

Environmental correlates for tropical tree diversity and distribution patterns in Borneo

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ABSTRACT

Aim Identify environmental correlates for tropical tree diversity and composition.

Location Borneo, Southeast Asia.

Methods A GIS-environmental database with 5 arc minute (*c.* 10 × 10 km) resolution was combined with tree inventory data. Tree diversity, phylogenetic diversity (PD) and the two main compositional gradients were determined for 46 tree inventories. Akaike's information criterion and a data jackknifing procedure were used to select 50 explanatory models for diversity and composition gradients. The average of these models was used as our final diversity and compositional model. We applied Moran's *I* to detect spatial autocorrelation of residuals.

Results Tree diversity, PD and the two main compositional gradients in Borneo were all significantly correlated with the environment. Tree diversity correlated negatively with elevation, soil depth, soil coarseness (texture) and organic carbon content, whereas it correlated positively with soil C:N ratio, soil pH, moisture storage capacity and annual rainfall. Tree PD was correlated positively with elevation and temperature seasonality and was largely determined by gymnosperms. However, angiosperm PD also correlated positive with elevation. Compositional patterns were strongly correlated with elevation but soil texture, cation-exchange-capacity, C:N ratio, C and N content and drainage were also important next to rainfall seasonality and El Niño Southern Oscillation drought impact.

Main conclusions Although elevation is the most important correlate for diversity and compositional gradients in Borneo, significant additional variability is explained by soil characteristics (texture, carbon content, pH, depth, drainage and nutrient status) and climate (annual rainfall, rainfall seasonality and droughts). The identified environmental correlates for diversity and composition gradients correspond to those found in other tropical regions of the world. Differences between the regions are mainly formed by differences in the relative importance of the environmental variables in explaining diversity and compositional gradients.

Keywords

Borneo, floristics, meta-analysis, phylogenetic diversity, Southeast Asia, tropical forest.

INTRODUCTION

Explaining the diversity and distribution of tree species remains a challenging subject in tropical ecology. Only recently have

people combined available local tree inventory data to address questions at regional and continental scales (Gentry, 1988; Oliveira-Filho & Fontes, 2000; Slik *et al.*, 2003; ter Steege *et al.*, 2003, 2006; Parmentier *et al.*, 2007; Punyasena *et al.*, 2008).

However, these studies have mainly focused on the Neotropics posing the question whether observed correlations between tree diversity and composition gradients there are also valid in other parts of the tropics. Parmentier *et al.* (2007) found only limited similarity in environmental correlates of tree diversity and composition when they compared African and South American tropical forests in a single meta-analysis. This suggests that the world's tropical forests differ in the environmental structuring of their tree communities, and illustrates the importance of replicating such studies on different continents.

We studied tree diversity and compositional gradients in Borneo as an example of Southeast Asian tropical forest. Borneo has been identified as a biodiversity hotspot, and its lowland forests are among the world's most diverse (Kier *et al.*, 2005). Most of Borneo's forests are dominated by the Dipterocarpaceae, which is atypical compared to other tropical forests around the world (Gentry, 1988; Slik *et al.*, 2003). The structure of Borneo's forests also differs from other tropical regions because of the higher density and taller height of emergent trees, resulting in a relatively open upper canopy (Dail *et al.*, 2004; Paoli *et al.*, 2008). Borneo is also an island of large biophysical ranges having a rainfall gradient of almost 3 m (1585 to 4566 mm annually) and an altitudinal gradient of more than 4000 m. It contains a mosaic of forest types including: mangroves; peat and fresh water swamps; forest on ultramafic, poor white sand (kerangas/heath) and limestone soils; lowland mixed dipterocarp forest; montane and alpine forests (MacKinnon *et al.*, 1996). Borneo's recent geological history is unusual because of the island's repeated connection to the Southeast Asian mainland, Sumatra and Java, during lowered sea levels of Pleistocene glacial periods (Morley, 2000).

There have been few studies addressing island-wide tree diversity and composition gradients on Borneo. Most were carried out at local and regional scales identifying elevation, annual rainfall and soils as environmental correlates for tree diversity and composition gradients (Newbery & Proctor, 1984; Potts *et al.*, 2002; Miyamoto *et al.*, 2003; Slik *et al.*, 2003; Cannon & Leighton, 2004; Aiba *et al.*, 2005). Despite this lack of Borneo-wide analyses, the island has been divided into seven bio-units (MacKinnon & MacKinnon, 1986; Ridder-Numan, 1998; Wong, 1998) based on a few plant and animal groups, unclear methods, spatially biased data and/or expert opinion. It therefore remains unclear to what extent island-wide floristic patterns are spatially structured in relation to the environment. Here we combine available Bornean tree inventory and environmental data into a single meta-analysis to identify environmental correlates for Borneo's tree diversity and compositional gradients.

