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

Raes, N.

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CHAPTER 1
General Introduction

▶ Niels Raes

BORNEO AND THE MALESIAN FLORISTIC REGION

The island of Borneo straddles the equator between latitudes 7° N and 4° S, and belongs, together with Amazonia and New Guinea, to the botanically most diverse terrestrial regions on earth (Myers et al., 2000; Barthlott et al., 2005; Kier et al., 2005). Borneo is part of the Malesian floristic region, first recognized by the Swiss botanist and explorer Heinrich Zollinger in 1857 (Zollinger, 1857; Johns, 1995). Zollinger comments on the demarcation of the 'Flora of the Dutch Indies' by F.A.W. Miquel , and argues that a floristic region should not be confused with the boundaries of a country's colonies. Based on a very limited number of distribution data and with mainly straight lines, Zollinger (1857) defined the boundaries of the Malesian floristic region (Fig 1.1; total grey area). He named his floristic region - Flora Malesiana - after the common use of the Malay language throughout the entire Archipelago. For colleagues at the time, who found the delimitation to extensive, Zollinger (1857) even recognized a 'Flora Malesiana' in a more restricted sense (Fig. 1.1; dark-grey area). He acknowledged that the western peninsular Malesia probably should be split up into three different regions: a northern-, central-, and southern region. According to Zollinger the southern region definitely belonged to the Malesian floristic region, and indeed this boundary corresponds with one of the demarcation knots of Van Steenis (1948, 1950; see below) . The reported sightings of snow-covered mountain peaks led him to conclude that the flora of New Guinea likely resembled that of a temperate mainland more than that of an island flora, hence excluded most of New Guinea from the Malesian floristic region.

Almost a century later, Van Steenis largely confirmed the Malesian floristic boundaries of Zollinger's initial delimitation, based on distribution maps of 2178 genera (van Steenis, 1948, 1950). This work was a continuation of the physiognomic map of the Dutch East Indies colonies, currently known as Indonesia, which he published in 1935 (van Steenis, 1935a, b). Van Steenis identified four contact zones and three principal 'demarcation knots' of Malesia with adjacent floral regions, viz. between the Malay Peninsula (e.g. the very south of Thailand) and Asia, between the Philippine Islands and Taiwan, the Torres Strait between New Guinea and Australia, and a less clear contact zone between the Bismarck- and Solomon islands and the Pacific islands (van Steenis, 1950). The later arbitrarily taken as eastern border because of lack of data (Fig. 1.1). The natural eastern boundary of the region lies in fact east of the Pacific Islands (van Balgooy et al., 1996). It should also be noted that the demarcation knot between the Malay Peninsula and Asia is not located at the Isthmus of Kra, but through the southernmost provinces of Thailand (van Steenis, 1950). The phytogeographical status of Malesian floristic region was recently confirmed by Van Welzen et al. (2005), who found that 70% of 6616 sampled species was endemic to Malesia.

