Borneo : a quantitative analysis of botanical richness, endemicity and floristic regions based on herbarium records

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CHAPTER 6

Borneo's remaining forests – Where to from here?

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In this chapter we summarize the results of the previous chapters, show how much the botanical diversity and floristic regions of Borneo have been impacted, and discuss the conservation/policy implications of these results. Finally, we make suggestions for future research to answer questions raised as result of our studies, and to further improve our understanding of what shapes macroecological biodiversity patterns. Although it is widely recognized that Borneo is one of the world's most important biodiversity hotspots (Myers *et al.*, 2000), the spatial patterns of botanical richness, endemicity, 'centres of endemicity', and Borneo's floristic regions, have until now largely been based on informal expert opinion. Recent digitization of the botanical collections of Borneo, housed at the National Herbarium of the Netherlands, has provided a database that allowed a quantitatively spatial analysis of the components of biodiversity of Borneo. We have shown that botanical richness and endemicity are not evenly distributed over Borneo, and also that clear floristic regions, with meaningful ecological correlates can be identified. Much of Borneo has been impacted by man, however (Curran *et al.*, 2004; Dennis & Colfer, 2006; Langner *et al.*, 2007; Stibig *et al.*, 2007), but to what extent this has affected the species rich areas, the centres of endemicity and the various floristic regions remains unknown.

The 'road map' to patterns of botanical diversity and the floristic regions of Borneo

We selected species belonging to families treated in Flora Malesiana (Anon., 1959-2007), together with those of the revised genera of the Annonaceae, Euphorbiaceae, and Orchidaceae. To georeference the collections we used online- and printed gazetteers. Mapping of the georeferenced collections revealed an uneven, or biased, distribution of collection localities on Borneo (Fig. 3.3). To reduce bias to a minimum we applied a technique known as georegistration in order to georeference as many collections as possible from the severely under-collected provinces of Kalimantan (Raes *et al.*, 2009 - Chapter 2). Our efforts resulted in a database comprising 66,262 georeferenced records belonging to 102 plant families representing 2,273 species.

To develop Borneo-wide biodiversity patterns at high spatial resolution we used a technique known as species distribution modelling. Species distribution models (SDMs) predict the potential distribution of a species by describing relationships between a species' presence/absence-, or presence-only data, and a set of environmental predictors across an area of interest. Depending on the availability of meaningful environmental predictors, in combination with sufficiently accurate collection localities, SDMs can predict the presence and absence of species across the entire area of investigation at the spatial resolution of the environmental predictors (Guisan & Zimmermann, 2000; Araújo & Guisan, 2006; Peterson, 2006). From the available suite of modelling applications (Elith *et al.*, 2006; Pearson *et al.*, 2006) we selected Maxent (ver. 3.0.4) (Phillips *et al.*, 2006) for our data, because Maxent was a) specifically developed to model species distributions with presence-only data (typical of herbarium data), b) has shown to outperform most other modelling applications (Elith *et al.*, 2006; Pearson *et al.*, 2007; Wisz *et al.*, 2008), and c) is least affected by georeferencing errors (Graham *et al.*, 2008).

The application of predictive models, like SDMs, require testing of their predictive accuracy. We showed, however, that currently used SDM accuracy measures based on presence-only data, and pseudo-absences instead of true absences (which are often not available), cannot reliably be applied (Raes & ter Steege, 2007 - Chapter 3). Therefore, we introduced a newly developed null-model methodology that tests whether an SDM's AUC value - a threshold independent and prevalence insensitive measure of model accuracy (Fielding & Bell, 1997; McPherson *et al.*, 2004; Raes & ter Steege, 2007 - Chapter 3) - is significantly different from random chance expectation, taking into account the uneven distribution of collection localities.

