | 289 | 103 | | | 175* | 179* | 180* | | | | | | |
| 3000–3300 | 191 | 68 | | | 134* | 136* | 136* | 111* | 120* | 105* | 86.3* | | |
| 3300–3600 | 56 | 38 | 45.51 | 47.4* | 50.1* | 50.0* | 50.3* | 46.5* | 48.1* | 45.6* | 41.3 | 37.2 | |
| 3600–3900 | 36 | 23 | 31.39 | 32.2* | 33.5* | 33.5* | 33.6* | 31.9* | 32.5* | 31.5* | 29.4* | 27.1 | 28* |

*The 95% confidence interval of the rarefied species richness does not include the observed species richness. Note that some pair-wise comparisons are not made because intervals have same number of specimens.

the species richness pattern of all vascular plants along a whole gradient in the Tropics. Kessler (2002) reported that total species richness decreased monotonically with elevation when the whole flora of Ecuador was investigated, and Grytnes & Vetaas (2002) reported a humped species richness pattern with the whole flora in sub-tropical Nepal. Neither of these studies included a factor for sampling effort. In the latter study it was demonstrated that interpolation of species ranges may be at least partly responsible for the observed hump.

The climatic variables most commonly related to species richness of vascular plants, and especially to variation in primary productivity, are typically measures of energy (e.g. temperature or potential evapotranspiration) or measures of energy in combination with water availability (e.g. actual evapotranspiration) (O'Brien, 1993; Odland & Birks, 1999; Grytnes, 2003a; Currie et al., 2004; Rahbek, 2005). Area is a profoundly important factor for species richness that may have a large influence on elevational species richness patterns (Rosenzweig, 1995; Körner, 2000; Lomolino, 2001). Relating this pattern directly to explanatory factors is difficult, because some appropriate data are unavailable. The lack of reliable metadata makes a statistical evaluation of the factors influencing richness patterns difficult, and a further discussion of these factors is not included here. However, for the sake of completeness we have added available information about climatic factors and area and a short discussion of these factors in Appendix S1 in the Supplementary Material. The mid-domain effect is a hypothesis that has received much attention recently in connection with elevational gradients (Colwell & Hurtt, 1994; Grytnes & Vetaas, 2002; Grytnes, 2003b; Zapata et al., 2003; Colwell et al., 2004; McCain, 2005). We do not discuss this further here as we will examine this factor in more detail in a forthcoming paper.

The elevational species richness pattern differs between the different functional groups. Factors that would have been expected to influence species richness in the same way for all groups, for example area and the mid-domain effect, cannot therefore be the only factors determining the elevational species richness pattern. The observed differences in species richness patterns indicate that some group-specific ecophysiological or evolutionary traits play a role in determining what richness pattern is observed.

After dividing the species into functional groups it is only trees that do not have the statistically significant humped pattern. However, even trees do not have their maximum diversity in the lowermost interval, but in the interval above (from 600 to 900 m). The number of tree species in the two lowest intervals cannot be differentiated statistically by the methods we use because of the low number of specimens in the lowermost interval, and the resulting large variance in the rarefaction analysis. The pattern of tree species richness partly confirms previous studies based on plot sampling along the same elevational gradient (Kitayama, 1992; Aiba & Kitayama, 1999). These studies found an exponential decrease in species richness of trees with elevation; that is, a much more dramatic decrease in species richness with elevation than observed here,

at least in the lower part of the mountain. Kitayama (1992) compared species richness patterns of different sized plots from 600 to 3400 m. At 600 m he found 153 species, at 800 m richness was reduced to 102 species, and at 1200 m that richness was further reduced to 79 species. A very similar trend for tree species richness was observed by Aiba & Kitayama (1999). Even though the lowermost interval is not covered in either of these two studies, it is evident that they found a much clearer increase in species diversity towards the lowermost elevations studied than is indicated in the present study. There are two possible explanations that may account for this difference in observed pattern between the previous studies and this study. First, the use of rarefaction may mask the differences in the number of rare species along the altitudinal gradient, and rarefaction analyses will in addition dampen differences in richness as diversity becomes very high. Second, scale has been demonstrated several times to have a profound effect on how we perceive species richness patterns and on what factors are important at the different scales (Rahbek & Graves, 2001; Whittaker et al., 2001; Rahbek, 2005). While the observed pattern based on plot sampling at a fine scale may reflect local-scale processes such as species interactions, the observed pattern in the present study, meant to represent all species found in an elevational interval, may be more a reflection of the effects of evolutionary history and dispersal than of local processes.