Wallace's Line, the Sunda Shelf, Wallacea, and the Sahul Shelf

Since the first recognition of Malesia as a floristic region, a debate is ongoing about its internal subdivision. The most famous division is in a western- and eastern sub-region, separated by Wallace's Line (Fig. 1.1; Wallace, 1860). Wallace (1860) found a distinct boundary between the Southeast Asian- and the New Guinean-Australian fauna, located east of the Philippines, between Borneo and Sulawesi and finally between Bali and Lombok. Other authors have recognized similar lines, or western and
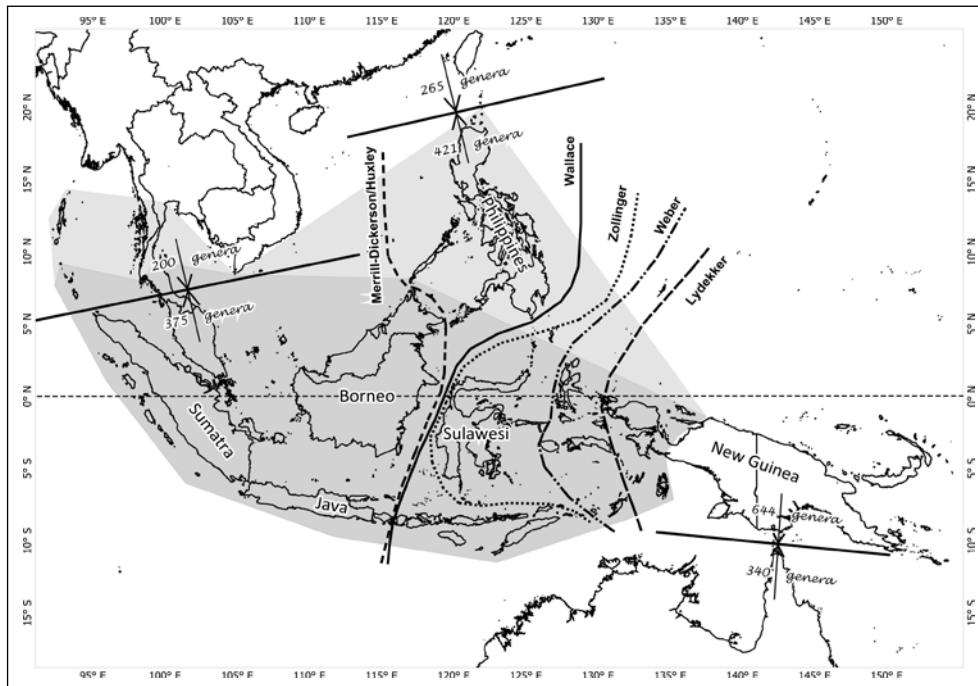
Figure 1.1. The boundaries of the Malesian floristic region defined by Zollinger (1857) in the widest sense (total grey area) and in the more restricted sense (dark-grey area); and the delimitation by Van Steenis (1948, 1950) indicated by the three demarcation knots. The numbers indicate the number of genera not crossing the knots. The different lines indicate Wallace's Line and the eastern and western variants by different authors.

Figure 1.2. Results of the Principal Coordinate Analysis (PCO) based on presence/absence data of 7043 plant species for the nine island groups of the Malay Archipelago (from Van Welzen & Slik, 2009; Fig. 1a therein).

eastern variants of Wallace's Line (Fig. 1.1). A recent study of the evidence of the different lines based on botanical records of 6616 species showed that for all lines per side twice as many, or far more, species stop than cross the lines, and that the lines become stronger moving from west to east, meaning that less species pass a line (van Welzen *et al.*, 2005). The strong boundary of the eastern Lydekker's line indicates the very different nature of the New Guinean flora. This finding was also supported by the Principal Coordinate analysis on a slightly larger dataset containing data of 7043 species, showing the separate position of New Guinea (Fig. 1.2; van Welzen & Slik, 2009). Note that the Merrill-Dickerson/Huxley Line actually includes Java with Borneo, Sumatra and the Malay Peninsula (explained below). The floristic separation in three regions

