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Meng Zhang · Shuichiro Tagane · Hironori Toyama
Tsuyoshi Kajisa · Phourin Chhang · Tetsukazu Yahara

Constant tree species richness along an elevational gradient of Mt. Bokor, a table-shaped mountain in southwestern Cambodia

Abstract Some previous studies along an elevational gradient on a tropical mountain documented that plant species richness decreases with increasing elevation. However, most of studies did not attempt to standardize the amount of sampling effort. In this paper, we employed a standardized sampling effort to study tree species richness along an elevational gradient on Mt. Bokor, a table-shaped mountain in southwestern Cambodia, and examined relationships between tree species richness and environmental factors. We used two methods to record tree species richness: first, we recorded trees taller than 4 m in 20 uniform plots (5×100 m) placed at 266–1048-m elevation; and second, we collected specimens along an elevational gradient from 200 to 1048 m. For both datasets, we applied rarefaction and a Chao1 estimator to standardize the sampling efforts. A generalized linear model (GLM) was used to test the relationship of species richness with elevation. We recorded 308 tree species from 20 plots and 389 tree species from the general collections. Species richness observed in 20 plots had a weak but non-significant correlation with elevation. Species richness estimated by rarefaction or Chao1 from both data sets also showed no significant correlations with elevation. Unlike many previous studies, tree species richness was nearly constant along the elevational gradient of Mt. Bokor where temperature and precipitation are expected to vary. We suggest that the table-shaped landscape of Mt. Bokor, where elevational interval areas do not significantly change between 200 and 900 m, may be a determinant of this constant species richness.

Introduction

Terrestrial plant diversity varies with both latitude and elevation (Guo et al. 2013). Tropical areas are well known to harbor the highest levels of plant diversity in the world along an elevational gradient (Whitmore 1999; Kreft and Jetz 2007; Kerkhoff et al. 2014). Ecologists have had a continuing interest in this high species richness in tropical lowland rain forests (Whitmore 1999; Hubbell et al. 2008). While most studies related to the species richness in tropical areas, particularly of plants, have been conducted in lowlands, some studies along an elevational gradient on a tropical mountain have documented that plant species diversity decreases with increasing elevation (see Aiba and Kitayama 1999 for a review). However, most of previous elevational studies did not attempt to standardize the amount of sampling effort (Rahbek 1995; Guo et al. 2013). Grytnes (2003) and Carpenter (2005) made a pioneering transect survey using uniform sampling to standardize sampling effort. Subsequently, Grytnes and Beaman (2006) applied a rarefaction model to densely collected specimen data of Mt. Kinabalu, a prominent mountain on the island of Borneo in Southeast Asia, and estimated total species richness for each elevational interval. The result showed that a weakly hump-shaped elevational pattern of species richness exists, peaking in the interval between 600 and 900 m or between 900 and 1200 m.

A hump-shaped pattern of species richness with a mid-elevational peak has been observed in many studies made on various organisms worldwide (McCain and

M. Zhang · T. Yahara (✉)
Graduate School of Systems Life Sciences, Kyushu University, 744 Motooka, Nishi Ward, Fukuoka 819-0395, Japan
E-mail: tet.yahara@gmail.com
Tel.: +81-092-802-4335

S. Tagane · H. Toyama · T. Kajisa · T. Yahara
Center for Asian Conservation Ecology, Kyushu University, 744 Motooka, Nishi Ward, Fukuoka 819-0395, Japan

P. Chhang
Department of Forestry Management and Community Forestry, Forestry Administration, Ministry of Agriculture Forestry and Fisheries, 40 Preah Norodom Blvd, Phnom Penh, Cambodia

Grytnes 2010; Guo et al. 2013). This pattern agrees with the prediction of the "mid-domain effect" model developed by Colwell and Hurtt (1994) who claimed that a hump-shaped pattern can arise from the random placement of species ranges within a bounded domain, even under uniform environmental conditions. This model triggered a series of empirical studies on species richness along elevational gradients. By reviewing those studies, Currie and Kerr (2008) concluded that observed broad-scale patterns of species richness are not consistent with the mid-domain hypothesis.

Additional empirical studies are needed using a standardized method to examine the pattern of species richness and identify major factors determining variation of species richness with elevation. Thus, we are conducting a series of field surveys in many mountainous areas of tropical Southeast Asia by recording plant species richness within 5- × 100-m plots placed at different elevations on a mountain (Yahara et al. 2012; Tagane et al. 2015). While many studies of tropical lowland forests have used fewer and larger plots, our strategy employs placing smaller plots in many more locations than have been employed in many previous studies of the elevational patterns of plant species richness (Gentry et al. 1995; Grytnes 2003; Sanchez-Gonzalez and Lopez-Mata 2005; Kluge et al. 2006). While our previous studies using 5- × 100-m plots revealed significant changes of species richness along an elevational gradient in most mountains we studied, including Mt. Honba in southern Vietnam, we found a non-significant correlation between species richness and elevation on a table-shaped mountain, Mt. Bokor, in southwestern Cambodia. Mt. Honba and Mt. Bokor are located approximately 400 km apart on the southern Indochina Peninsula, where annual rainfall is very high (Rundel et al. 2003; Stuart and Emmett 2006; Tagane et al. 2015). It would be interesting to know why two geographically proximate mountains under similar climatic conditions would show a notable difference in patterns of species diversity along an elevational gradient.

The main purpose of this study is to describe a pattern of plant species richness along an elevational gradient from 200 to 1048 m in Mt. Bokor, Cambodia. Additionally, we compare these observations with elevational changes of tree density and discuss plausible factors determining the plant species richness pattern along the elevation gradient of Mt. Bokor.

