UNDERSTOREY VEGETATION AT TWO MUD VOLCANOES IN NORTH-EAST BORNEO

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TING TM & POULSEN AD. 2009. Understorey vegetation at two mud volcanoes in north-east Borneo. Mud volcanoes constitute one of the natural causes of disturbance in tropical rainforest but the actual effect on the surrounding vegetation is little studied. The objective of this study was to document the effects of mud volcanoes on the species richness, abundance and composition of the surrounding vegetation. The study was conducted at two mud volcanoes in Tabin Wildlife Reserve, Sabah, Malaysia to determine the effect of mud flow disturbance on the distribution of plant species. Both the mud volcanoes have a central area free of vegetation. Four series of plots were established at increasing distance from the periphery of the open area towards N, E, S and W into the surrounding forest. The estimates of canopy openness using the Crown Illumination Ellipses were highest closest to the volcano. At both volcanoes, the abundance decreased, and the species richness and Shannon index of the plots increased with distance from the central area up to 30 m. Species composition was highly correlated with distance from the mud volcano. Plots close to the mud volcanoes had species adapted to open canopies and the adverse soil conditions caused by the mud flows. Some of these species are otherwise mostly known from mangroves, a vegetation type which is at least 10 km away. The study provides baseline data on a rarely studied natural cause of disturbance and thus contributes to a better understanding of the dynamics of tropical forests.

Keywords: *Acrostichum*, Crown Illumination Ellipses, edaphic preference, Mantel test, disturbance, Sabah

TING TM & POULSEN AD. 2009. Tumbuhan tingkat bawah kanopi di dua volkano lumpur di timur laut Borneo. Volkano lumpur merupakan salah satu daripada punca gangguan semula jadi dalam hutan hujan tropika tetapi kesan sebenarnya terhadap tumbuhan sekitar kurang dikaji. Kajian ini bertujuan untuk mendokumentasikan kesan volkano lumpur terhadap kekayaan spesies, kelimpahan spesies dan komposisi spesies tumbuhan di sekitarnya. Kajian ini dijalankan di dua volkano lumpur di Simpanan Hidupan Liar Tabin, Sabah, Malaysia, untuk menentukan kesan gangguan aliran lumpur terhadap taburan spesies tumbuhan. Kedua-dua volkano lumpur mempunyai kawasan tengah yang tidak mempunyai tumbuhan. Sebanyak empat siri plot masing-masing pada arah utara, timur, selatan dan barat didirikan dengan jarak yang semakin bertambah dari tepi kawasan terbuka menghala ke hutan. Anggaran pembukaan kanopi menggunakan Elips Pencahayaan Silara mencatatkan nilai tertinggi di plot yang terdekat dengan volkano. Bagi kedua-dua volkano lumpur, kelimpahan spesies berkurang dan kekayaan spesies serta indeks Shannon bertambah dengan jarak dari kawasan terbuka sehingga kira-kira 30 m jauhnya. Komposisi spesies mempunyai korelasi yang tinggi dengan jarak dari volkano lumpur. Plot yang berdekatan dengan volkano lumpur menampung spesies yang dapat menyesuai kepada bukaan kanopi dan keadaan tanah yang teruk akibat aliran lumpur. Sesetengah spesies yang biasanya hidup di hutan bakau turut dijumpai. Hutan bakau terdekat terletak 10 km dari kawasan kajian. Kajian ini membekalkan data asas tentang punca gangguan semula jadi, suatu aspek yang jarang diselidiki. Ia dapat menyumbang kepada pemahaman kita tentang kedinamikan hutan tropika.

INTRODUCTION

Natural disturbances in tropical forest can be of different magnitude—from the impact of a single fallen tree to destruction of several hundred km^2. Large-scale disturbance may be caused by wind, landslide, river dynamics, volcanoes or fires (Whitmore & Burslem 1998). Even though disturbance caused by humans has occurred for a long time (Boerboom & Wiersum 1983), recent change in landuse has resulted in large areas of forest be converted into secondary forest or monoculture of woody or herbaceous plants.

Mud volcanoes are geological structures formed as a result of emission of argillaceous material on the earth's surface and a way for fluid and gases to escape from sedimentary basins (Dimitrov 2002). Buoyancy from gas exsolution or the excess pressure of the fluid source will cause the water–mud mix to move to the surface (Brown 1990). When the extruded material is very fluidized and gassy, the crater collapses and a mud pool is formed in the depression. Mud with low porosity forms cones or ridges, more consistent mud with intermediate fluid content may give rise to mud volcanoes with large diameters and elevation, and high porosity mud creates mud pies with great areal extent (Yusifov & Rabinovitz 2004). Variable geometry and size from one metre to several hundred metres in height can be formed. The eruptions of mud are not necessarily hot but mud deposition will affect the surrounding vegetation physically and catastrophically, if of sufficient size. In addition, geochemical anomalies of the water–mud mix deposited at an area will prevent plants from colonizing. The water–mud mix extruded is very saline with high contents of Cl, Na, K, Ca and Mg (Dia *et al.* 1999, You *et al.* 2004, Ting & Jopony 2008), which may create extreme stress to the affected plants. Thus one would expect the vegetation close to a mud volcano to reflect this impact.