We developed SDMs for the 2273 species based on their presence records, and 11 meaningful and independent environmental predictors at 5 arc-minute (ca. 100 km^2) spatial resolution (Raes *et al.*, submitted - Chapter 4). All models were tested against a bias corrected null-model, resulting in 1439 significant SDMs (63.3%), covering 8577 grid cells. We converted the continuous Maxent predictions to discrete presence/absence maps by applying a 10-percentile threshold. Significant SDMs were superimposed to generate the botanical richness pattern of Borneo (Fig. 6.1A). As measure of endemicity we used the weighted endemism index (Crisp *et al.*, 2001; Kier & Barthlott, 2001; Küper *et al.*, 2006; Slatyer *et al.*, 2007). We developed the endemicity pattern by summing the weights of all 1439 significant SDMs for all grid cells (Fig. 6.1C). The 'centres of endemicity' were identified by mapping the relative residuals of the species richness – weighted endemism relationship (Fig. 6.1E).

The 50 percent highest diversity grid cells cover 15.8% of Borneo (Table 6.1, quartile 3 & 4); for weighted endemism this is less than 5%. Only 2.1% of Borneo's surface has more than 150% endemics than can be expected based on their diversity values (Table 6.1, '50-100' & '>100'). These areas are the 'centres of endemicity'. The areas of high diversity and endemicity are characterized by a relatively small range in annual temperature, but with seasonality in temperatures within that range. Furthermore, these areas are least affected by the El Niño Southern Oscillation drought events. The 'centres of endemicity' are found in areas that are ecologically distinct in altitude, edaphic conditions, annual precipitation, or a combination of these factors.

To identify the floristic regions of Borneo we constructed a presence/absence matrix based on 1439 significant SDMs for the 8577 grid cells of Borneo (Raes *et al.*, submitted - Chapter 5). This matrix was then analysed using a hierarchical cluster analysis, and the resulting cluster dendrogram was pruned using indicator species analysis (ISA) to partition the 11 floristic regions (Fig. 6.1G; Table 6.1, Floristic Region). The relationship between the 11 floristic regions and environmental conditions was explored using a classification and regression tree (CART) analysis. CART identified meaningful ecological thresholds defining each floristic region, largely in accordance with the known ecology of the represented 'forest types' (Whitmore, 1984a; Wikramanayake *et al.*, 2002). This method allowed the quantitative confirmation of the floristic distinctiveness and extent of montane rain forest (Floristic Region 1 & 3), kerangas (4), peat swamps (5), and fresh water swamp forest (9). The lowland rain forest, previously recognized as one floristic region (Whitmore, 1984b; MacKinnon, 1997; Wikramanayake *et al.*, 2002) was divided in at least four (and possibly six) distinct floristic regions, viz. the lowlands of (i) Sabah and Sarawak (10), (ii) East Kalimantan (11), (iii) southern Borneo (6, 7 & 8), and (iv) the Wet hill forest of Sarawak (2). Due to the 100 km^2 resolution of our analysis, we could not distinguish, but do recognize, the 'Kinabalu highlands', mangroves, and forests on limestone and ultramafic rock.

Borneo's remaining forests

The use of SDMs to generate quantitative patterns of botanical richness, weighted endemism, 'centres of endemicity', and floristic regions of Borneo, resulted in potential forested extents of these areas (Fig. 6.1, 'Total'), with 100% of Borneo covered by forest. Much of Borneo has been impacted by man, however, and few areas have been put aside in conservation areas. To analyse the extent of deforestation and conservation in areas of high diversity, high endemicity and the different floristic regions, we overlaid our maps with those of forest change and conservation areas. As a proxy for Borneo's remaining forests we used the Global Land Cover 2000 dataset (GLC2000, 2003) for South East Asia

Table 6.1. The percentages of Borneo's surface covered by the four quartiles of 'Species Diversity' and 'Species Weighted Endemism', the four 'Relative Residual Weighted Endemism' classes, and the 11 'Floristic Regions' for its entire surface - 'Total', divided in 'Forested' and 'Non-Forested' extents, and for 'Protected-' and 'Non-Protected Areas' divided in 'Forested' and 'Non-Forested' extents. Between brackets percentages deforestation.