Methods

Study area

We conducted field surveys on the southern slope of Bokor National Park, Kampot Province, southwest Cambodia, facing towards the Gulf of Thailand

(Fig. 1). Bokor National Park covers the entire range of Mt. Bokor, a mountain covering approximately 140,000 ha where the land area per elevational interval (100 m) does not decrease with the elevation except for on the plateau above 900 m (Figs. 1, 2a). The southern slope of Mt. Bokor has an elevational gradient from sea level to a maximum of 1079 m (Rundel et al. 2003; Stuart and Emmett 2006) and the slopes above 200 m are covered with mesic tropical rainforest (Tagane et al. 2015).

The topographic map of Bokor National Park and Mt. Bokor (Fig. 1) was created using Quantum GIS 2.4.0-Chugiak (Quantum GIS Development Team 2014a). A digital elevation model (DEM) was obtained from the Shuttle Radar Topography Mission 90 m database, which is maintained by the Consultative Group for International Agriculture Research Consortium for Spatial Information (Jarvis et al. 2008).

We also conducted field surveys on Mt. Honba (Fig. 1a), in the vicinity of Nha Trang City in southern Vietnam using the same sampling methods employed on Mt. Bokor. The results from Mt. Honba will be discussed elsewhere, but the relationship between elevation and species richness in Mt. Honba is included here to demonstrate that our methods can detect a significant trend.

Climate

We extracted various climate variables from the Worldclim database (Hijmans et al. 2005; http://www.worldclim.org/), including mean temperature and annual precipitation. Mean temperature on Mt. Bokor decreases with elevation, from 25.7 °C at 266 m to 21.9 °C at 1048 m, indicating a decrease of approximately 0.5 °C per 100 m. However, the data cited by Rundel et al. (2003) showed that mean temperature is about 20.4 °C at 950 m; therefore, the temperature data extracted from Worldclim may not be sufficiently reliable at the scale of the elevational gradient in Bokor. According to the Worldclim database, annual precipitation of Mt. Bokor decreases with elevation, from 2726 mm at 266 m to 2450 mm at 1048 m. Furthermore, thick fog surrounds the upper elevation of Mt. Bokor for much of the year (Grismer et al. 2008), and the decreasing trend of annual precipitation derived from the Worldclim database is likely to be inaccurate. In addition, Rundel et al. (2003) reported that annual precipitation on top of Mt. Bokor exceeds 5000 mm and Stuart and Emmett (2006) noted that annual precipitation in Bokor National Park as a whole varies from 3000 to 5000 mm because the summer southwestern monsoon from the Gulf of Thailand causes high rainfall on Mt. Bokor. Considering those inconsistencies, we did not use climatic variables but used elevation itself in our analysis of species richness.
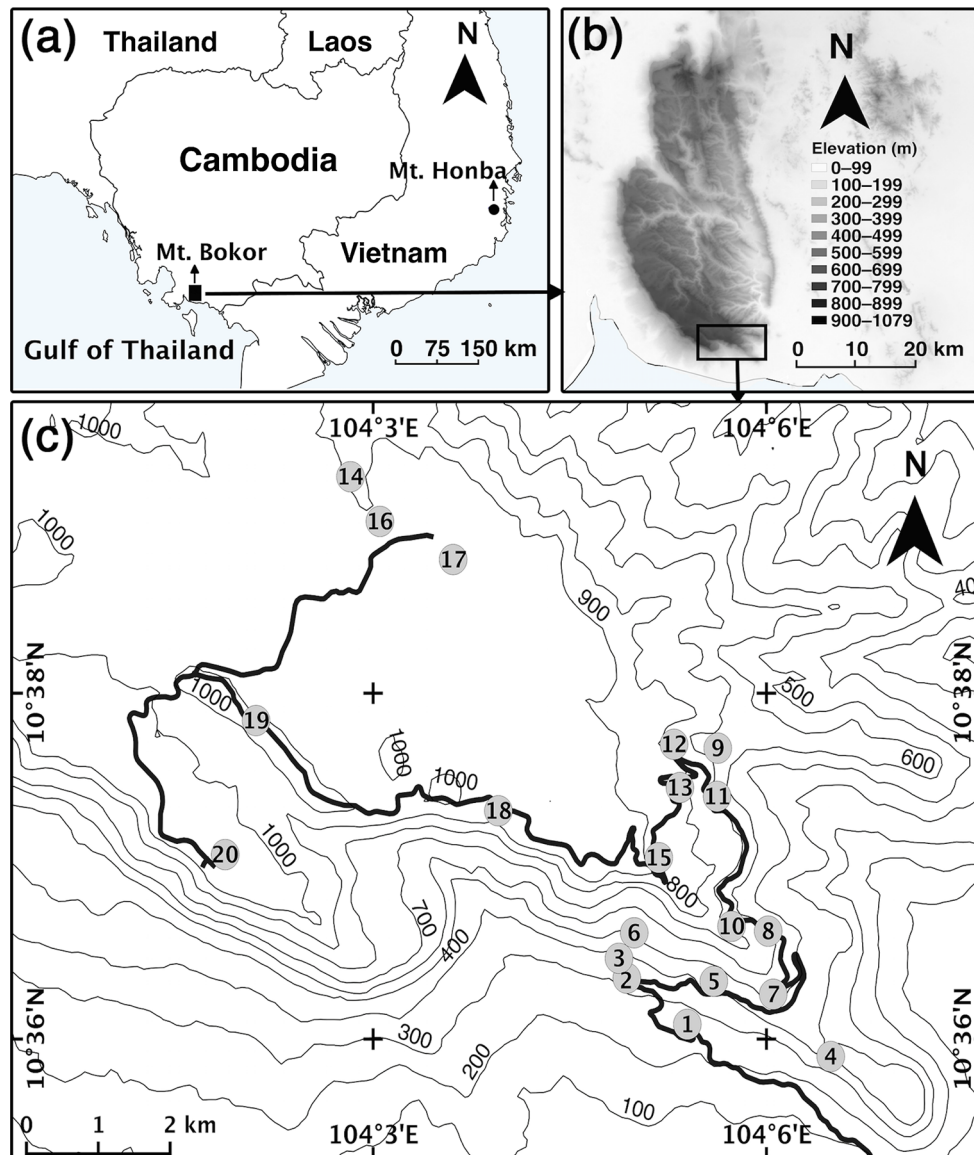
Fig. 1 Study area: **a** locations of Bokor National Park (*black rectangle*) and Mt. Honba (*black solid circle*), **b** topography of Bokor National Park, **c** the locations of plots in the southern slope and top area of Mt. Bokor (*circles with numbers*, sampling plots; *thick line*, main route along which we made general specimen collection; *thin lines*, contours; *plus mark*, cross graticules)