Gaps in the forest can encourage the growth of shade-intolerant herbs due to higher light intensity (Collins *et al.* 1985, Kiew 1987). The mud volcano, however, not only creates a large gap but also changes the soil chemistry. The effect of the mud flow is likely to be repeated at the same location several times but the eruption size, frequency and the number of years a mud volcano remains active have not been recorded.

In the temperate region, three studies have focused on mud volcanoes and succession of the vegetation (Russia: Ivanov *et al.* 1989, USA: Moral & Wood 1993, Japan: Adikari *et al.* 2007). The earliest mud volcanism in Sabah was recorded in 1897 at Lambian, Klias Peninsula (Wilson 1964), and the earliest record of mud volcanoes at Tabin was possibly by Reinhard and Wenk (1951) (cited by Haile & Wong 1965). Although mud volcanoes have been present for many years, to our knowledge, the vegetation surrounding the mud volcanoes in Borneo has not been studied quantitatively.

The aim of this study was to provide baseline information on plant species distribution in the vicinity of mud volcanoes. The primary objective was to document the effects of mud volcanoes on species richness, abundance and composition, and to establish how far into the forest vegetation the effects could be documented. One would hypothesize that the increased light conditions would result in an increased abundance of plants. However, the soil chemical factors may select species capable of colonizing the recently deposited mud and therefore a lower species richness.

MATERIALS AND METHODS

Study area

The Tabin Wildlife Reserve with an area of 120 ha is located in the middle of the Dent Peninsula in eastern Sabah, Malaysia (Figure 1). Lowland dipterocarp forest dominates the area, most of which is secondary as a consequence of logging, with over 100 plant families (Sale 1994). The primary forest is dominated by Dipterocarpaceae, while the secondary forests, *Macaranga*, gingers and ferns.

The most unique feature of the Tabin Wildlife Reserve is the presence of mud volcano activity, rendering the nature of the vegetation dynamic (Figure 2). The reserve has two prominent mud volcanoes: Lipad (05° 12.6' N, 118° 30.5' E; 180 m elevation) and Tabin (05° 12.2' N, 118° 39.9' E; 239 m elevation) that are 25 km apart. Both mud volcanoes form up to 120 m wide circular or elliptical opening in the forest vegetation comprising two distinct vegetation types, namely, an inner zone with very limited plant growth and an outer zone with dense vegetation cover. The Lipad mud volcano is situated within the Lipad Virgin Jungle Reserve and located approximately 2 km north of Tabin Wildlife Headquarters. The Tabin mud volcano is located in the centre of the Tabin Virgin Jungle Reserve. Since the mud volcanoes are located in reserves, the nearby vegetation is relatively undisturbed, even if the large part of the Tabin Wildlife Reserve had been logged in the past.

Both volcanoes continue to be active but are not explosive; continuous gentle activity can be observed with frequent mud–water mix being extruded to the surface. A few eruptions of variable sizes take place every year. The biggest eruption observed during this study occurred at Lipad on 5 April 2000 and covered an area of approximately 2500 m^2 (Figure 2). The mud volcanoes appear within the mélange formation which comprises rock blocks such as chert, ultrabasic, plutonic rocks, basalts and sandstones (Sanudin 1989). Based on elemental analyses

Figure 1 Location of Tabin Wildlife Reserve (black) in eastern Sabah. The approximate positions of Lipad and Tabin mud volcanoes are indicated by small, white circles.

Figure 2 Lipad mud volcano a day after the 5 April 2000 eruption

of mud or soil, the parent material consists of a mixture of basic igneous rock, shale and sandstone (Ting & Jopony 2008).

Sampling procedure

The fieldwork was conducted from March–June 2000. Transects of 10 × 50 m were established starting at the periphery of the open, inner zone of the volcano towards the four cardinal compass bearings (Figure 3). Each transect was divided into five continuous 10 × 10 m plots labelled A, B, C, D and E; plot A being closest to the mud volcano. Four additional plots of 10 × 10 m were placed 200 m away from the periphery of the inner zones (labelled F). Each plot was subdivided into four subplots of 5 × 5 m for easier enumeration and accuracy.

All plants below 2 m height within each plot were recorded and voucher specimens collected. Single-stemmed individuals such as trees, bunch-grasses and single-stemmed herbs were easily counted. The stems and ferns coming from the same rhizome were counted as one single individual. For the perennial herbs, such as rhizomatous ginger, the stems that were coming from the same rhizome were counted as a single individual (Causton 1988).