		Total	Forested	Non-Forested	Protected Area		Non-Protected Area	
					Forested	Non-Forested	Forested	Non-Forested
Species	**1**	62.4	40.3	22.1 (35.4)	5.7	0.9 (13.6)	34.6	21.2 (38.0)
Diversity	**2**	21.7	14.0	7.7 (35.3)	1.1	0.4 (28.0)	12.9	7.2 (35.9)
	3	10.2	6.8	3.4 (33.7)	0.7	0.3 (27.8)	6.1	3.2 (34.3)
	4	5.6	2.4	3.2 (57.4)	0.4	0.2 (33.0)	2.1	3.1 (59.9)
Species	**1**	81.3	52.3	28.9 (35.6)	6.4	1.3 (16.9)	45.9	27.6 (37.6)
Weighted	**2**	14.5	9.2	5.3 (36.6)	1.0	0.3 (24.4)	8.2	5.0 (37.9)
Endemism	**3**	3.3	1.4	1.9 (56.8)	0.2	0.1 (32.2)	1.2	1.8 (59.6)
	4	0.9	0.6	0.3 (35.7)	0.2	0.0 (14.3)	0.4	0.3 (43.7)
Relative	**<0**	59.8	36.5	23.3 (39.0)	2.5	1.1 (30.5)	34.0	22.2 (39.5)
Residual	**0-50**	38.0	25.2	12.8 (33.6)	4.5	0.6 (12.3)	20.7	12.2 (37.0)
Endemism	**50-100**	1.9	1.6	0.3 (16.6)	0.7	0.0 (4.4)	0.9	0.3 (24.8)
(in %)	**>100**	0.2	0.2	0.0 (5.9)	0.1	0.0 (3.5)	0.1	0.0 (7.6)
Floristic	**1**	14.3	13.1	1.2 (8.5)	2.4	0.1 (5.2)	10.7	1.1 (9.2)
Region	**2**	4.5	4.2	0.3 (7.2)	0.0	0.0 (0.6)	4.1	0.3 (7.3)
	3	5.3	5.2	0.1 (1.5)	1.5	0.0 (1.7)	3.6	0.1 (1.4)
	4	5.8	3.1	2.6 (45.7)	0.6	0.1 (15.3)	2.6	2.5 (49.6)
	5	8.3	4.5	3.8 (46.3)	0.6	0.2 (26.6)	3.8	3.6 (48.6)
	6	9.0	6.1	2.9 (32.2)	0.9	0.2 (14.7)	5.2	2.7 (34.5)
	7	6.9	3.4	3.5 (50.5)	0.0	0.0 (70.7)	3.4	3.4 (50.4)
	8	14.3	7.9	6.4 (44.7)	0.8	0.2 (24.1)	7.1	6.1 (46.2)
	9	7.4	3.8	3.7 (49.6)	0.2	0.1 (32.7)	3.5	3.6 (50.3)
	10	12.6	6.9	5.6 (44.9)	0.7	0.3 (28.1)	6.3	5.4 (46.2)
	11	11.7	5.4	6.3 (53.5)	0.1	0.5 (84.4)	5.4	5.8 (52.0)
Total		**100.0**	**63.6**	**36.4**	**7.8**	**1.8 (18.4)**	**55.7**	**34.7 (38.4)**