METHODS

Our GIS-environmental database consisted of the five least correlated bio-climatic variables (Pearson's $r < 0.75$) of the WORLDCLIM dataset (<http://www.worldclim.org>) for Borneo (Hijmans *et al.*, 2005): elevation, temperature seasonality, temperature annual range, annual rainfall and rainfall seasonality. To this we added El Niño Southern Oscillation (ENSO) drought

impact defined as the relative difference between the normalized difference vegetation index (NDVI) of a severe ENSO year (July 1982–June 1983) and a non-ENSO year (July 1981–June 1982). We also selected 15 soil variables from the Food and Agriculture Organization (FAO) database for poverty and insecurity mapping (FAO, 2002). Principal component analysis (PCA) was used to summarize these data in five independent soil axes that together explained 83% of soil data variance (Table 1). Pearson's correlation was used to determine which of the original 15 FAO soil predictors were significantly correlated with each of the 5 PCA axes (Table 1). Soil axis 1 (31.6% data variance) was positively correlated with soil water availability and storage capacity, organic matter content, nitrogen content and base cation availability, but negatively with soil drainage; soil axis 2 (22.5% data variance) was positively correlated with topsoil organic carbon content, but negatively with soil pH, water storage capacity and topsoil base saturation; soil axis 3 (16.6% data variance) was negatively correlated with soil texture (coarseness) and topsoil clay-cation-exchange capacity; soil axis 4 (7.5% data variance) was negatively correlated with soil depth; whereas soil axis 5 (4.9% of data variance) was positively correlated with soil C:N ratio. All data layers were set at 5 arc minute resolution (~10 km at the equator) covering Borneo by 8577 grid cells. Our final data selection contained 11 environmental variables (Fig. 1). All data layer manipulations were performed with Manifold GIS (Manifold Net Ltd).

Plot tree inventory data with diameter at breast height (d.b.h.) ≥ 10 cm for 46 Bornean GIS-grid cells were available (Fig. 1a; Table 2). These locations covered a wide range of climatic, soil and altitudinal gradients (Fig. 2). Tree communities were assessed using generic data to avoid problems with incomplete

Table 1 PCA factor loadings for the five soil axes (between brackets the amount of explained data variance) used in this study. Soil variables with a significant Pearson's correlation coefficient > 0.5 are indicated in bold. Cation-exchange-capacity (CEC); carbon (C); nitrogen (N).

Factor	Axis 1 (31.6%)	Axis 2 (22.5%)	Axis 3 (16.6%)	Axis 4 (7.5%)	Axis 5 (4.9%)
Base saturation topsoil	-0.047	-0.462	0.042	0.135	0.350
CEC clay topsoil	0.262	-0.189	-0.336	0.313	-0.082
CEC soil topsoil	0.342	-0.106	0.148	0.035	0.137
C:N ratio topsoil	0.234	0.159	-0.267	-0.287	0.623
Easy available water	0.362	-0.260	-0.027	0.123	-0.091
Effective soil depth	0.112	-0.171	-0.094	-0.793	-0.272
Nitrogen topsoil	0.338	0.133	0.232	0.145	-0.234
Organic carbon topsoil	0.254	0.289	0.207	0.065	-0.349
Organic carbon pool	0.350	0.216	0.157	-0.089	0.078
pH topsoil	-0.202	-0.370	0.086	0.203	-0.091
Soil drainage	-0.382	0.121	-0.096	-0.062	-0.292
Soil moisture storage	0.327	-0.295	0.005	-0.018	-0.186
Soil production index	-0.022	-0.470	0.046	-0.236	-0.152
Textural class subsoil	0.133	0.017	-0.555	0.030	-0.158
Textural class topsoil	0.018	0.100	-0.578	0.142	-0.155