Field surveys

We conducted seven field surveys (December 3–23 in 2011; May 8–16, July 14–20, and October 15–26 in 2012; and February 16–17, August 6–13, and December 7–12 in 2013) on the southern slope and top of Mt. Bokor (Tagane et al. 2015). We used occurrences of tree species recorded by two different sampling methods, namely, plot-based surveys and general collection of specimens. We used not only the former but also the latter method that was employed by Grytnes and Beaman (2006). For the former, we placed 20 rectangular plots (5 × 100 m) along an elevational gradient from 266 to 1048 m (Fig. 1c). All these plots were chosen in areas of natural forest with little human disturbance; we did not place any plot below 200 m because these low-elevation for-

ests are highly disturbed or have been cleared. The start and end points of each plot were georeferenced using GPS. Each plot was divided into 10 subplots (5 × 10 m) and we recorded all tree species above 4 m in each subplot. Species were distinguished in the field, recorded with field names, and carefully identified later using voucher specimens collected in the plots. Specimens of tall trees were collected using a long flexible fiberglass rod equipped with a sickle on the top. In addition to surveying the flora generally, we collected 1120 specimens along the elevational gradient of Mt. Bokor, including the southern slope, along the main road and on the top the plateau. For each species, we counted the number of collection localities in each of nine elevational intervals from 200–299 to 1000–1048 m. In plot and general surveys, we collected a total of 2995 specimens
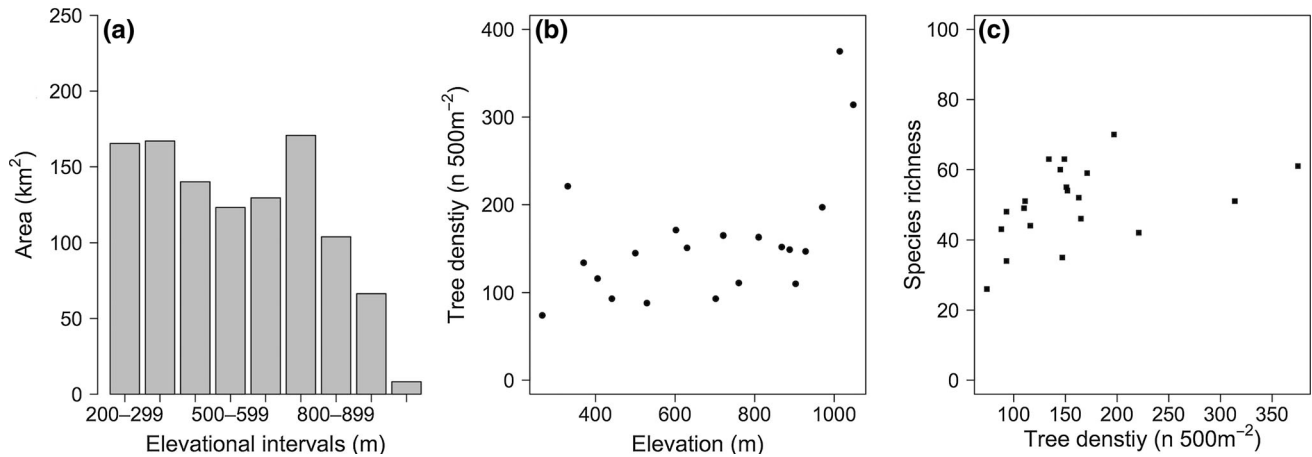
Fig. 2 a Distribution of land area per elevation zone, **b** the relationship between tree density and elevation ($P = 0.013$), and **c** the relationship between species richness and tree density ($P = 0.077$)

(excluding duplicates). Each specimen collected included a leaf sample dried with silica-gel and used for DNA extraction. We followed the methods of Toyama et al. (2015) for DNA isolation and sequencing. Then, species were identified using two DNA barcode regions, *rbc*L and *mat*K, taxonomic literature and authentic specimens including types (Tagane et al. 2015; Toyama et al. 2015). Endemic species of Mt. Bokor are specified based on the most recent taxonomic study of trees of Mt. Bokor (Tagane et al. 2015; Tagane et al. unpublished).