The abundance of species is the total number of individuals present per 10 × 10 m plot and species richness, the number of species per plot. The Shannon diversity index is the number of species and their evenness per plot (Magurran 1988).

$$H' = -\Sigma p_i (\ln p_i)$$

where
n_i = the abundance of species i
N = the total number of individuals

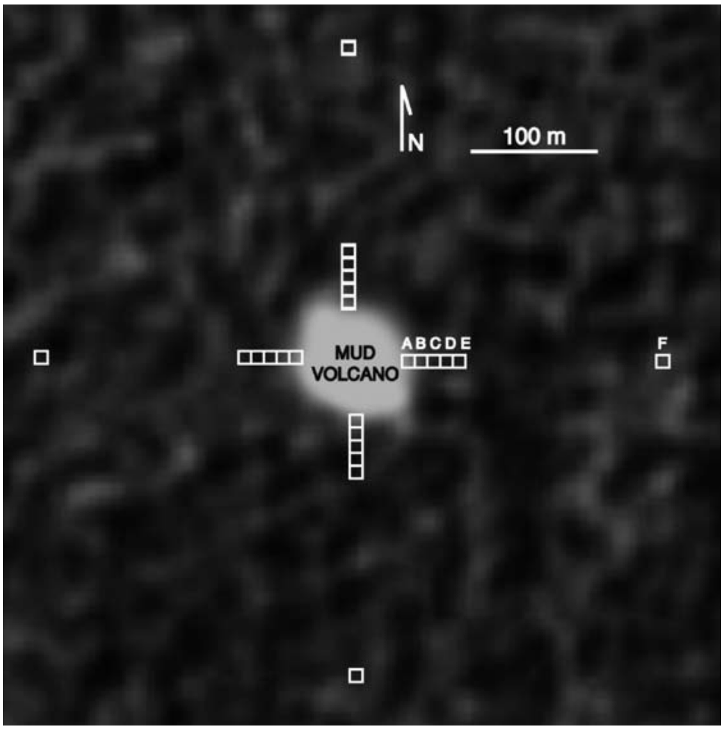

Figure 3 Schematic diagram of the sampling design in the vegetation surrounding the open area of a mud volcano

p_i = the relative abundance of each species, calculated as the proportion of a given species to the total number n_i /N.

The Shannon diversity index was calculated using the program EstimateS (Version 5.0; Colwell 1997).

Identification

The voucher specimens were sorted out into morpho-species of which 24% could be identified to species level by experts at the herbarium in Sepilok (SAN) and Aarhus University (AAU).

Light estimate

The method of Crown Illumination Ellipses (CIE) described by Brown *et al.* (2000) was used to assess the forest understorey light environments. The understorey light environment in the vegetation area in all plots was assessed in the centre of each 10 × 10 m plot. This method consisted of drawing ellipses of three different sizes on a plexi-glass sheet. To use the CIE method, the plexi-glass sheet was fixed in all directions to get as high a reading as possible for each plot. The score was determined by the size of the ellipse that fitted entirely into the largest canopy opening visible anywhere in the canopy while standing at the point of measurement.

Numerical analysis

Simple correlations were carried out using Pearson correlation coefficients performed by SPSS program version 10.0. The other analyses were performed using Le Progiciel R, available on the Internet (http://www.bio.umontreal.ca/casgrain/fr/labo/). Detailed explanations of all the methods were found in Legendre and Legendre (1998).

Resemblance matrices were constructed using the Sørensen index (which is binary and hence only takes into account species presence and absence) and the Steinhaus index (which is mathematically similar but also takes into account species abundance) to measure floristic similarity between plots. When similarities needed to be converted to distances, the formula Distance = 1 – Similarity was used. A matrix of ln-transformed geographic distances of plots to volcano gap was computed. Due to dispersal, this reflects the rapid decline of similarity at short distances between plots better than a linear relationship (Condit *et al.* 2002). Euclidian distance was used when this matrix was computed. To obtain information of the floristic gradients within the plot, Principal Co-ordinates Analysis (PCoA) was performed. Correlations between distance matrices were computed using the Mantel test. The standardized form of the Mantel statistic was used, which is mathematically similar to the Pearson correlation coefficient but is computed between the cell values of two resemblance matrices rather than the measured values of the original variables. The statistical significance of each correlation was determined by a Monte Carlo permutation test using 999 permutations, which allowed testing of the statistical significance at the $p < 0.001$ level.

RESULTS

Canopy openness

The highest CIE values (Figure 4) were recorded in the plots closest to the mud volcano (A and B). On average, the CIE index was lower in plots further away from the mud volcanoes. The variation in CIE index was most obvious between plots A and B.

Abundance

A total of 7827 and 4838 individuals were encountered at Lipad and Tabin mud volcanoes respectively (Figure 5). The numbers of individuals per plot for the first two plots (A and B) were significantly higher than the remaining plots. This was more apparent at Lipad. Plots A and B were dominated by Asteraceae, Poaceae and Cyperaceae. Most of the individuals were small. The abundance of plots further inside the forest remained more or less constant from plot C onwards.