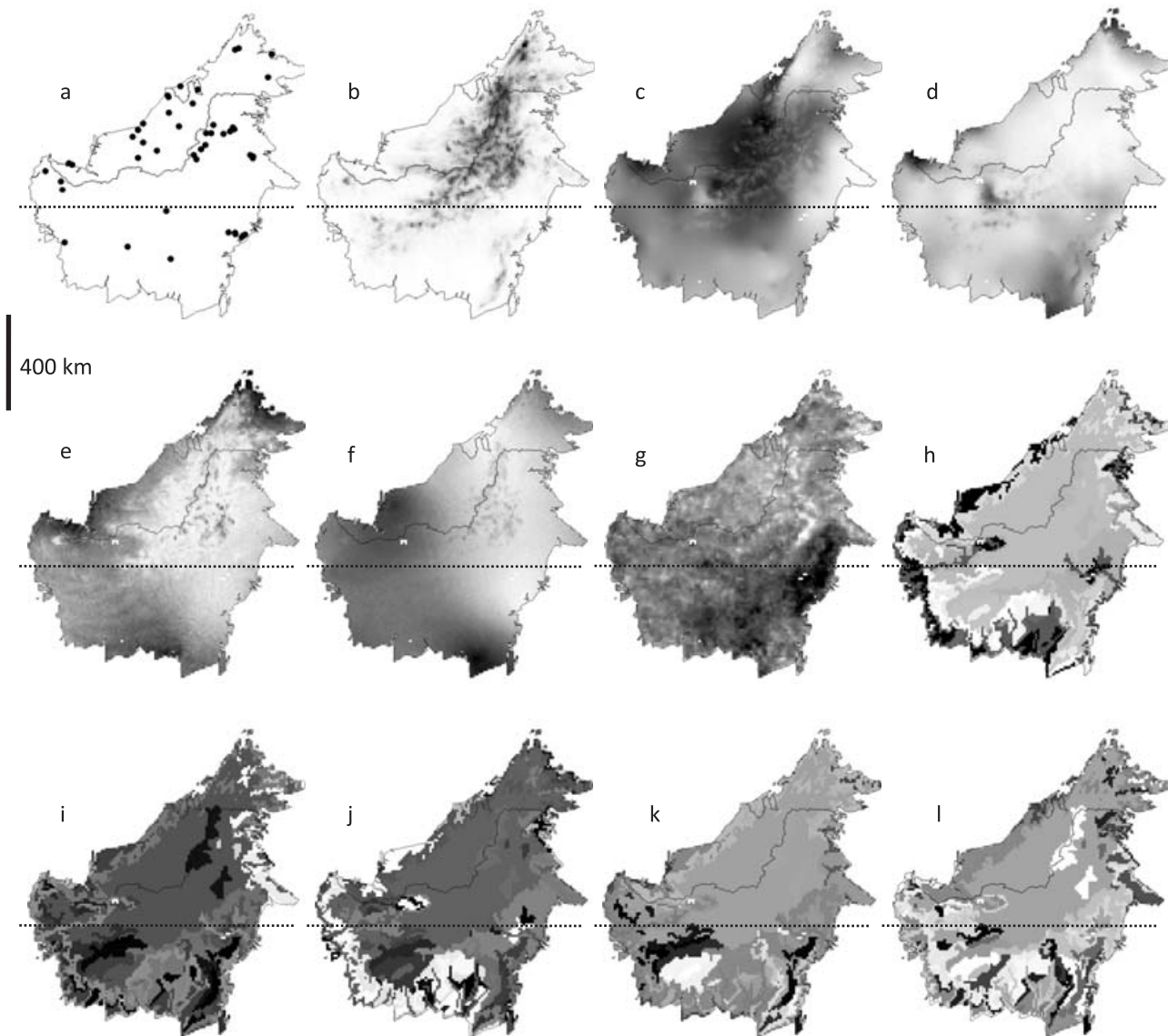


Figure 1 Data locations and environmental variables used in this study: (a) locations; (b) topography; (c) annual rainfall; (d) rainfall seasonality; (e) temperature seasonality; (f) temperature annual range; (g) ENSO drought impact; (h) soil axis 1, (i) soil axis 2, (j) soil axis 3, (k) soil axis 4, (l) soil axis 5. Values increase from white to black.

species identifications (Slik *et al.*, 2003). Patterns in generic diversity and composition match those of species well (Higgins & Ruokolainen, 2004). Inventories were standardized by pooling all plots and stems in each grid cell and randomly drawing 400 individuals. This was repeated five times for each grid cell to calculate reliable average tree species diversity and compositional values (Slik *et al.*, 2003). The number of individuals per genus and the number of genera per 400 individuals were determined for each random draw.

We determined two diversity measures for each location; rarefied and phylogenetic diversity (PD). Rarefied diversity represents the average number of genera in five random samples of 400 stems per location. This procedure removed effects of

different sample sizes on diversity estimates (Slik *et al.*, 2003). To determine phylogenetic diversity we pruned down the angiosperm phylogeny group (APG (Stevens, 2001)) to the tree families present in our dataset using Phylomatic (Webb *et al.*, 2007), choosing the maximally resolved seed plant tree option. Using published phylogenies we manually resolved this tree to genus level for most families (see Appendix S1 in supporting information). Genera that could not be resolved were placed as basal polytomies within their families. This phylogeny was used as input in PhyloCom's Bladj application (Webb *et al.*, 2007). The Bladj application scales phylogenetic branch lengths to estimated time of evolutionary origin using known family ages (Wikstrom *et al.*, 2001). The PD application in PhyloCom was used to calculate

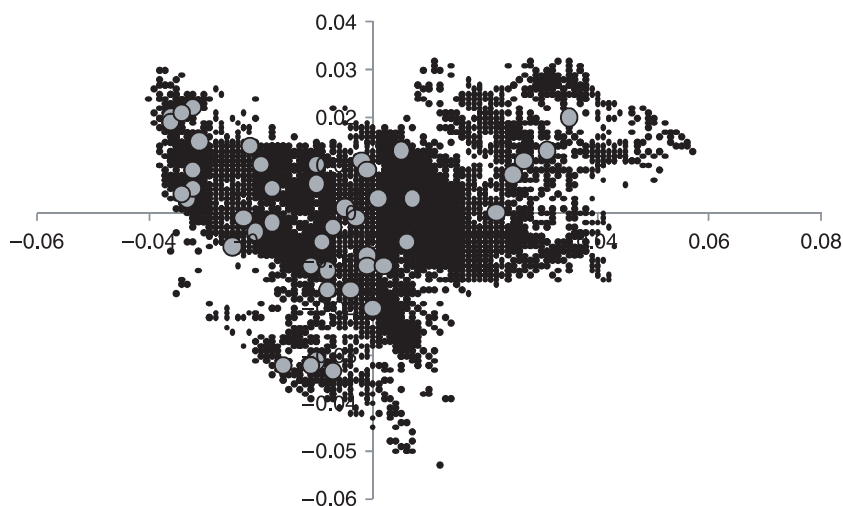


Figure 2 The first two axes, which together explain 39.9% of environmental data variance, of a principal components analysis of the 8577 Bornean grid cells used in our study (small black dots) based on the 11 environmental variables. The grid cells with tree inventory data are indicated with large grey dots to illustrate how much of environmental variability was encompassed by these locations.

phylogenetic diversity (Faith, 1992), which represents proportion of total phylogenetic branch length captured by the species in the input sample. Phylogenetic diversity in each location was based on the average of 5 random selections of 38 genera (based on the lowest number of genera found in our random samples of 400 individuals). Because gymnosperms, as the most basal group in the phylogeny, can greatly influence the outcome of phylogenetic diversity calculations, we repeated the analysis with angiosperms only (based on 37 randomly selected genera, the lowest number found in our random samples of 400 individuals).