Elevational land area and species pool

In this study, sampling area had no direct effect on species richness because all plots sampled were the same size (500 m^2) along the elevational gradient (Grytnes 2003). However, species richness in a sampling plot is influenced by the number of individuals sampled and the number of species in the species pool (Zobel et al. 1998). The species area relationship indicates that a larger area tends to have a larger number of species (Rosenzweig 1995), and thus has a larger species pool (Grytnes 2003). Here, we calculated the areas of elevational intervals per 100 m (from 200–299 to 1000–1079 m) in the entire mountain range of Mt. Bokor, starting at the Shuttle Radar Topography Mission layer, but excluding the areas below 200-m elevation (Fig. 2a). Elevational interval areas decreased with elevation ($R^2 = 0.67$; $P = 0.007$), but this pattern became non-significant if we excluded the areas above 900 m ($R^2 = 0.18$; $P = 0.19$) (Fig. 2a).

Data analysis

Rarefaction and Chao1 richness estimator

Reducing sampling limitations and biases presents a challenge for ecologists who desire to compare species

richness and analyze diversity patterns (Chao et al. 2005; Colwell et al. 2012). To meet this challenge, a rarefaction model has been proposed (Colwell et al. 2012). In our study, we applied individual-based rarefaction models to the number of species recorded in plots and the number of specimens collected in each of nine elevational intervals. In addition, we calculated Chao1 with a confidence interval (95 %), a widely used estimator of total species richness (Colwell et al. 2004; Colwell 2013) for all the plots and elevational intervals. All of the above approaches were processed using EstimateS version 9.1.0 software with a set of 100 randomizations for estimators (Colwell 2013).

Species richness patterns

Species richness observed in the 20 plots and nine elevational intervals was compared as "point diversity" (Carpenter 2005; Kluge et al. 2006). Species richness was considered to have a Poisson distribution because of its discrete values (McCullagh and Nelder 1989). Thus, simple scatter diagrams and a generalized linear model (GLM) up to the second polynomial with quasi-Poisson regression with a logarithmic link were explored to illustrate the changes of species richness and tree density as a function of elevation as well as the relationship between species richness and tree density. A quasi-Poisson distribution was used to account for overdispersion. In addition, we calculated Moran's I (Fortin et al. 2002; Paradis et al. 2004), one of the most widely used coefficients of spatial autocorrelation, to check for the significance of two-dimensional spatial autocorrelation in our species richness within 20 plots. We calculated Moran's I of all 20 plots and also for neighbors at a geographic distance less than 2 km. All the above calculations and illustrations were made with R 3.0.2 (R Core Team 2014b), using the *ape* package (Paradis et al. 2004) for Moran's I test.

Results

Plots and specimen data

In the 20 plots, we recorded 3029 individual trees with height above 4 m, including 308 species of 178 genera and 76 families (Table 1). Among them, only two species, *Gironniera subaequalis* and *Toxicodendron succedaneum*, were deciduous. *G. subaequalis* was found from 266 to 970 m (58 individuals) and *T. succedaneum* was found above 1000 m (two individuals). The four most abundant species were *Archidendron quocense* (154 individuals), *Lithocarpus elephantum* (67) and *Macaranga andamanica* (66) and *Mallotus paniculatus* (112). Tree density varied from 65 individuals per plot (500 m^2) at 266 m to 348 at 1014 m. Table 2 summarizes the GLM analysis results based on plot data. A significantly positive correlation was observed between elevation and tree density (Fig. 2b, Table 2; $P = 0.013$); however, note that tree density records at 1014 m (348) and 1048 m (295) were much higher than 188 individuals at 970 m, 138 at 928 m and other density records at lower elevations. If the data collected at 1014 m (348) and 1048 m (295) were excluded, the correlation became non-significant (Table 2; $P = 0.148$). Species richness varied from 27 at 266 m to 70 at 970 m (Fig. 3); a weak but non-significant correlation existed between species richness and elevation (Table 2; $P = 0.064$). Moreover, the second polynomial regression also showed species richness had no significant correlation with elevation (Table 2; for elevation, $P = 0.267$; for elevation squared, $P = 0.396$). Additionally, the correlation between tree density and species richness was not significant (Fig. 2c, Table 2; $P = 0.077$). The number of families and genera was also minimal at 266 m and maximal at 970 m. However, on Mt. Honba, a significant increase in species richness was found from 225 to 1200 m with species richness decreasing at 1336 m and 1500 m (Fig. 3, Table 2; fitted to a quadratic curve, for elevation, $P = 0.008$; for elevation squared, $P = 0.014$). As a general floristic survey, we collected 1120 specimens of tree species which represented 389 species of 200 genera and 79 families (Table 3). The number of collected specimens per 100-m interval varied from 45 at 300–399 m to 223 at 900–999 m. Species richness per 100-m interval varied from 42 at 300–399 m to 150 at 900–999 m. The number of specimens was positively correlated with elevation (Dev. = 96.62, $P = 0.021$). However, observed species richness was not significantly correlated with elevation (Fig. 4b; Dev. = 69.3, $P = 0.094$). The numbers of endemic species collected from the highest to the lowest interval were 12, 29, 11, 6, 2, 0, 2, 2, and 0, respectively.

Rarefaction and richness estimator

According to rarefaction curves of 20 plots, if 65 individuals (minimal sample size in Plot 1) are assumed to be sampled, species richness and its 95 % confidence interval vary from 20.91 (CI range: 16.23–25.6) at 330 m to 41.3 (CI range 35.01–47.58) at 888 m (Fig. 5a). However, the 95 % confidence intervals of the Chao1 richness estimator (Fig. 4a) overlapped with each other except in the following two cases: (1) expected richness at 928 m was significantly lower than that in the neighboring plots at 903 m and 970 m, and (2) expected richness at 330 m was significantly lower than that in the neighboring plot at 370 m.