A total of 14 and 12 families had more than 100 individuals at Lipad and Tabin mud volcanoes respectively (Table 1). At both volcanoes,

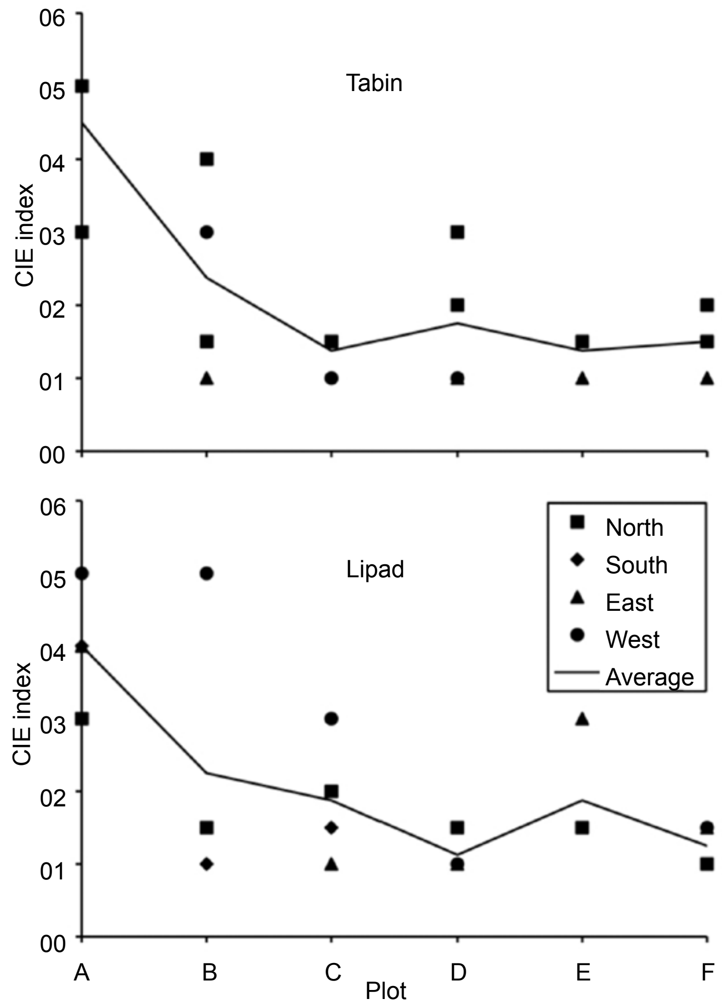

Figure 4 The Crown Illumination Ellipses index in 10 × 10 m plots towards the north, south, east and west of the two mud volcanoes. F is 200 m from the volcano.

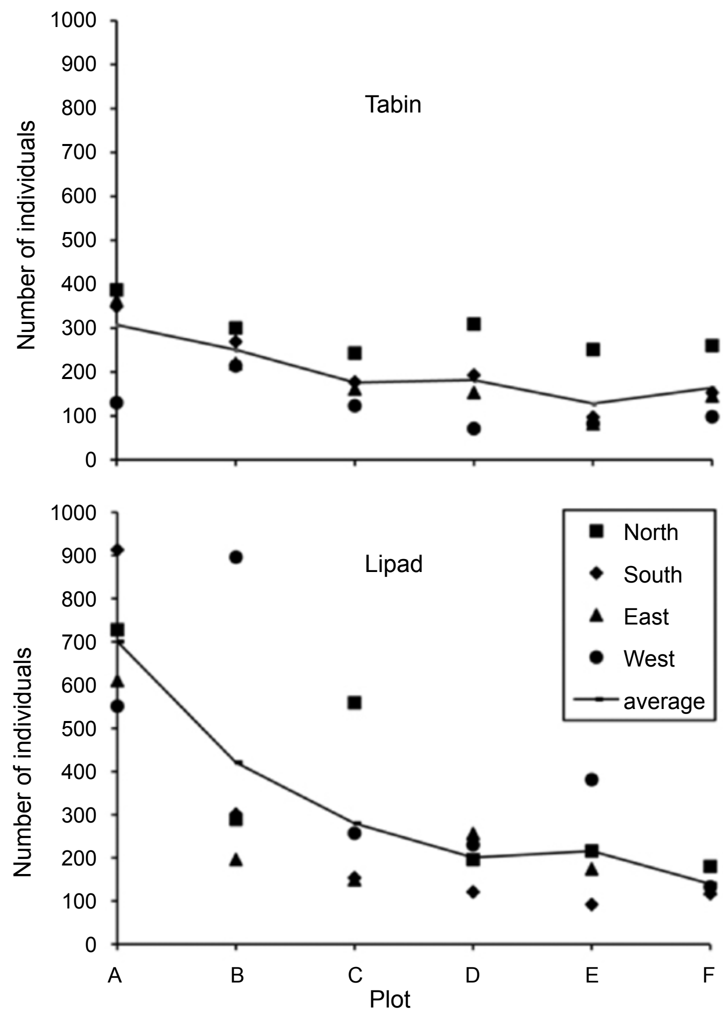

Figure 5 The abundance in 10 × 10 m plots towards the north, south, east, and west of the two mud volcanoes

Cyatheaceae, Cyperaceae, Piperaceae, Poaceae, Zingiberaceae were the most abundant families. There were 40 and 35 species with only one individual recorded at Lipad and Tabin mud volcanoes respectively (results not shown).