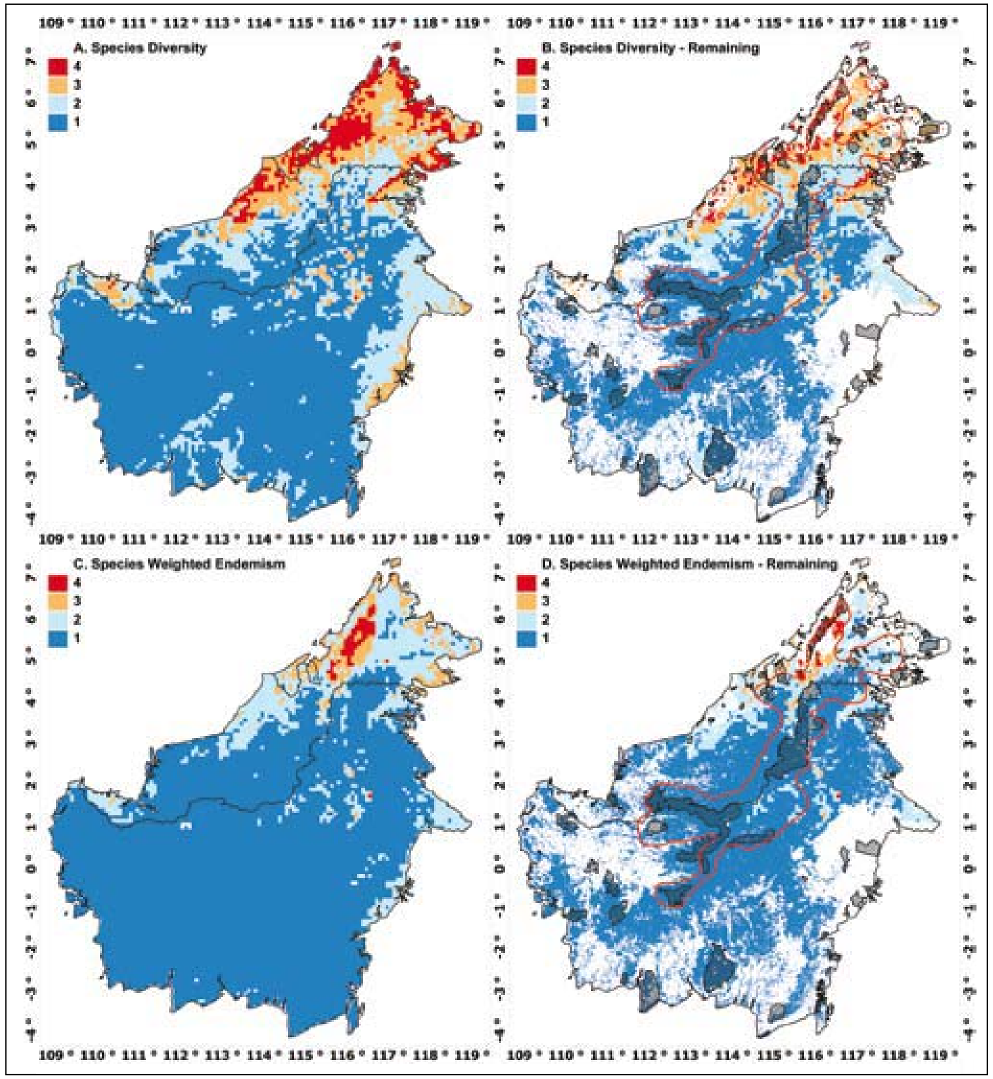

Figure 6.1. A. The four quartiles of species diversity (1=lowest diversity; 4= highest diversity); B. The four quartiles of species diversity still forested; C. The four quartiles of species weighted endemism; D. The four quartiles of species weighted endemism still forested. Red line – the proposed trans-boundary WWF 'Heart of Borneo' protected area.

based on SPOT-VEGETATION satellite data for the years 1998-2000 (Stibig *et al.*, 2007). The average annual deforestation rate on Borneo of 1.7% (Langner *et al.*, 2007) suggests that our estimates of the forested extent of Borneo are probably conservative. We re-sampled our 5 arc-minute maps to the '1 km at equator' (0.00893 decimal degree) resolution of the South East Asian land-cover map, and kept only those grid cells with values for both maps. We used land-cover forest classes 1-5 as our proxy for forested extent, and assessed the