Rarefaction curves for all nine elevational intervals (Fig. 5b) also showed curves that fell within a narrow interval. For species richness and its 95 % confidence interval, rarefaction from the minimum number of

Table 1 Elevations, tree density, the number of families, genera, and species in 20 plots in Mt. Bokor

Plot	Elevation (m)	Individuals	Families	Genera	Species
1	266	65	20	25	27
2	330	221	25	40	42
3	370	134	32	54	64
4	405	115	26	36	43
5	441	93	25	34	34
6	500	145	35	48	60
7	529	95	30	39	43
8	602	145	32	52	59
9	630	142	32	48	54
10	702	93	30	44	48
11	721	136	32	43	47
12	760	111	31	44	51
13	810	163	33	46	52
14	868	152	30	44	54
15	888	140	30	45	63
16	903	110	32	42	49
17	928	138	20	29	34
18	970	188	36	53	70
19	1014	348	33	50	61
20	1048	295	27	41	51

Table 2 Summary of statistical tests using a generalized linear model for: (1) the relationships between observed species richness and species density as a function of elevation, and the relationship between species richness and tree density of plot data on Mt. Bokor; and (2) the relationship between species richness and elevation on Mt. Honba

Study sites	Indicators	Order	Preditors	D.f.	Dev.	P
Mt. Bokor	Richness	2	Elevation	17	38.04	0.267
		2	Elevation^2	17	38.04	0.396
		1	Elevation	18	39.76	0.064
	Density	1	Density	18	40.86	0.077
		1	Elevation	18	388.76	0.013*
	Density.e	1	Elevation.e	16	200.84	0.148
Mt. Honba	Richness	2	Elevation	5	9.29	0.008*
		2	Elevation^2	5	9.29	0.014*

Richness species richness, *density* species density, *density.e* species density excluding the data above 1000 m, *Elevation^2* elevation squared, *elevation.e* elevation below 1000 m, *d.f.* degree of freedom, *Dev.*, residual deviance

* $P < 0.05$ indicates significance

specimens (45), varied from 38.5 (CI range: 34.25–43.64) at 1000–1048 m to 43.61 (CI range 34.07–53.15) at 200–299 m (Fig. 5b). The Chao1 estimated species richness value peaked at the 400–499-m elevational interval of and was the least at the interval of 1000–1048 m. The 95 % confidence intervals of the Chao1 richness estimator (Fig. 4b) did not overlap between the neighboring elevational intervals in one case: between 900–999 and 1000–1048 m.

Spatial autocorrelation

Based on Moran's I of the complete set of 20 plots (obs. = −0.01; exp. = −0.05; SD = 0.06; P = 0.51) no spatial autocorrelation of species richness was observed among the 20 plots. Additionally, Moran's I between the plots with a geographic distance of less than 2 km (obs. = −0.01; exp. = −0.05; SD = 0.16; P = 0.77) also indicated no spatial autocorrelation between them.

Discussion

Constant species richness along the elevational gradient

In this study, we quantified the pattern of tree species richness of a wet tropical rainforest along an elevational gradient on a table-shaped mountain, Mt. Bokor. The observed species richness of 20 plots had no significant pattern along the elevational gradient from 266 to 1048 m. However, species richness data from Mt. Honba, obtained using the same plot size, showed a hump-shaped pattern with a significant increase in species richness from 225 to 1200 m. Also, species richness estimates by Chao1 from the plot data (266–1048 m) showed no significant correlations with elevation (Fig. 4a), and rarefaction estimates standardized for a minimal sample size (65 individuals) showed no significant difference among plots (Fig. 5a). For the general collection data summed for nine elevational intervals (200–299 to 1000–1048 m), observed species richness also had no significant correlations with elevation (Fig. 4b). In addition, species richness estimates by Chao1 from the general collection data showed no significant correlations with elevation (Fig. 4b) and rarefaction estimates standardized for a minimal sample size (45 specimens) showed no significant difference (Fig. 5b). This constant richness pattern agreed neither with the "mid-domain effect" model (Colwell and Hurtt 1994) nor with any of the four common patterns summarized by McCain and Grytnes (2010), where the hump-shaped pattern is considered to be the most common pattern among several elevational gradient research studies involving plants (Rahbek 1995, 2005; McCain and Grytnes 2010; Guo et al. 2013). Thus, our findings in Mt. Bokor provide a unique opportunity to
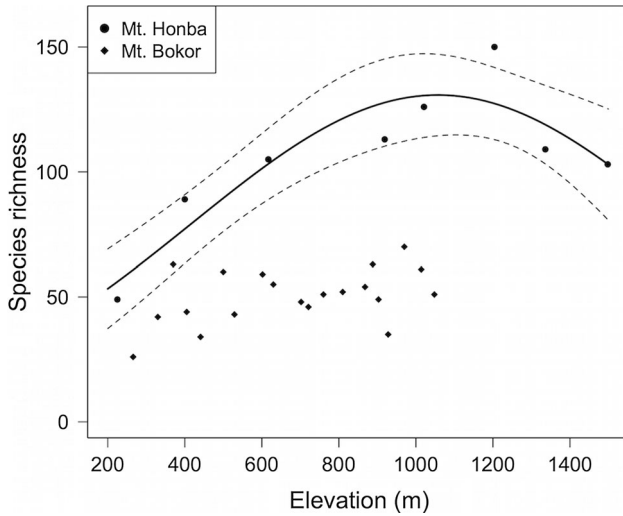
Fig. 3 Relationships between observed species richness and elevation in Mt. Honba (*solid circles*, species richness; *firm curve line*, fitted by generalized linear regression (GLM) with the 95 % confidence interval shown by dash lines, for elevation, $P = 0.008$; for elevation squared, $P = 0.014$) and Mt. Bokor (*solid square*, the relationship was not significant, $P = 0.064$)

understand the relationship of species richness with several factors that can vary with elevation.