Tree compositional gradients were determined using Detrended Correspondence Analysis (DCA) in multi-variate statistical package (Kovach Computing Services, Anglesey, Wales, UK). DCA was performed using a log₁₀ transformed matrix to reduce the effect of abundant genera. The DCA contained all random draws of 400 individuals. The scores of the locations on each of the DCA axes were determined by averaging the DCA axis scores of the five random draws per location.

Because our data came from different studies, the number of sampled trees, plots and sampled surface area differed for each grid cell introducing potentially confounding sampling effects. In combination with the fact that the exact locations of subplots within study areas were mostly unknown, this heterogeneous plot layout made it difficult to exclude the possibility that beta diversity was included in our diversity estimates. To minimize these sampling biases we applied multiple regression analysis with backward selection between the diversity and compositional values and the log-transformed number of plots, stems and sample area for each GIS-grid cell with inventory data (Statgraphics Plus for Windows 2.1, Rockville, MD, USA). This procedure identified significant correlations: (1) tree diversity with number of plots; (2) phylogenetic diversity with sample area; (3) CCA compositional axis 2 with number of plots, trees and sample area. The regression equations were used to calculate expected diversity and compositional values for each grid cell, which were subtracted from the observed values, to minimize confounding sample effects. All further analyses are based on these corrected diversity and composition values.

Relations between diversity and compositional gradients and the environmental variables were determined using Akaike's Information Criterion (AIC) using the model selection application Spatial Analysis in Macroecology (SAM, version 3.0, Rangel *et al.*, 2006). This procedure always produces a single best model given a certain dataset. However, because data selection can greatly influence final model choice, especially in small datasets, we used AIC in combination with data jackknifing. Therefore, we produced 50 sub-datasets, each with 6 randomly excluded locations, selecting the best model (AIC) for each. Although this reduces the power of each separate analysis slightly (40 instead of all 46 locations used) it will produce 50 equally likely models, giving an estimate of data variability on model choice. For each of the 50 models we determined the multiple regression equations, which were used to calculate 50 diversity and composition estimates for each location. The average of these 50 values was used as our final diversity and compositional estimate for each location. The performance of our final model (correlation coefficients, R^2 -adjusted, F -ratio and P -values) was tested by regressing estimated against observed values. We tested for residual spatial autocorrelation (RSA) of our diversity and compositional models using Moran's I . Finally, the 50 regression equations were used to calculate average diversity and compositional values (\pm SD) for each grid cell in Borneo.

RESULTS

Tree diversity, phylogenetic diversity and CCA composition axes 1 and 2 were significantly correlated with environmental variables (Table 3). Only tree diversity showed significant spatial autocorrelation of residuals in the first distance class (69 km, Table 3). All models performed well with correlation coefficients between 0.52–0.92 and adjusted R^2 -values between 25.4–84.1%.

Tree diversity had a correlation coefficient of 0.52 with the environment explaining 25.4% of data variability (Table 3). Tree diversity correlated negatively with elevation and positively with soil axis 5, indicating increasing diversity with increasing topsoil C:N ratio. Other, less important positive soil correlates for

Table 2 Tree inventory locations with their sample size, sample area, number of plots surveyed, the longitude/latitude of the centre of the GIS-grid cells where they were situated, average altitude of the grid cells, diversity (number of genera in 5 random draws of 400 individuals \pm confidence interval), phylogenetic diversity (percentage of reference phylogeny covered by 38 randomly selected genera \pm confidence interval), and data source.