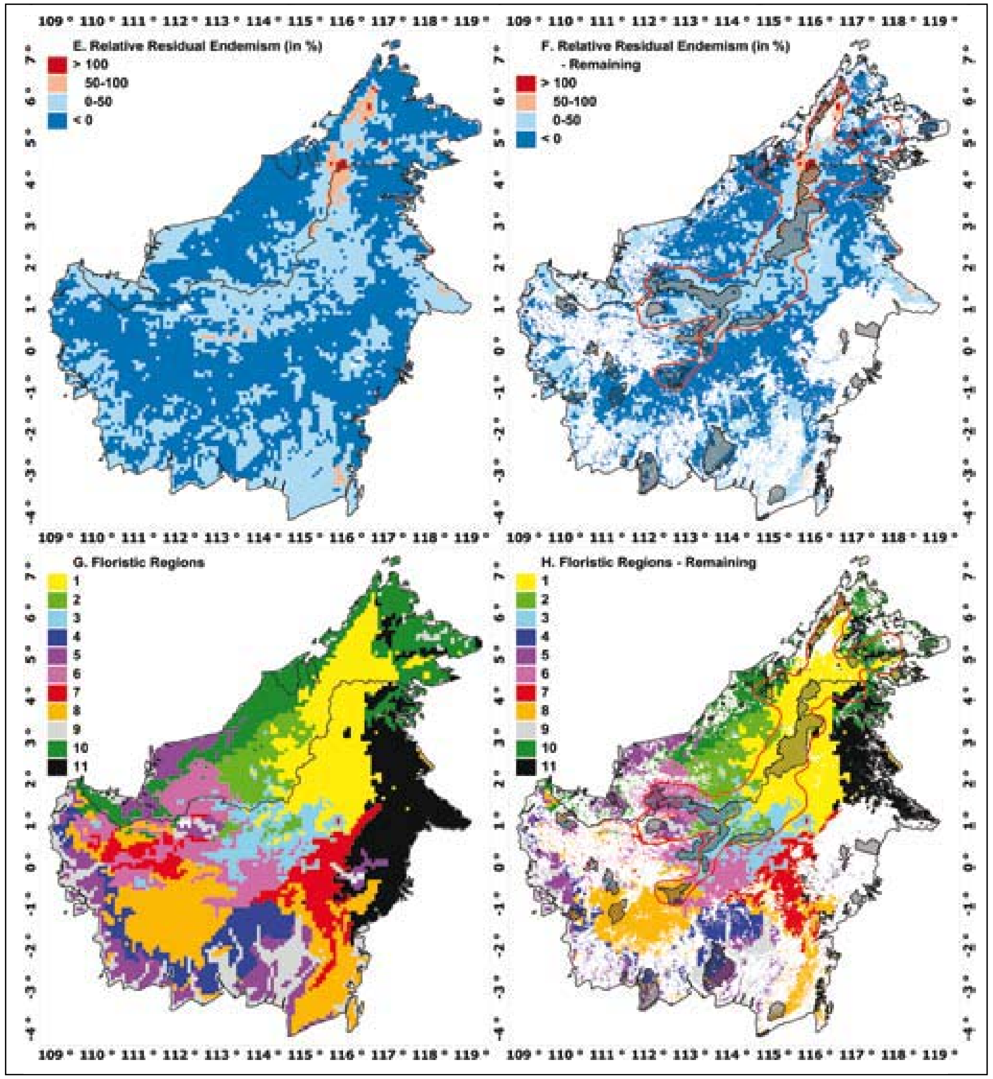

Figure 6.1. (continued) E. The four classes of relative residual weighted endemism ('<0' =less than expected, '0-50' = up to 50% more endemism than expected, '50-100' = 50-100% more endemism than expected, '>100' = more than 100% more endemism than expected); F. The four classes of relative residual weighted endemism still forested; G. The 11 floristic regions of Borneo; H. The 11 floristic regions of Borneo still forested. Hatched areas indicate the IUCN recognized protected areas (WDPA, 2007). Red line – the proposed trans-boundary WWF 'Heart of Borneo' protected area.

percentage of each area covered by these five land-cover forest classes (Fig. 6.1B, D, F, H; Table 6.1, 'Forested/Non-Forested'). The analysis reveals that 36 % of Borneo's total surface, and 57% of its most diverse areas (Table 6.1, Species Diversity - 4th quartile) are already very heavily impacted. Especially the most diverse lowlands of Sabah and Sarawak (Floristic Region 10), and those of East Kalimantan (11) have been severely hit by deforestation caused by logging, forest fires and land-use change (Table 6.1, Fig. 6.1) (Sodhi *et al.*, 2004; Dennis & Colfer, 2006; Langner *et al.*, 2007; Stibig *et al.*, 2007).