Plausible mechanisms behind the constancy of species richness

The fact that species richness is not significantly correlated with elevation implies three possibilities. First, our sample size may be too small to detect the relationship between species richness and elevation. Second, neither temperature nor precipitation had any significant effect on species richness in Mt. Bokor. Third, effects of temperature and precipitation may cancel each other out completely.

Because our survey is based on a small plot size (500 m^2), observed species richness is not saturated within this plot size (Fig. 5), and also because the relationship between species richness and elevation was not significant ($P = 0.064$), further surveys using larger plots may detect a correlation of species richness with elevation. However, a data set from Mt. Honba using the same plot size showed a hump-shaped pattern with the significant increase in species richness from 225–1200 m (Fig. 3). Thus, we can conclude that the correlation between species richness and elevation in Mt. Bokor is, if any, weaker than the significant correlations previously observed on other mountains.

For the second possibility, temperature and precipitation have been considered to be important determinants of species richness along elevational gradients in other situations (Rahbek 1995; Lomolino 2001; Hawkins et al. 2003; Körner 2007; McCain 2007; McCain and Grytnes 2010; Guo et al. 2013). The relationship between tree species richness and temperature is generally hump-shaped (O'Brien et al. 1998). However, our study found no significant change in tree species richness with elevation while the temperature decreases with elevation, implying that temperature alone is not a significant factor restricting species richness in Mt. Bokor. Tree species richness is known to decrease with annual precipitation at a global scale (Francis and Currie 2003; Hawkins et al. 2003) and also in tropical Southeast Asia (Slik et al. 2009). While annual precipitation on top of Mt. Bokor exceeds 5000 mm (Rundel et al. 2003), annual precipitation in Bokor National Park as a whole varies from 3000–5000 mm (Stuart and Emmett 2006). Thus, it is likely that annual precipitation is higher at higher elevations, although the precipitation data ex-
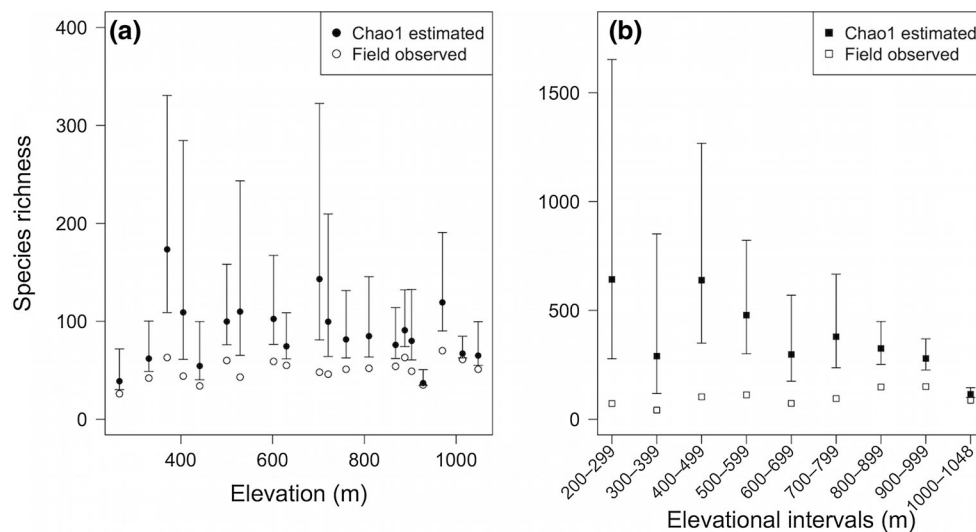

Fig. 4 Field observed species richness and Chao1 estimated richness for the **a** 20 plots and **b** nine elevational intervals. *Open circles/squares*, field observed richness; *solid circles/squares*, point estimates; bars, confidence intervals (95 %)
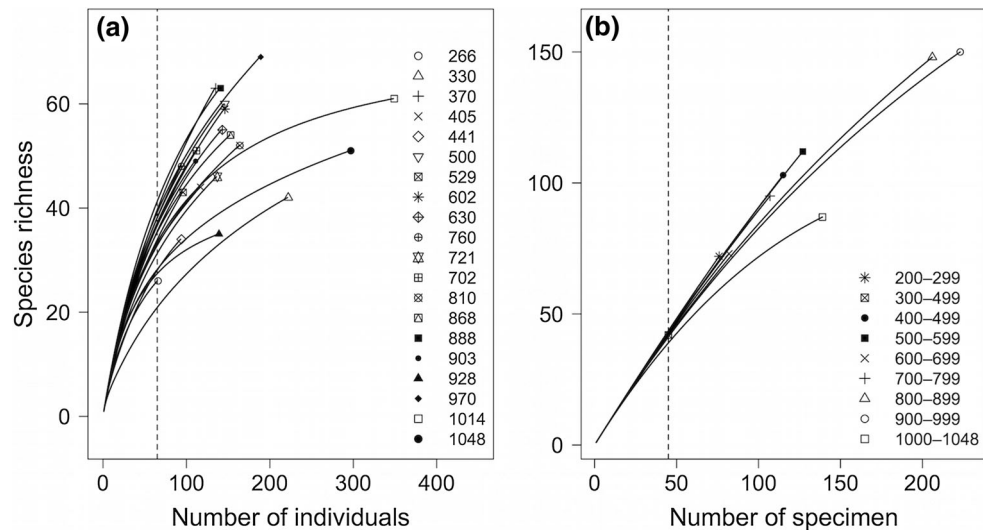
Fig. 5 a Rarefaction curves for 20 plots and **b** nine elevational intervals; a *dash line* in **a** indicates 65, the minimum of individuals recorded, and a *dash line* in **b** indicates 45, the minimum of specimens collected. Legends refer to 20 plots or nine elevational intervals. For simplicity, confidence intervals are not illustrated. Units in both parts of the figure are in m