Location	Sample size (trees)	Sample area (ha)	Plot number	Longitude	Latitude	Elevation (m)	Diversity ($n = 400$) (\pm conf.)	Phylogenetic diversity (\pm conf.)	Source
Andalau	12,648	20.2	10	114.5407E	4.6240N	61	81.2 \pm 2.7	17.6 \pm 0.4	Ashton
Bako	1892	2.4	4	110.4575E	1.7075N	58	85.0 \pm 0.6	17.8 \pm 0.6	Ashton
Long Barang	695	1.3	4	115.1240E	1.8740N	1026	105.6 \pm 2.3	18.8 \pm 1.0	Valkenburg
Barito Ulu	1562	2.5	3	114.0407E	0.1258S	287	88.8 \pm 7.0	17.4 \pm 0.9	Brearley
Belalong	9157	20.2	10	115.2073E	4.5407N	332	91.0 \pm 3.3	16.6 \pm 0.6	Ashton, Poulsen
Berau 1	1137	1.5	5	117.2906E	1.9575N	74	78.0 \pm 1.9	18.3 \pm 1.2	Slik
Berau 2	832	1.3	1	117.1239E	2.0408N	59	73.8 \pm 3.2	17.5 \pm 0.7	Slik
Berau 3	7195	12.0	3	117.2072E	1.8741N	105	85.4 \pm 4.2	17.3 \pm 0.9	STREK
Bukit Iju	9267	9.1	15	112.7074E	2.7074N	111	89.2 \pm 1.6	16.6 \pm 0.6	Ashton
Bukit Raya	7522	9.1	15	112.9574E	1.9575N	141	91.6 \pm 3.6	17.4 \pm 0.5	Ashton
Bukit Bangkirai	827	1.6	3	116.8678E	1.0300S	72	79.4 \pm 2.9	17.4 \pm 0.2	Slik
Bok Tisam	3533	6.1	10	114.1240E	3.6241N	77	86.6 \pm 3.9	16.9 \pm 0.7	Ashton
Danum Valley	3454	8.0	2	117.7906E	4.9573N	300	73.2 \pm 2.1	17.2 \pm 0.5	Newbery
Enggeng	1900	4.0	4	115.7906E	3.2074N	819	57.6 \pm 1.0	17.8 \pm 0.3	Wulffraat
Gunung Mulu	652	1.4	3	114.9573E	3.9574N	551	97.4 \pm 1.8	17.7 \pm 0.4	Martin, 1977
Gunung Meratus	575	1.4	62	116.2906E	0.8758S	103	96.8 \pm 3.1	17.3 \pm 0.7	Slik
Gunung Mersing	11,032	18.2	30	113.1241E	2.5407N	231	91.6 \pm 4.0	17.3 \pm 1.4	Ashton
Gunung Palung	2862	4.5	28	110.2075E	1.2924S	280	85.4 \pm 3.2	17.1 \pm 0.7	Webb
Gunung Santubong	907	1.2	2	110.3742E	1.6241N	9	71.4 \pm 2.4	16.6 \pm 0.9	Ashton
ITCI 1	1132	2.4	3	116.6239E	0.9591S	141	81.0 \pm 4.1	16.8 \pm 1.2	Eijk-Bos
ITCI 2	1813	4.8	4	116.5406E	0.9591S	322	99.8 \pm 6.2	17.5 \pm 1.3	Eijk-Bos
Kinabalu 1	974	2.0	2	116.7073E	6.0406N	774	91.8 \pm 2.9	17.2 \pm 0.9	Aiba
Kinabalu 2	2969	2.4	5	116.5406E	6.0406N	1958	55.4 \pm 2.3	22.4 \pm 1.0	Aiba
Lahei	1561	2.0	2	114.2074E	1.8757S	39	56.0 \pm 3.1	17.9 \pm 1.3	PLOTNET
Lambir	12,473	15.3	13	114.0407E	4.2074N	111	109.6 \pm 6.0	17.3 \pm 0.8	Ashton, Nagamasu
Langap	1421	1.0	35	116.4573E	3.1242N	118	100.6 \pm 3.8	17.9 \pm 0.4	Sheil
Lio Mutai	520	1.0	13	116.3739E	2.9574N	234	99.6 \pm 0.5	17.9 \pm 0.8	Sheil
Long Jalan	440	0.7	11	116.1240E	2.8741N	581	107.8 \pm 1.0	18.4 \pm 1.3	Sheil
Lurah	2711	5.0	5	115.4573E	2.8741N	991	44.8 \pm 1.9	17.9 \pm 0.7	Wulffraat
Malinau	480	0.8	12	116.5406E	3.0407N	257	95.2 \pm 2.5	17.7 \pm 0.6	Sheil
Nyabau	2848	3.0	5	113.1241E	3.2074N	44	76.4 \pm 3.8	17.5 \pm 0.5	Ashton
Puak	2267	4.5	5	115.7073E	2.8741N	1349	42.4 \pm 2.1	20.2 \pm 0.6	Wulffraat
Saan	416	0.5	1	115.4573E	2.4574N	855	35.0 \pm 0.0	19.7 \pm 0.0	Wulffraat
Samboja	6793	13.4	66	116.9573E	0.9591S	62	99.4 \pm 3.7	17.8 \pm 0.4	Slik
Sangai	7886	15.0	15	112.5408E	1.4591S	97	92.4 \pm 2.0	17.1 \pm 1.1	Wilkie
Segan	2467	3.0	5	112.9574E	2.9574N	160	95.0 \pm 3.3	17.7 \pm 1.4	Ashton
Sempatung	472	1.0	1	110.0409E	1.0408N	501	53.0 \pm 1.1	17.9 \pm 0.6	Suzuki
Semule	594	1.0	1	115.2907E	2.2908N	929	52.0 \pm 1.4	18.9 \pm 0.6	Wulffraat
Sepilok	18,745	48.0	12	117.9572E	5.8740N	32	87.0 \pm 1.1	16.9 \pm 0.5	Nilus
Serimbu	1082	2.0	2	110.1242E	0.7075N	129	93.4 \pm 2.0	16.6 \pm 0.5	Suzuki
Sungai Iwan	2306	5.6	6	115.0407E	2.0408N	737	53.6 \pm 2.8	17.8 \pm 0.6	Wulffraat
Sungai Wain	1976	2.8	200	116.7906E	1.1257S	35	87.6 \pm 3.5	17.3 \pm 0.9	Slik
Sunujuh	1254	2.0	2	109.4576E	1.4575N	27	77.6 \pm 2.5	17.5 \pm 1.0	Suzuki
Ulu Bakong	1705	3.0	5	114.0407E	4.2907N	41	81.0 \pm 5.5	16.5 \pm 0.5	Ashton
Ulu Dapoi	986	1.2	2	114.4574E	3.1241N	213	99.2 \pm 1.1	17.1 \pm 1.3	Ashton
Ulu Temiai	491	0.6	1	113.6241E	2.2074N	442	95.6 \pm 2.0	18.0 \pm 0.8	Ashton

diversity were soil pH, moisture storage capacity and topsoil base saturation, whereas tree diversity decreased with increasing soil depth, soil coarseness (texture), organic carbon content and topsoil cation-exchange-capacity of the clay fraction. Increasing annual rainfall also correlated positive with tree diversity.