corresponds very closely with the geological history of the Malay Archipelago (Hall, 1998). The western part, west of the Merrill-Dickerson/Huxley Line in Fig. 1.1, including Borneo, Sumatra, the Malay Peninsula, and Java is also known as the Sunda Shelf. This continental shelf formed one continuous landmass during glacial maxima, when the sea levels were ~120m lower than at present, caused by an increase in land ice on the polar caps (Voris, 2000; Bird *et al.*, 2005). Under these conditions species were able to disperse to other areas on the Sunda Shelf. This has resulted in relatively high similarities in the floras of the different islands on the Sunda Shelf (Fig. 1.2; filled circles). Java is an exception, which is - contrary to the other everwet islands on the Sunda Shelf - for a large part of its surface characterized by a dry
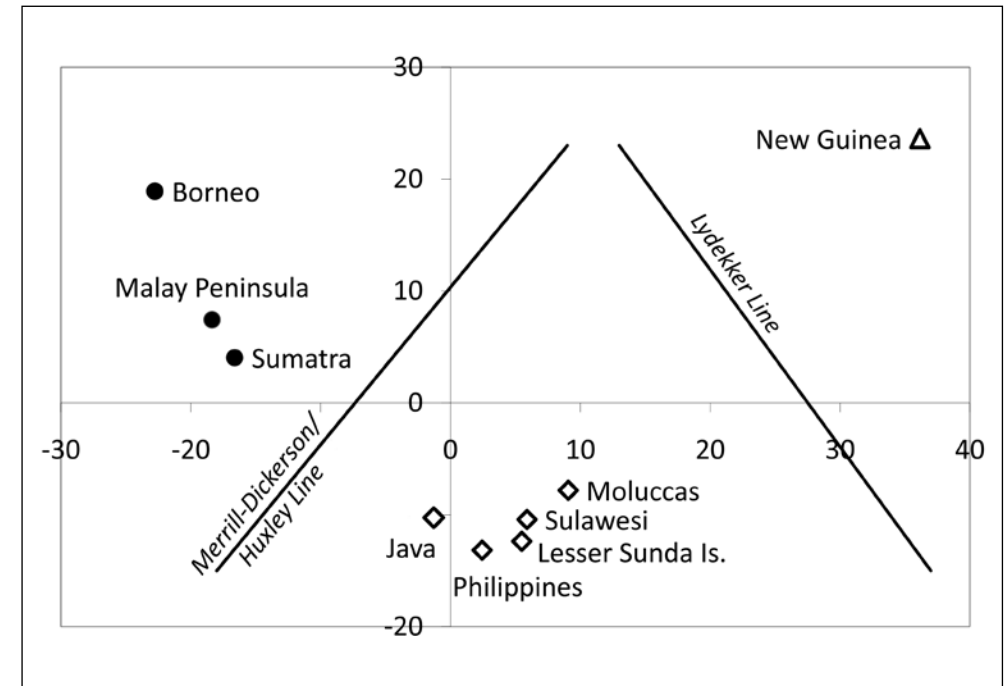
monsoon climate (van Steenis, 1979). Hence, it clusters with the islands of central Malesia, which have similar climatic conditions (Fig. 1.2; diamonds). This central Malesian region is known as Wallacea, and is located between the Merrill-Dickerson/Huxley- and Lydekker's Line, both variants of Wallace's Line. Like the continental Sunda Shelf, this central Malesian region consists of microplates which have remained submerged, only to emerge after they collided, which for Sulawesi happened only 15-10 Ma (Hall, 1997, 1998; van Welzen *et al.*, 2005). Hall (1997, 1998) provides a comprehensive overview of how the different microplates and continental platelets of Wallacea have moved, collided, emerged and submerged during the last 50 Ma. To illustrate the tectonic complexity of the Malesian region I included an image (Fig. 1.3) of one of Hall's papers (Hall, 2009).

The absence of land bridges in Wallacea, disconnected the western Sunda Shelf from the eastern part of Malesia, the Sahul Shelf, also known as Papuasia (Johns, 1995). Like the Sunda Shelf, the eastern Sahul Shelf is a continental shelf which connected New Guinea to Australia during glacial maxima. The separation of the western Sunda Shelf from the eastern Sahul Shelf by Wallacea has resulted in a distinct floristic compositions on both shelves (Fig. 1.2), as is shown by Van Welzen and Slik (2009).

Botanical diversity patterns and floristic regions of Borneo

The unique status of Borneo in the Malesian region was already recognized as early as 1857 by Zollinger, who divided Malesia in five 'natural' groups, among which the 'Central-land Borneo'. He stated that the 'Central-land Borneo', in comparison to the other groups, most resembled mainland areas, and that the Malesian floristic character will likely be best expressed on Borneo (Zollinger, 1857). He also recognized that Borneo was one of the least known islands of Malesia. Since 1857 not much has changed, and Borneo with only 35 collections per 100km² is, after Sumatra and

Sulawesi, the least collected island of Malesia (Johns, 1995). Furthermore, the Indonesian Kalimantan provinces, covering 2/3 of Borneo have the lowest collection density of the entire Malesian region with only 12 collections per 100km²; whereas Sabah, with Mt. Kinabalu, and Sarawak together with Brunei, have 126 and 76 collections per 100km², respectively (Johns, 1995). This bias in collection intensities is better known as the 'Wallacean shortfall' (Whittaker et al., 2005).