Table 3 Tree diversity revealed by general collections of specimens in nine elevational intervals on Mt. Bokor

Elevational interval (m)	Specimens	Families	Genera	Species
200–299	76	35	54	72
300–399	45	21	31	42
400–499	115	37	72	103
500–599	127	48	79	112
600–699	82	36	56	73
700–799	107	41	70	95
800–899	206	57	102	148
900–999	223	51	95	150
1000–1048	139	39	65	87

tracted from the Worldclim database shows the reverse trend. Because our study showed no significant change of tree species richness with elevation, it is unlikely that a precipitation gradient alone constrains species richness.

We cannot exclude the third possibility that the combined effects of decreasing temperature and increasing annual precipitation with elevation would have negative and positive effects on species richness, respectively, and therefore could cancel each other. To test this possibility, we need more reliable annual precipitation data from different elevations of Mt. Bokor.

An implication for the land area hypothesis

One of the difficulties in studying patterns of species richness along an elevational gradient is that many factors change with elevation creating confounding conditions with each other (Körner 2007). Temperature decreases with elevation by an average of 0.6 °C for each 100-m increase (Barry 2013). However, land area usually decreases with elevation (Körner 2007). Therefore, when

studying the correlation between elevation and species richness, it is usually difficult to determine whether the correlation reflects a direct coupling or the results of the combining effects of several other factors (Rahbek 1995; Körner 2007). If land area per elevational zone is a major determinant of species richness, then species richness is expected to not decrease with elevation on a table-shaped mountain. This prediction is consistent with our findings on Mt. Bokor that neither Chao1 nor land area per elevation zone significantly vary with elevation below 900 m but Chao1 is significantly lower on the top of the plateau above 1000 m where land area per elevation zone is very limited.

However, the decrease of Chao1 above 1000 m may be associated with the unique environment on the plateau where the landscape is very flat (Fig. 1). We found unique features in the two plots on the plateau (1014 and 1048 m). Tree density was significantly higher (Fig. 2a) while tree height was lower on the plateau. Those observations suggest that some of the forest that has developed on the top of the plateau of Mt. Bokor can be considered to be a kind of kerangas (heath) forest that develops under frequent flooding on a flat landscape (Proctor et al. 1983). In addition, endemism peaks on the plateau, suggesting that the environments on the plateau have been historically unique and have driven adaptive speciation.

Conclusion

We found that Mt. Bokor, an isolated, table-shaped mountain, shows a nearly constant pattern of tree species diversity along an elevational gradient. This pattern does not agree with any of the four common patterns between species richness and elevation summarized by

McCain and Grytnes (2010). We suggest that the table-shaped landscape may be a determinant of this constant species richness. In this study, we focused on trees because the tree species had been mostly completely identified. Subsequent taxonomic studies related to vines, shrubs and herbs that are currently in progress will enable us to examine whether species richness patterns are similar among different life forms. Further studies on other mountains are also needed to deepen our understanding of the patterns of species richness in the tropical rain forests of Southeast Asia.

References

Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. Plant Ecol 140:139–157. doi:10.1023/A:1009710618040

Barry RG (2013) Mountain weather and climate. Routledge, London

Carpenter C (2005) The environmental control of plant species density on a Himalayan elevation gradient. J Biogeogr 32:999–1018. doi:10.1111/j.1365-2699.2005.01249.x

Chao A, Chazdon RL, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol Lett 8:148–159. doi:10.1111/j.1461-0248.2004.00707.x

Colwell RK, Chang XM, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecol 85:2717–2727. doi:10.1890/03-0557

Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J Plant Ecol 5:3–21. doi:10.1093/jpe/rtr044

Colwell RK, Hurtt GC (1994) Nonbiological gradients in species richness and a spurious rapoport effect. Am Nat 144:570–595. doi:10.1086/285695

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples, version 9.1.0. URL http://purl.oclc.org/estimates

Currie DJ, Kerr JT (2008) Tests of the mid-domain hypothesis: a review of the evidence. Ecol Monogr 78:3–18. doi:10.1890/06-1302.1

Fortin M, Dale M, Hoef J (2002) Spatial analysis in ecology. Encycl Environ 4:2051–2058. doi:10.1002/9780470057339.vas039

Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. Am Nat 161:523–536. doi:10.1086/368223

Gentry AH, Churchill SP, Balslev H, Forero E, Luteyn JL (1995) Patterns of diversity and floristic composition in Neotropical montane forests. In: Biodiversity and conservation of Neotropical montane forests. Proceedings of a symposium, New York Botanical Garden, 21–26 June 1993. New York Botanical Garden, pp 103–126