Species richness

In the open area of the mud volcanoes, where no plots were established, three species occurred: *Acrostichum aureum* (pteridophyte), *Imperata cylindrica* (Poaceae) and *Chromolaena odorata* (Asteraceae) but in very low abundance. Plots nearest to the mud volcano (A) had lower number of species at both sites. Only few (< 5) species were recorded in the inner vegetation zone. Species richness increased in plots further into the forest and remained fairly constant in the last four plots (Figure 6).

A total of 335 species belonging to 76 families were recorded at Lipad compared with 269 morpho-species belonging to 65 families at Tabin, indicating that species richness was 25% higher at the former site. Eighty-seven species could be found at both mud volcanoes (Table 1). Species such as *Acrostichum aureum*, *Acrostichum speciosum*, *Glochidion rubrum* (Euphorbiaceae), *Imperata cylindrica* and *Chromolaena odorata* were found only at the first plots (A–B–C) of Lipad and Tabin mud volcanoes.

Family occurrence

Of the 84 families recorded, 57 (68%) could be found at both sites. Nineteen (23%) and eight families (10%) were restricted to Lipad and Tabin respectively, indicating a regional difference in the overall forest composition (Table 1).

Table 1 Families represented in the understorey at the Lipad and Tabin mud volcanoes

Lipad mud volcano	Both sites		Tabin mud volcano
Acanthaceae: 4(59)	Actinidiaceae: 1(10); 1(7)	Meliaceae: 7(20); 7(59)	Anacardiaceae: 1(1)
Alangiaceae: 2(6)	Annonaceae: 16(47); 17(76)	Menispermaceae: 5(16); 1(18)	Blechnaceae: 3(12)
Amaranthaceae: 1(21)	Apocynaceae: 3(13); 1(4)	Moraceae: 6(37); 6(11)	Convolvulaceae: 2(7)
Boraginaceae: 2(2)	Araceae: 21(162); 6(48)	Myrsinaceae: 2(12); 5(15)	Dracaenaceae: 2(5)
Davalliaceae: 1(7)	Asclepiadaceae: 3(10); 2(2)	Myrtaceae: 8(294); 5(150)	Guttiferae: 4(35)
Elaeocarpaceae: 1(1)	Aspleniaceae: 3(27); 2(15)	Oleaceae: 3(8); 5(46)	Monimiaceae: 1(3)
Fagaceae: 1(2)	Begoniaceae: 1(2); 1(2)	Oleandraceae: 2(152); 1(117)	Ophioglossaceae: 1(6)
Flagellariaceae: 2(4)	Celastraceae: 1(1); 3(35)	Orchidaceae: 3(27); 5(23)	Symplocaceae: 1(1)
Labiatae: 1(4)	Combretaceae: 1(1); 2(19)	Palmae: 8(75); 5(47)	
Loranthaceae: 1(3)	Commelinaceae: 2(44); 2(25)	Piperaceae: 20(**731**); 11(**639**)	
Magnoliaceae: 1(2)	Compositae: 3(231); 4(230)	Poaceae: 7(**1249**); 5(**263**)	
Marantaceae: 2(8)	Connaraceae: 5(22); 2(43)	Polygalaceae: 3(6); 2(10)	
Myristicaceae: 3(9)	Cucurbitaceae: 3(12); 1(1)	Polypodiaceae: 3(23); 4(6)	
Onagraceae: 2(21)	Cyatheaceae: 1(**608**); 3(**260**)	Proteaceae: 1(5); 1(13)	
Pandanaceae: 1(1)	Cyperaceae: 6(**1391**); 7(**552**)	Pteridaceae: 2(150); 1(246)	
Passifloraceae: 1(7)	Dichapetalaceae: 1(2); 1(3)	Rhamnaceae: 5(52); 4(33)	
Sapotaceae: 2(5)	Dilleniaceae: 3(18); 2(15)	Rhizophoraceae: 1(19); 1(7)	
Theaceae: 2(25)	Dipterocarpaceae: 12(66); 5(25)	Rubiaceae: 24(144); 26(220)	
Verbenaceae: 1(13)	Ebenaceae: 3(24); 2(6)	Rutaceae: 2(54); 3(42)	
	Euphorbiaceae: 22(223); 17(231)	Sapindaceae: 7(60); 4(56)	
	Fabaceae: 18(319); 12(179)	Schizaeaceae: 1(46); 2(25)	
	Flacourtiaceae: 2(10); 4(8)	Smilacaceae: 1(7); 2(15)	
	Gesneriaceae: 6(18); 2(8)	Sterculiaceae: 1(32); 1(2)	
	Icacinaceae: 1(1); 1(1)	Thymelaeaceae: 3(10); 3(6)	
	Lauraceae: 4(17); 8(30)	Tiliaceae: 3(53); 3(15)	
	Lecythidaceae: 2(5); 1(2)	Urticaceae: 1(3); 4(45)	
	Leeaceae: 1(128); 1(96)	Vitaceae: 7(85); 7(36)	
	Loganiaceae: 1(5); 1(31)	Zingiberaceae: 17(**806**); 16(**582**)	
	Melastomataceae: 5(34); 3(67)		
22.6%	67.9%		9.5%

Number of species is followed by abundance in parenthesis.
Numbers in bold indicate the most abundant of families.