Deforestation has taken its toll even in the IUCN recognized protected areas (Curran et al., 2004), as can be concluded from the overlay of the World Database of Protected Areas (WDPA, 2007) on the remaining forested areas (Fig. 6.1B, D, F, and H; hatched areas). Only 0.6% of Borneo's surface belongs to the fourth quartile of species diversity, while at the same time having an IUCN protected status. By the year 2000, 33% of this area was already deforested, however. For the non-protected areas belonging to this category (5.2% of Borneo's surface), 60% was already lost by 2000. For areas in the highest weighted endemism categories (Table 6.1, Species Weighted Endemism, quartile 3 & 4), values in the same order of magnitude were found. Most catastrophic is the loss of 84% of East Kalimantan's lowland rain forests in protected areas (Table 6.1, Floristic Region 11). The 'centres of endemicity' are least affected by deforestation (Table 6.1, Relative Residual Endemism), as these are mainly found in the higher altitude, less impacted, floristic regions ('Montane rain forest' – Floristic Regions 1 & 3; Table 6.1).

Implications for conservation

The latest effort to conserve large part of Borneo's biodiversity is the 'Heart of Borneo' initiative (WWF-Germany, 2005; Stone, 2007). This area of more than 20 million ha straddles Borneo's trans-boundary highlands of Indonesia and Malaysia, and reaches out through the foothills into adjacent lowlands and to parts of Brunei (Fig. 6.1 B, D, F, H; red boundary). Although this initiative is a milestone for conservation on Borneo, many floristic regions will not be protected within its boundaries (Fig. 6.1H). To safeguard Borneo's genetic diversity, especially the last remaining high diversity lowland rain forest regions of 'East Kalimantan' (11) and 'Sabah and Sarawak' (10) should be awarded protected status.
For East Kalimantan, we suggest the Sungai Wain 'Protection' Forest close to Balikpapan, part of the Sangkulirang Peninsula, and the area between the Sembakung-Sesajap delta and the montane rain forest in northern East Kalimantan. For Sabah and Sarawak the areas west of the Crocker Mountains range, the valley between the Crocker Mountains and the central mountains range, and the last remaining lowlands of south-western Sarawak are suggested. Furthermore, the floristic regions that cover smaller percentages of Borneo's surface, such as 'Kerangas' (4), 'Peat swamp forests' (5), and 'Fresh water swamps' (9) should receive more conservation attention and a larger percentage of their extent should be protected. Finally, we suggest that parts of all southern Borneo lowland rain forest regions (6, 7 and 8) are conserved.

Future research prospects

The quantitative analysis of Borneo's botanical diversity, endemicity, and floristic regions has also raised several challenges that deserve to be addressed by future research.

1. The first is the introduction of error-surfaces, or the extent to which gradients in environmental predictors are covered by sample localities. These issues have started to be addressed (Kadmon *et al.*, 2004; Guralnick *et al.*, 2007; Loiselle *et al.*, 2008), but deserve additional research and incorporation in SDMs.
2. For our analyses we used single species distribution models that exclude many species on grounds of the required minimum number of presences. A recent review of community level modelling (Ferrier & Guisan, 2006) suggests that these methods can offer an approach for constructing distribution models for rare species with low occurrence data. It should be explored how results of these methods differ from our results.
3. The application of large scale analysis of combined phylogenetics and bioclimatic modelling, known as phyloclimatic modelling (Yesson & Culham, 2006b; Yesson & Culham, 2006a) should be explored to improve LGM refugial reconstructions (Waltari *et al.*, 2007), and to assess when, and under which environmental conditions speciation most likely has taken place.
4. Modelling of species traits of dispersal in relation to the post-glacial dispersal lag hypothesis (Svenning *et al.*, 2008) may lead to better founded reconstructions of LGM refugia.
5. Projection of 'local' SDMs on an SDM derived from the global set of occurrence records allows testing whether local populations occupy their entire potential niche, and whether their predictive accuracy improves, or deteriorates. Geographically separated populations can occupy a different spectrum of their niche due to genetic drift or competition with other species. Vice versa, projection of SDMs to a global environmental predictor dataset can reveal biogeographical boundaries and regions prone to invasion.
6. The combination of diversity measures from plot studies (Slik *et al.*, 2003) with biodiversity patterns derived from SDM to potentially introduce abundance measures to SDMs.
7. The projection of SDMs under different Global Climate Change scenario's (Millennium-Ecosystem-Assessment, 2005) to identify those areas which potentially can preserve most of the world's genetic diversity in a changing world.