Grismer LL, Thy N, Thou C, Grismer JL (2008) Checklist of the amphibians and reptiles of the Cardamom region of southwestern Cambodia. Cambodian J Nat Hist 2008:12–28

Grytnes JA (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. Ecography 26:291–300. doi:10.1034/j.1600-0587.2003.03358.x

Grytnes JA, Beaman JH (2006) Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. J Biogeogr 33:1838–1849. doi:10.1111/j.1365-2699.2006.01554.x

Guo Q, Kelt DA, Sun Z, Liu H, Hu L, Ren H, Wen J (2013) Global variation in elevational diversity patterns. Sci Rep. doi:10.1038/srep03007

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecol 84:3105–3117. doi:10.1890/03-8006

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. doi:10.1002/joc.1276

Hubbell SP, He F, Condit R, Borda-de-Agua L, Kellner J, Ter Steege H (2008) Colloquium paper: how many tree species are there in the Amazon and how many of them will go extinct? Proc Natl Acad Sci USA 105(Suppl):11498–11504. doi:10.1073/pnas.0801915105

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled SRTM for the globe Version 4. Available from the CGIAR-CSI SRTM 90 m Database. URL http://srtm.csi.cgiar.org

Kerkhoff AJ, Moriarty PE, Weiser MD (2014) The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. Proc Natl Acad Sci USA 111:8125–8130. doi:10.1073/pnas.1308932111

Kluge J, Kessler M, Dunn RR (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Glob Ecol Biogeogr 15:358–371. doi:10.1111/j.1466-822X.2006.00223.x

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proc Natl Acad Sci USA 104:5925–5930. doi:10.1073/pnas.0608361104

Körner C (2007) The use of "altitude" in ecological research. Trends Ecol Evol 22:569–574. doi:10.1016/j.tree.2007.09.006

Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. Glob Ecol Biogeogr 10:3–13. doi:10.1046/j.1466-822x.2001.00229.x

McCain CM (2007) Area and mammalian elevational diversity. Ecol 88:76–86. doi:10.1890/0012-9658(2007)88[76:AAMED]2.0.CO;2

McCain CM, Grytnes JA (2010) Elevational gradient of Species Richness. Wiley, Chichester, UK. URL http://www.els.net. doi:10.1002/9780470015902.a0022548

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. CRC Press, London

O'Brien EM, Whittaker RJ, Field R (1998) Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. Ecography 21:495–509. doi:10.1111/j.1600-0587.1998.tb00441.x

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinforma 20:289–290. doi:10.1093/bioinformatics/btg412

Proctor J, Anderson JM, Fogden SCL, Vallack HW (1983) Ecological Studies in Four Contrasting Lowland Rain Forests in Gunung Mulu National Park, Sarawak: II. Litterfall, Litter Standing Crop and Preliminary Observations on Herbivory. J Ecol 71:261–283. doi:10.2307/2259976

Quantum GIS Development Team (2014) Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. version 2.4.0. URL http://qgis.osgeo.org

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 2:200–205. doi: 10.1111/j.1600-0587.1995.tb00341.x

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol Lett 8:224–239. doi: 10.1111/j.1461-0248.2004.00701.x

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Rundel PW, Middleton DJ, Patterson MT, Monyrak M (2003) Structure and ecological function in a tropical montane sphagnum bog of the elephant mountains, Bokor National Park, Cambodia. Nat Hist Bull 51:185–196

Sanchez-Gonzalez A, Lopez-Mata L (2005) Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. Divers Distrib 11:567–575. doi: 10.1111/j.1366-9516.2005.00186.x

Slik JWF, Raes N, Aiba SI, Cannon CH, Meijaard E, Nagamasu H, Nilus R, Paoli G, Poulsen AD, Sheil D, Suzuki E, Van Valkenburg JLCH, Webb C, Wilkie P, Wulffraat S (2009) Environmental correlates for tropical tree diversity and distribution patterns in Borneo. Divers Distrib 15:523–532. doi: 10.1111/j.1472-4642.2009.00557.x

Stuart BL, Emmett DA (2006) A Collection of Amphibians and Reptiles from the Cardamom Mountains, Southwestern Cambodia. Fieldiana Zool 109:1–27

Tagane S, Toyama H, Chhang P, Nagamasu H, Yahara T (2015) Flora of Bokor National Park, Cambodia & #x0399;: Thirteen New species and One Change in Status. Acta Phytotax Geobot 66:95–135

Toyama H, Kajisa T, Tagane S, Mase K, Chhang P, Samreth V, Ma V, Sokh H, Ichihashi R, Onoda Y, Mizoue N, Yahara T (2015) Effects of logging and recruitment on community phylogenetic structure in 32 permanent forest plots of Kampong Thom, Cambodia. Philos Trans R Soc B Biol Sci 370:20140008. doi:10.1098/rstb.2014.0008

Whitmore TC (1999) Arguments on the forest frontier. Biodivers Conserv 8:865–868. doi:10.1023/A:1008836306030

Yahara T, Akasaka M, Hirayama H, Ichihashi R, Tagane S, Toyama H, Tsujino R (2012) Strategies to observe and assess changes of terrestrial biodiversity in the Asia-Pacific regions. Biodivers Obs Netw Asia Pacific Reg. doi: 10.1007/978-4-431-54032-8

Zobel M, van der Maarel E, Dupré C (1998) Species pool: the concept, its determination and significance for community restoration. Appl Veg Sci 1:55–66. doi:10.2307/1479085