Nevertheless, Borneo with an estimated number of 14,423 species was found to be the most diverse island of the whole Malesian region (Roos et al., 2004). A more recent analysis, based only on species treated in Flora Malesiana (Anon., 1959-2007) placed Borneo as second most diverse island, after New
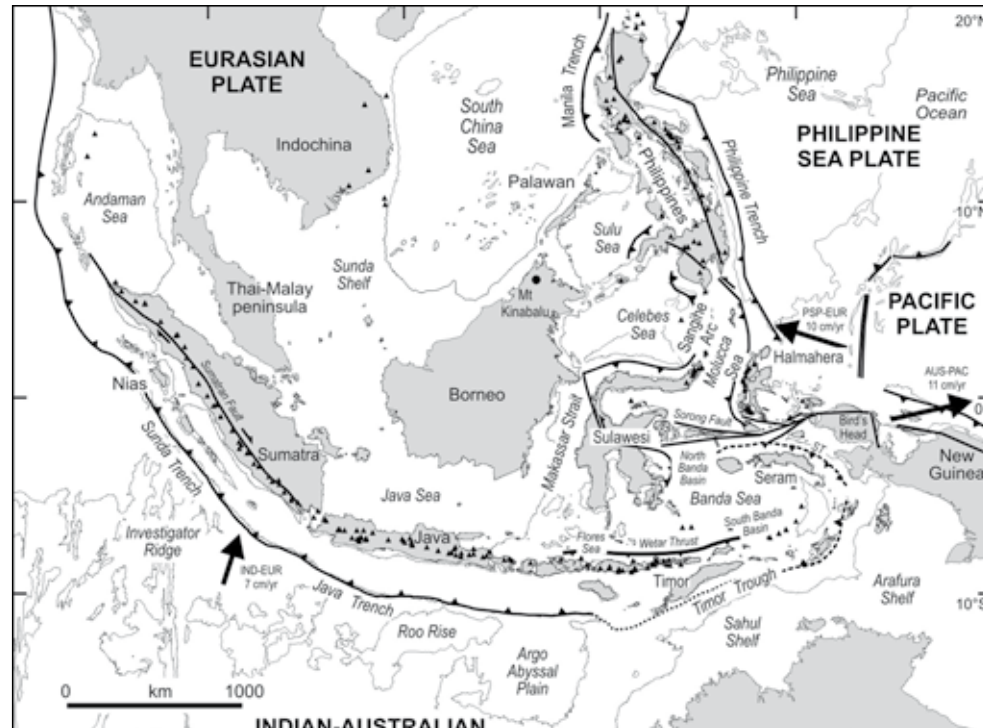
Guinea (van Welzen & Slik, 2009). The same study found that 37% of Borneo's vascular plant species are endemic. Furthermore, Borneo harbours four of the 'Global 200' priority ecoregions for global conservation, together covering virtually the whole island, i.e. the 'Borneo lowland and montane forests', the 'Kinabalu montane shrublands', the 'Greater Sundas Mangroves', and the 'Sundaland rivers and swamps' (Olson & Dinerstein, 2002) (See last page, Fig. a). Except for the 'Centres of Plant Diversity for Australasia' (WWF & IUCN, 1995), indicating that the centres of plant diversity on Borneo are found in smaller areas in the north, on the central mountain chain, and in the south-eastern Meratus Mountains (See last page), and a number of 'local' diversity studies (Aiba et al., 2002; Potts et al., 2002; Ashton, 2005; Beaman, 2005; Grytnes & Beaman, 2006) remarkable little is known about the spatial distribution of these two biodiversity components. The only study covering a larger area is the lowland Dipterocarp forests plot study of Slik et al. (2003).

The same accounts for the spatial pattern of floristic regions of Borneo. The first map delineating the different forest types (~floristic regions) of Indonesia, the former Dutch East Indies, was published in 1935 (van Steenis, 1935a). It was Van Steenis' map that served as basis for most of the following vegetation maps of Malesia (Hannibal, 1950; van Steenis, 1958b; Whitmore, 1984b; MacKinnon, 1997), ultimately resulting in the WWF 'ecoregion' map of the Indo-Pacific (Olson et al., 2001; Wikramanayake et al., 2002). The Bornean region of these maps is shown on the last page. Although these maps probably reflect reality to a large extent, the delineation of the floristic regions is mainly based on informal expert opinion.