Shannon diversity index

The Shannon diversity index calculated based on the overall vegetation data at Lipad and Tabin mud volcanoes were 3.95 and 4.42 respectively, whereas the values for individual plots were lowest near the volcanoes (Plot A, Figure 7).

Floristic composition and Mantel test

The ordination of all 48 plots from both volcano areas produced by the PCoA based on matrices involving Sørensen and Steinhaus similarities between plots showed a similar pattern (Figure 8). The ordinations had the typical arch-shape with the plots less disturbed by the mud volcano to the left and the plots closest to the volcanoes to the right. The surrounding forest of the two volcanoes appeared to be different and in the ordination diagram (Figure 8, lower row), plots from the two volcanoes separated along axis 3 (Tabin plots were mostly below and Lipad mostly above). The first three axis of the ordination explained 29% of the variation using Sørensen and 26%, using Steinhaus.

The Mantel test showed that the floristic composition was significantly correlated with distance from mud volcano ($r = 0.50$ (Sørensen), $r = 0.46$ (Steinhaus), $p < 0.001$).

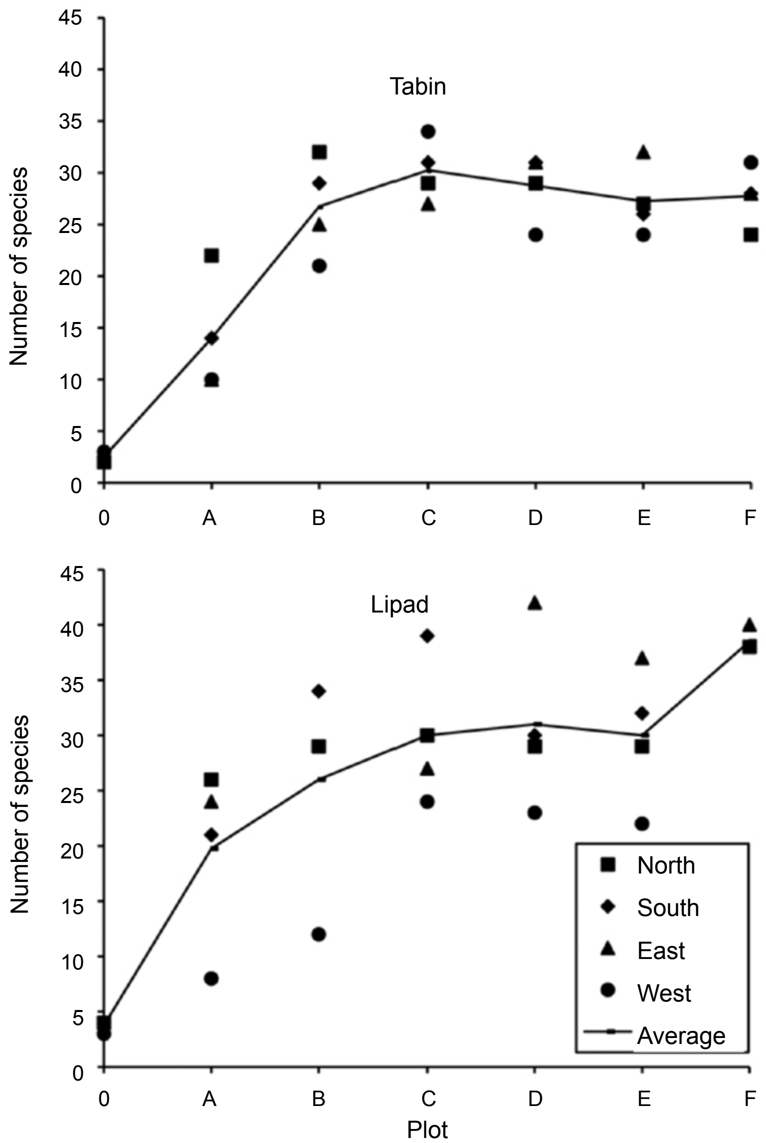

Figure 6 Species richness in 10 × 10 m plots towards the north, south, east, and west of the two volcanoes. The zero on the *x*-axis represents the periphery of the inner vegetation-free zone.

DISCUSSION

The effects of mud volcanoes on forest structure, abundance and species richness

The environment of the primary forest differs from that of the disturbed forest, primarily due to a reduced canopy cover. The lower canopy cover in the disturbed forest is presumed to increase light penetration through the canopy and thus, the light intensity at the forest floor (Congdon & Herbohn 1993). Consequently, a denser understorey is found in contrast to the closed-canopy forest where the understorey is rather clear. Unless a tree falls and creates a gap, the lack of light reaching the forest floor will generally discourage growth of plants.

Not surprisingly, the most open plots were found within 20 m of the two mud volcanoes (Figure 4). The abundance of understorey plants was highest in these plots (Figure 5) but the species richness and Shannon index were lowest (Figures 6 and 7) and these were correlated with the openness of the canopy (Table 2). The abundance near the volcano gap at Lipad was, however, much more pronounced. The eruption history of the volcanoes may explain the difference. The recent mud flows may have wiped out many individuals close to the volcano and there has not been sufficient time for recolonization.