Tree phylogenetic diversity correlated strongly with environmental variables (0.84), and these explained 70.5% of data variability (Table 3). Elevation and temperature seasonality were the most important positive correlates for tree phylogenetic diversity, whereas annual rainfall, rainfall seasonality and temperature

Table 3 Model performances (correlation coefficient, R^2 adjusted, F -ratio, d.f. and P -values), significant environmental correlates (with direction of correlation and model selection percentage between brackets) and residual spatial autocorrelation (significant Moran's I -values indicated in bold).

	Tree species diversity	Phylogenetic diversity all	Phylogenetic diversity angiosperms	Tree species composition axis 1	Tree species composition axis 2
Correlation	0.52	0.84	0.57	0.92	0.55
R^2 (%)	25.4	69.0	31.2	84.1	28.4
F -ratio	16.3	101.4	21.4	239.9	18.9
d.f.	45	45	45	45	45
P	0.0002	< 0.0001	< 0.0001	< 0.0001	0.0001
Multiple regression					
Variable 1	(–) Elevation (84)	(+) Elevation (100)	(+) Elevation (100)	(+) Elevation (100)	(+) Rain seas. (88)
Variable 2	(+) Soil 5 (64)	(+) Temp. seas. (82)	(–) Soil 2 (6)	(–) Soil 3 (94)	(+) Enso (34)
Variable 3	(–) Soil 2 (14)	(–) Annual rain (48)	(+) Annual rain (4)	(–) Soil 5 (36)	(–) Soil 5 (22)
Variable 4	(+) Soil 3 (12)	(–) Temp. range (34)	(–) Soil 5 (2)	(+) Soil 1 (18)	(–) Soil 3 (14)
Variable 5	(+) Annual rain (12)	(–) Rain seas. (12)	(–) Enso (2)	(–) Annual rain (4)	(+) Soil 4 (12)
Variable 6	(+) Soil 4 (10)	(–) Soil 2 (8)		(–) Enso (4)	(+) Temp. seas. (10)
Variable 7		(–) Soil 5 (4)		(+) Soil 2 (2)	(–) Temp. range (4)
Variable 8		(–) Soil 3 (2)		(–) Temp. seas. (2)	(–) Soil 1 (2)
Variable 9		(+) Soil 1 (2)			(–) Soil 2 (2)
Moran's I residuals distance classes (km)					
68.9	–0.200*	–0.045	–0.107	–0.101	–0.138
186.5	0.017	–0.016	–0.012	0.012	0.092
272.2	0.097	–0.023	–0.069	0.063	–0.138
345.7	–0.060	–0.094	0.066	–0.032	–0.104
412.9	–0.029	–0.018	0.112	0.006	0.039
488.7	0.062	0.086	–0.079	0.043	–0.023
577.7	–0.009	–0.011	–0.103	–0.071	0.075
683.7	–0.040	0.001	0.011	–0.135	–0.005
957.1	–0.036	–0.081	–0.018	0.015	0.004

yearly range correlated negatively. Soil variables were of limited importance for tree phylogenetic diversity. Phylogenetic diversity was almost entirely determined by gymnosperms, which explained 74.2% of data variance between locations (correlation coefficient = 0.86, F -ratio = 126.3, d.f. = 45, $P < 0.0001$). Therefore, we repeated the analysis with angiosperms only, which lowered the correlation with the environment (0.52) and amount of explained data variability (31.2), but still resulted in a strong positive correlation between elevation and angiosperm phylogenetic diversity.

The main compositional gradient in Borneo (DCA axis one, explaining 9.5% data variability) was strongly associated with environmental variables (correlation coefficient 0.92, R^2 -adjusted 84.1%). Elevation was the major correlate in association with soil axis 3, indicating the importance of soil texture and topsoil cation-exchange-capacity of the clay fraction. Other variables affecting composition gradients were the soil C:N ratio, N content, C content and drainage.

The second compositional gradient in Borneo (DCA axis two, explaining 3.8% data variability) was significantly associated with environmental variables (correlation coefficient 0.55 and R^2 -adjusted 28.4%). This compositional gradient was mainly associated with rainfall seasonality and ENSO-drought impact.

Other, less important correlates were temperature seasonality and soil texture, topsoil cation-exchange-capacity of the clay fraction, soil depth and topsoil C:N ratio.