Despite Borneo's exceptional botanical

richness and levels of endemicity, large areas of Borneo's lowland rain forests are already deforested (Stibig et al., 2007), and annual deforestation still averages 1.7% (Langner et al., 2007). Even more worrying is the fact that 56% of the protected lowland forests in Kalimantan has been lost between 1985 and 2001 (Curran et al., 2004). For these reasons the Sundaland hotspot, with Borneo as major component, is recognized as one of the top 5 biodiversity hotspots of the world (Myers et al., 2000).

Recent digitization of the botanical collections of Borneo, housed at the National Herbarium of the Netherlands, has resulted in a database containing 166,757 records. It is this database that has provided the opportunity to quantitatively analyse the spatial patterns of botanical richness, -endemicity, and the floristic regions of Borneo, without having to rely on any informal expert opinion. Most databases containing collection records, however, suffer from a biased spatial distribution of collection records, the previously mentioned 'Wallacean Shortfall' (Whittaker et al., 2005). The need to be able to predict the presence and absence of species, even for areas where no collections have been made, has resulted in a suite of species distribution modelling applications (Guisan & Zimmermann, 2000; Elith et al., 2006; Peterson, 2006). 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 (i.e. annual precipitation, altitude, soil depth, etc.) across an area of interest, in this case Borneo. One of the remaining challenges in the field of species distribution modelling concerns the validation of SDMs developed with presence-only data, typical for herbarium collections; i.e. it is very difficult, if not impossible, to establish

Figure 1.3. A simplified presentation of the complex present-day tectonic configuration of the Malesian region (taken from Hall, 2009; Fig. 1 therein).

the absence of a species from an area. Most measures of SDM accuracy currently applied were developed for presence/absence datasets (Fielding & Bell, 1997; McPherson *et al.*, 2004; Pearson *et al.*, 2006), and severe problems do exist when applied to presence-only data. This was also acknowledged by other authors, who placed the improvement of SDM validation high on their list of research priorities (Olden *et al.*, 2002; Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Phillips *et al.*, 2006).

Borneo's botanical diversity is unique, but its threatened conservation status is of major concern. The large amount of recently digitized herbarium records, the available spatial data on global climate and soil properties, together with recent developments of species distribution modelling techniques that allow to predict the presence and absence of species even for areas that never have been sampled, make it possible to analyse the spatial patterns of botanical richness, -endemicity, and floristic regions of Borneo quantitatively at a high spatial resolution. This in turn can inform better conservation strategies for this unique natural resource.

Objectives

The objectives of this thesis are:
1. To introduce a technique known as georegistration to georeference as many collections as possible, especially for the least represented regions, to reduce the effects of collection bias to a minimum.
2. To develop a new statistical test to assess the significance of species distribution models.
3. To develop high spatial resolution botanical richness and -endemicity maps of Borneo, and to relate these patterns to

environmental conditions.
4. To identify the different floristic regions of Borneo based on actual collection data, and to characterize the different regions by their environmental conditions.
5. To assess the priority regions for nature conservation on Borneo based on botanical richness, -endemicity, floristic regions and the level of deforestation.

Outline of the thesis

In Chapter 2 we introduce a technique known as georegistration. The Kalimantan provinces, in contrast to the rest of Borneo, have besides less collections also a larger proportion of the collections without coordinates required for modelling. By matching expedition maps with satellite images we attempt to georeference as many collection localities from the Kalimantan provinces as possible, thereby reducing the impact of collection bias to a minimum.
The erroneous application of the measures of model accuracy applied to presence-only species distribution models, led us to develop a new statistical significance test for this specific type of models. This method is described in chapter 3.
In chapter 4 we used all significant species distribution models to develop the botanical richness and -endemicity patterns of Borneo. The main driving factors of high levels of botanical richness and -endemicity were assessed by variance partitioning and multiple regression analyses.
In Chapter 5 we delineate the different floristic regions, based on the same significant models that were used in Chapter 4, with a hierarchical cluster analysis on the presence/absence species matrix for 8577 grid cells of Borneo. A classification and regression tree (CART) was used to characterize the ecological conditions

under which each floristic region occurs.
In the final Chapter 6 we combine all results, and assess which areas of high botanical richness, -endemicity, and different floristic regions are already heavily deforested, and require most conservation efforts. Furthermore, we make suggestions for future research.

Note to the reader:
All chapters have been printed, are submitted, or are in preparation to be submitted to SCI journals. Therefore some overlap in the content of the chapters does occur.