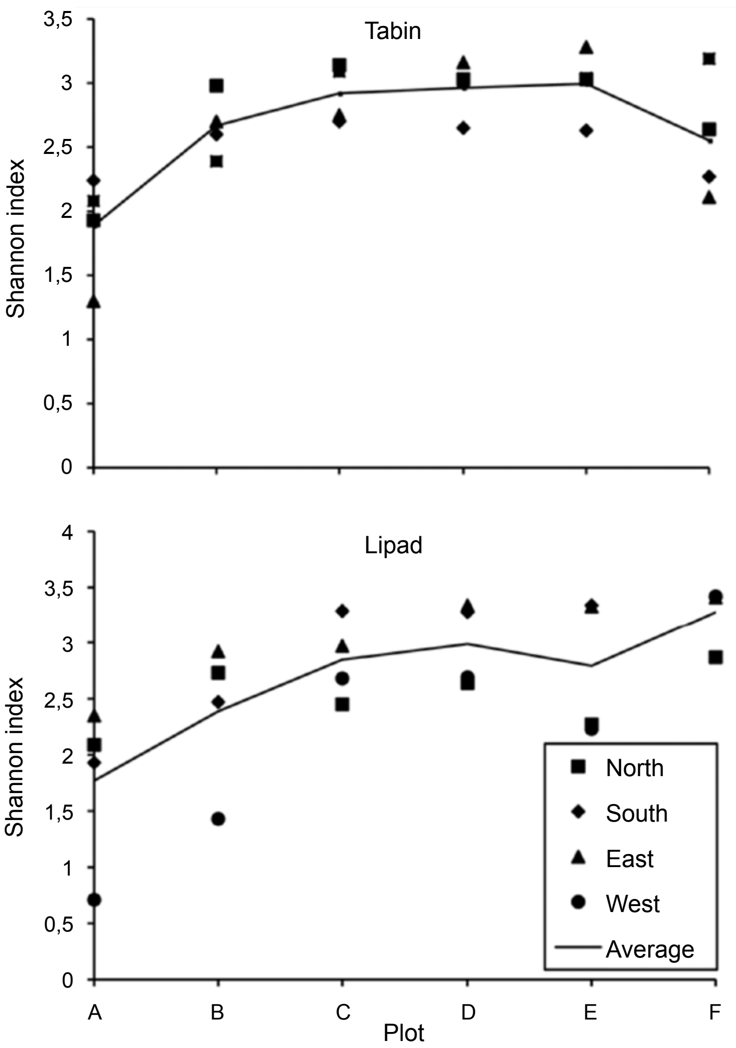

Figure 7 Shannon diversity index in 10 × 10 m plots towards the north, south, east and west of the two volcanoes

Table 2 Pearson correlation coefficients between CIE, species richness of plants, abundance of plants and Shannon diversity index

	CIE	Species richness	Abundance	Shannon diversity index
CIE index		0.722	0.601	-0.693
Species richness			0.456	0.835
Abundance				-0.684
ln(distance from volcano)	-0.647	0.603	-0.567	0.559

$p < 0.01$

The importance of forest structure (primary forest versus selective logged) was studied at Danum Valley, Sabah and the study found slightly higher numbers of species of ground herbs in the disturbed forest sample plots (Magintan 2000). Soils at the Tabin Wildlife Reserve are not similar to those in Danum Valley. Therefore, a direct comparison in plant distribution cannot be made. Nevertheless, since soils at the two mud volcanoes have similar characteristic and elevation, the overall dissimilarity in species richness (Figure 6) observed between these two mud volcano areas is most likely due to the effect of forest structure. Another possible difference between the Lipad and Tabin areas would be the topography; the area around Tabin mud