Borneo-wide extrapolations of diversity and compositional gradients are shown in Fig. 3. Tree diversity is highest in lowland forests, decreasing steadily with elevation (3a). Variations in lowland tree diversity are mainly linked to soil axis 5, with highest diversity in areas with high topsoil C:N ratios. Tree phylogenetic diversity and angiosperm phylogenetic diversity both show an increase with altitude across Borneo (Fig. 3b,c). Phylogenetic diversity, contrary to angiosperm phylogenetic diversity, is also relatively high in lowland Sabah (northeastern Borneo). The most important compositional gradient across Borneo identifies montane, sub-montane, keranga, peat swamp and dipterocarp forests (Fig. 3d), whereas the second compositional gradient reflects rainfall seasonality in combination with ENSO-drought impact (Fig. 3e).

DISCUSSION

Diversity patterns

Tree diversity and phylogenetic diversity were strongly associated with elevation albeit in contrasting ways: tree diversity declined

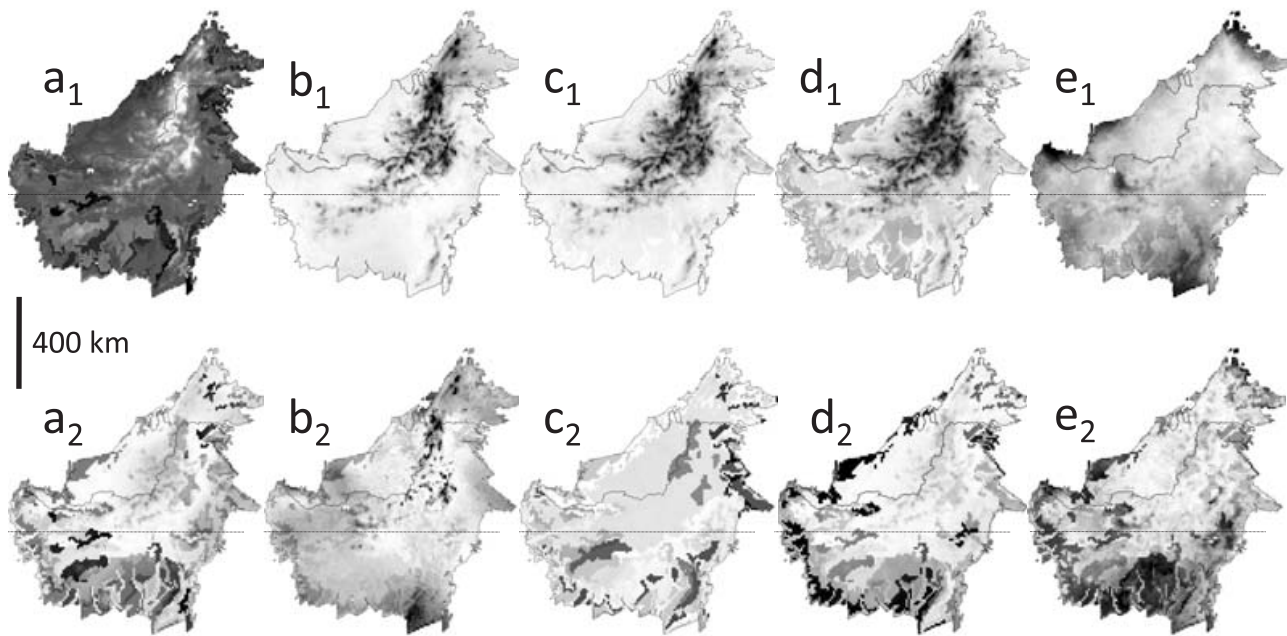


Figure 3 Borneo-wide modelling results for: tree diversity ($a_1 \pm SD$ (a_2)); tree phylogenetic diversity ($b_1 \pm SD$ (b_2)); tree phylogenetic diversity of angiosperms only ($c_1 \pm SD$ (c_2)); tree species compositional axis 1 ($d_1 \pm SD$ (d_2)); and tree species compositional axis 2 ($e_1 \pm SD$ (e_2)). Values increase from white to black.

whereas phylogenetic diversity increased with elevation. Decline in tree diversity with elevation confirms findings elsewhere on Borneo (Kitayama, 1992; Pendry & Proctor, 1997; Aiba *et al.*, 2005) and other tropical regions (Gentry, 1988; Romdal & Grytnes, 2007), although with exceptions (Lovett *et al.*, 2006). These changes are possibly linked to declining temperatures and area size with increasing altitude (Bachman *et al.*, 2004; Jimenez-Castillo *et al.*, 2007). A comparable phylogenetic diversity study in eastern African tropical forest also reports increasing phylogenetic diversity with elevation (Tallents *et al.*, 2005). In Borneo this increase in phylogenetic diversity is strongly determined by gymnosperms (*Agathis* Salsb., *Dacrycarpus* (Endl.) de Laub., *Dacrydium* Lamb., *Falcatifolium* de Laub., *Nageia* Gaertn. and *Podocarpus* L'Her. ex Pers.). However, when we repeated the analysis using only angiosperm genera, elevation was still the most important positive correlate for phylogenetic diversity. Apparently, basal plant lineages become more common at higher altitudes whereas lowland forests are characterized by communities of more closely related taxa. This suggests that lowland tropical forests serve as species sources (speciation centres) whereas high-elevation forests serve as species sinks. Such source–sink patterns are also observed along depth gradients in marine environments (Rex *et al.*, 2005) and along latitudinal gradients (Roy & Goldberg, 2007). This would mean that over evolutionary timescales lowland forests are essential for the maintenance of tree diversity in tropical montane floras.