There are a few other studies looking at elevational patterns in tree species richness in the Tropics. Lieberman et al. (1996) correlated tree species richness with elevation in Costa Rica and found that diversity peaked at 300 m. Their study was based on sampled plots of 1 ha, but they were also able to account for the number of specimens in the plots and found that the conclusion remained the same when the higher number of stems at 300 m was accounted for. Whittaker (1977, using data from Yoda, 1967) found a monotonically decreasing trend in tree species richness with elevation in subtropical Nepal, except for one plot at the lowest elevation (at c. 250 m judging from the figure shown in Whittaker, 1977), which had fewer species than the plots above (at c. 1100 m). Bhattarai & Vetaas (2003) investigated the richness pattern between 100 and 1500 m in the same area and found indications of a hump at 700 m when looking at tree species richness. Lovett (1999) counted the number of species per 20 individual trees and found no elevational trend in richness on Tanzanian mountains. Owing to the relatively few studies that contain enough data from the lowermost portions of elevational gradients in the Tropics, it is difficult to draw any general conclusions, but it seems likely that a peak in tree species richness is found somewhere not far from the bottom of the elevational gradient, at least in areas with relatively high humidity (Givnish, 1999).

Epiphytes have maximum species richness on Mount Kinabalu in the interval from 1200 to 1500 m. Ferns show a similar pattern and have maximum species richness in the same elevational interval. Many ferns are epiphytes, so it is not surprising that these show a similar pattern (on Mount Kinabalu, 236 of 609 fern species are epiphytes). As reported by Gentry & Dodson (1987) in their pantropical analysis of epiphytes, around two-thirds of the epiphytes are orchids on Mount Kinabalu (619 epiphytic orchid species out of 963 epiphytic species). The elevational richness pattern of epiphytes from Mount Kinabalu agrees well with that from a similar study of epiphytic elevational diversity from Chiapas in Mexico, where similar methods were used to estimate the elevational pattern in diversity (Wolf & Flamenco-S, 2003). In the Chiapas study, the highest diversity was found between 1000 and 1500 m. Similar results were found in two studies of neotropical epiphytes (Küper et al., 2004; Krömer et al., 2005; Cardelús et al., 2006). Gentry & Dodson (1987) compared different areas in the tropical Andes and found indications of a hump in the cloud zone between 2000 and 2500 m. They emphasized the importance of high moisture for high species diversity of epiphytes. On Mount Kinabalu, the peak in species richness of epiphytes is found c. 500 m below the lower level of the cloud zone. The cloud zone on Mount Kinabalu is considered to be the zone with the highest moisture (Kitayama, 1992). The peak in epiphytic richness on Mount Kinabalu therefore does not coincide with the zone with highest moisture as predicted by Gentry & Dodson (1987). However, a modifying factor that might be responsible for lowering the elevational peak in epiphyte richness is the number of niches available for the epiphytes. As observed in this study, the number of tree species decreases rapidly with elevation above 1500 m, reducing the heterogeneity of habitats for the epiphytes. The height of the canopy also shows a clear decrease with elevation (Kitayama, 1992). This may counteract the effect of moisture, giving a peak in richness below the zone with highest moisture.

Fern species richness was analysed earlier at a regional scale on Mount Kinabalu using the same data set as used in the present study but with a different treatment of data (Parris et al., 1992; Kessler et al., 2001). These studies found that fern species richness peaks at c. 1500 m, as also found in this study, but their finding of a very steep decrease in species richness below 1500 m is not supported by the analyses made here. Kessler et al. (2001) acknowledge that the steep decrease towards lower elevations in their study is probably related to differences in sampling intensities. With rarefaction analyses we find very similar species richness from 900 to 1800 m. Reducing the number of specimens to the lowest number (330) found in any of the three intervals results in 189 species (900–1200 m), 194 species (1200–1500 m), and 194 species (1500–1800 m), respectively. Kessler et al. (2001) also performed field sampling of ferns along the elevational gradient on Mount Kinabalu, which also revealed a humped pattern, but owing to the high variation in species richness between samples it is difficult to estimate the exact location of maximum species richness. Other studies of ferns similarly find a humped pattern, and when other plant groups are included it is generally the case that the peak in fern species richness is at a higher elevation than that in the other groups (Kessler, 2001; Bhattarai & Vetaas, 2003; Bhattarai et al., 2004; Watkins et al., 2006).

The main finding in this study is that, based on the elevational distribution of more than 28,000 specimens, the total species richness has a humped pattern with a peak in the lower part of the elevational gradient. Similar patterns are observed when looking at fern species richness and epiphytic species richness separately. The species richness of trees, however, shows a monotonically decreasing trend from the lowermost elevations to the summit. More specific analyses are needed to elucidate the potential factors that cause these patterns.

## ACKNOWLEDGEMENTS

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from http://www.Blackwell-Synergy.com:

**Appendix S1** A short discussion of the potential effects of climate and area on the elevational species richness pattern.

## BIOSKETCHES

**John Arvid Grytnes** is a postdoctoral researcher at the University of Bergen. His research interests are all aspects of species richness patterns at different spatial scales. His current projects focus mostly on elevational richness patterns and problems in quantifying and interpreting these patterns.

**John H. Beaman** is an Honorary Research Fellow in The Herbarium at The Royal Botanic Gardens, Kew. With a number of collaborators he recently completed an inventory of the flora of Mount Kinabalu, a project extending over 22 years, and published in five volumes, listing about 5000 species.

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