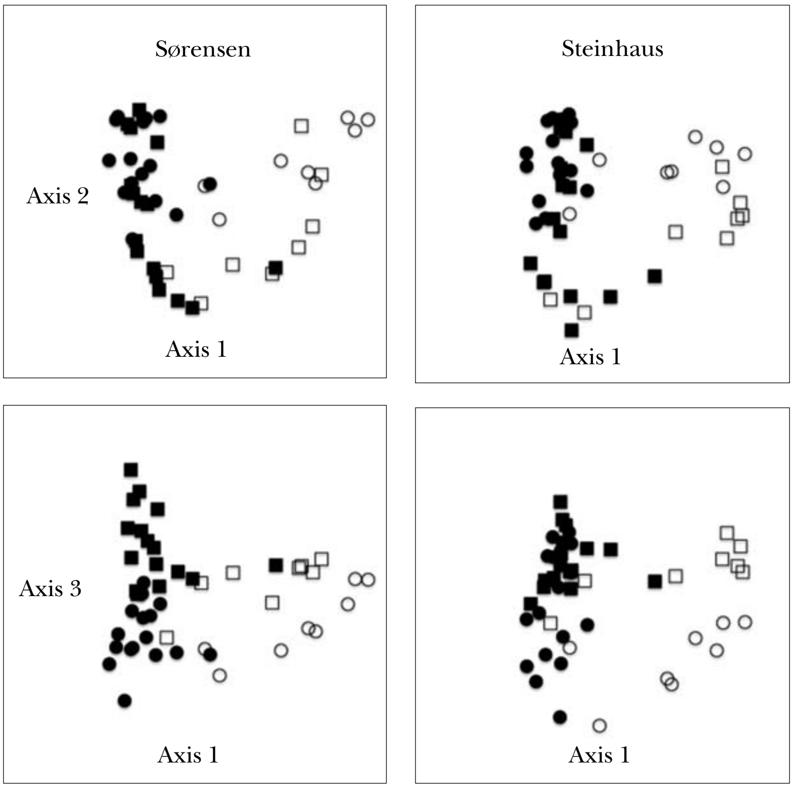

Figure 8 Ordination diagram (principal coordinate analyses) of 48 sample plots in the vegetation surrounding Lipad (squares) and Tabin (circles) mud volcanoes. Plots closest to the open volcano area are shown open and plots further away in closed symbols. Similarity matrices are based on species composition of understorey plants (< 2 m high) and two similarity indices were used: Sørensen (left) and Steinhaus (right). Upper row shows Axis 1 against Axis 2 and lower row Axis 1 against Axis 3.

volcano is topographically more rugged and situated towards the top of a hill. It has been shown that topography may affect the occurrence and distribution of plant species (Newbery *et al.* 1996). One would expect that the more varied topography at Tabin would contribute to higher species richness. Even though the topographic variation was not quantified in the present study, it appears that the lower species richness at Tabin is probably not caused by topographical heterogeneity and that forest structure is more important.

The chemistry of soils of the mud volcanoes is characterized by high amounts of dissolved solids and high conductivity (Ting & Jopony 2008). These factors are also likely to be important in preventing the growth of plants and thus contribute to maintaining an open canopy. Similar to tree fall gaps, a high abundance of plants is found close to the open zone but the present study differs in documenting low species richness probably due to the extreme soil conditions.

The intermediate disturbance hypothesis proposed by Connell (1978) provides an explanation to the maintenance of high species richness in tropical forests, even if this has been opposed (Sheil & Burslem 2003). The hypothesis predicts that the highest diversity occurs at intermediate disturbance regimes. In the present study, certainly the disturbance to the vegetation close to the volcano is too frequent or severe to allow many species to exist (Figure 6) and at Tabin there is at least a tendency for the highest richness and diversity (Figure 7) to be found in plots 20–30 m from the volcano, and thus give some support to the hypothesis even if only understorey plants are included in the present study. The pattern at Lipad, however, differs from Tabin in the far-most plots being more diverse. This may possibly be explained by the fact that the Lipad Jungle Reserve is also much smaller in area than the Tabin Jungle Reserve and has been subject to logging encroachment.

The effects of mud volcanoes on species composition

The ordination diagram illustrates that the plots closest to the mud volcanoes are floristically similar even when plots from both areas are pooled (Figure 8, top row). The gradient from the volcano into the nearby vegetation was highly correlated with the first axis. Plots closest to the volcano are situated to the right in Figure 8. These species-poor plots were dominated by a few, mainly herbaceous species, such as *Acrostichum* spp., *I. cylindrica* and *C. odorata*, which were shade-intolerant but able to colonize the unstable substrate of mud flats and cope with the chemical content of the mud.

Acrostichum aureum (mangrove fern) is well-known to occur in mangrove vegetation and two forms exist—the one with narrowly acuminate pinnae sometimes recognized as a separate species and *A. speciosum,* occurring in sites more frequently inundated by tides (Holttum 1954). In the present study, both species were found in plots at Lipad whereas Tabin only had *A. aureum.* This may reflect differences in eruption history and time available for rain to leach the salt content of the mud flows. It is perhaps surprising to have species mainly thought of as mangrove vegetation indicators in the plots especially as the nearest mangrove vegetation is at least 10 km away. This shows that ferns are able to colonize suitable habitats even if several kilometres away from the coast and underlines the special edaphic conditions of mud volcanoes. In coastal Puerto Rico, Medina (1990) found that the density of *A. aureum* was higher in full sun exposure with low salinity. At our study site these two factors are probably negatively correlated and this potential optimal condition is rarely found—lower salinity implies moving into shadier conditions.

CONCLUSIONS

The activity of mud volcano is an important natural factor in producing a major gap in the forest. As hypothesized, the increased light intensity resulted in an increased abundance and lower species richness of plants in plots closest to the mud volcanoes. In contrast to other large forest gaps, e.g. created by wind or fire, the mud volcano also modified the soil profile and chemical content of the soil which resulted in a unique vegetation, including plant species normally found in mangroves or tidal forests. More than 30 m away from the open area of the mud volcanoes, the effect on vegetation was limited. Characteristics of the prevailing forest type was expressed, which appeared to be different, both structurally and in species composition, between the two volcanoes.

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