Tree diversity showed a consistent positive correlation with increasing soil C:N ratio, pH, moisture storage capacity and topsoil base saturation, whereas it declined with soil depth, coarseness, organic carbon content and cation-exchange capacity of the topsoil clay fraction. This combination of soil factors

suggests increasing diversity in nitrogen limited, shallow soils with high water retention capacity, i.e. soils that are generally considered less fertile and productive. This seems to confirm findings from western Borneo, where diversity of Dipterocarpaceae increased with decreasing soil fertility (Paoli *et al.*, 2006).

Despite a 3-m gradient in Borneo, annual rainfall was only selected in 12% of models as a correlate for tree diversity, contrasting with its importance for diversity in African and Neotropical studies (Gentry, 1988; ter Steege *et al.*, 2003; Parmentier *et al.*, 2007; Punyasena *et al.*, 2008). This difference between Borneo and other tropical regions might be related to the fact that, measured over the long term, most areas in Borneo receive more than 100 mm of rain each month. This value is considered the minimum rainfall required to compensate for evaporation in the tropics, suggesting water stress plays a minor role in Borneo. This seems to be confirmed by the non-existent association between tree diversity and ENSO drought impact.

Composition patterns

Tree composition patterns were strongly associated with elevation, soil texture and, to a lesser extent, soil C:N ratio and fertility. Indeed, most studies in the tropics report shifts in tree species composition along altitudinal gradients (Gentry, 1988; Ashton, 2003) and soil types (Duivenvoorden, 1995; ter Steege *et al.*, 2006). The most obvious changes with increasing elevation in Borneo are the lowered abundance of Dipterocarps commensurate with increases in Fagaceae, Lauraceae, Myrtaceae and gymnosperms. Many of the montane genera are characterized by large distribution ranges that often include temperate regions, whereas characteristic lowland genera are usually confined to the tropics

(Qian *et al.*, 2003). Low-temperature tolerance probably plays a role in floristic shifts along altitudinal gradients, with increasing cold tolerance offset by lower competitive ability under warmer conditions.

Our study confirms the importance of soils as correlates for compositional gradients in the tropics. Soil texture, drainage and nutrient availability have repeatedly been shown to be associated with floristic shifts (Newbery, 1991; Duivenvoorden, 1995; Aiba & Kitayama, 2002; Tuomisto *et al.*, 2002; Phillips *et al.*, 2003). Soil nutrients impact tree communities by influencing forest turnover rates and dynamics, with fertile soils generally favouring trees with high growth rates and short life spans, and poor soils favouring slow growing long-lived trees (Phillips *et al.*, 1994). Soil texture and drainage are probably related to drought and flooding tolerance of trees, which can be potent selective forces (Slik, 2004; van Nieuwstadt & Sheil, 2005; McDowell *et al.*, 2008). Many studies report annual rainfall, rainfall seasonality and droughts as variables associated with tree floristics (Slik *et al.*, 2003; Chust *et al.*, 2006; ter Steege *et al.*, 2006; Parmentier *et al.*, 2007). Our results do indeed indicate that rainfall seasonality and ENSO-drought impact are important correlates for floristic shifts in Borneo.

Impact of data quality and quantity

We were faced with considerable problems when trying to perform a meta-analysis using inventory data that were collected differently in each location. In fact, the scarcity of taxonomically reliable inventory data in Borneo resulting in only 46 inventoried grid cells formed a problem by itself. As a result not all forest types were equally represented with only few locations in kerangas and none in freshwater/peat swamp forests leading to high standard deviations for these forest types in our Borneo-wide analysis. Although our locations were spatially biased towards northern Borneo, and some locations were close together, we only found significant RSA for tree diversity over small distances (< 70 km). This violates the assumption that residuals should be independent and results in inflated Type I errors (Dormann *et al.*, 2007). However, short-distance RSA, although causing inflated type I errors, does not seriously affect the interpretation of the regression coefficients estimated by ordinary least squares regressions (Diniz-Filho *et al.*, 2007; Hawkins *et al.*, 2007).

Different scales of environmental (*c.* 10 × 10 km grids) and inventory data form another complication as it is unlikely that plots covering a few hectares are representative of a 10 × 10 km area. Additionally, some grid cells contained more inventoried trees, plots or surveyed surface area than others, resulting in different levels of beta diversity captured per location. Although we have tried to correct our diversity and compositional values for these sampling biases, it is likely that they have at least partly influenced our results. Ideally, meta-analyses like ours should be performed on standardized plot layouts in combination with high-resolution environmental data. Unfortunately, such an approach is still difficult to realize in remote tropical areas like Borneo, where the availability of reliable inventory data itself

already forms a problem, let alone reliable high-resolution data on soils and climate. Given the enormous diversity stored in tropical forests and the alarming rate in which these forests are disappearing, it is urgently needed to set up large-scale baseline studies that sample the remaining tropical forests in a standardized manner. Current deforestation completely erases the natural patterns of ecological communities that exist in these forests in taxonomic and genetic terms. Soon it might be too late to reconstruct these natural patterns, which are key for our understanding of how these systems have originated and maintained themselves over millions of years.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Text file in Nexus format of phylogenetic reference tree used in this study.

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