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Species richness, lineages, geography, and the forest matrix: Borneo's 'Middle Sarawak' phenomenon

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ABSTRACT. Contemporary studies into the spectrum of plant life assembled on the island of Borneo continue to demonstrate an astonishing richness for some groups. Not all lineages are equivalent in their richness, and both biogeographic and ecological factors are the principal correlates of species richness and lineage diversification. The ways in which population genetic factors may influence the generation and persistence of variation, and their interaction with environmental change, could have fundamental importance in how diversity is maintained. Central Sarawak in the northwest Borneo hotspot is a premier ecological theatre where the interplay of such factors operates: its plant species richness is astounding, floristic documentation continues perhaps too slowly, and research and conservation priorities continue to loom large. Unfortunately, this resource has been severely modified in the several decades spanning the turn of the 21st century. The importance of increasing public perception, especially with well-illustrated accounts of this biological richness and its significance through a natural history perspective, will be as critical as the slowly advancing frontiers of the scientific platform on which our understanding depends.

Keywords. Biodiversity loss, Brunei, cauliflory, deforestation, polyploidy, rain forests, Sabah, speciation

Borneo and the frontiers of biodiversity knowledge

> *Today, the very topic of tropical rain forest ecology is endangered, in that the object of study is in retreat or radically changing.*
> – D.J. Mabberley (1992: 267)

Tropical rain forests evoke three major regions – tropical Africa, America and Asia. In Southeast Asia, Borneo and New Guinea are the largest landmasses. Perched on the eastern flank of the Sunda continental shelf, Borneo is the largest island there with the richest plant life. The Borneo lowlands ecoregion recognised by Kier et al. (2005) was rated by them as the number one hotspot in the world, and the only ecoregion to surpass 10,000 plant species. Barthlott et al. (2007) also considered North Borneo (northern and northwestern Borneo in the present context) as one of the world's top five biodiversity centres. The biogeographical significance of this region has received recent reviews including those by de Bruyn et al. (2014), Lohman et al. (2011) and Ashton (2014), emphasising the spectacular overall richness of landmasses like Borneo within the complex archipelagic setting of insular Southeast Asia. Others, such as Beaman & Anderson (2004) and Beaman (2005) have demonstrated how iconic features in this part of Asia are indeed floristically special.

Sarawak and its place in Northwest Borneo

Within Borneo, the state of Sarawak occupies the largest area of this biologically important part that is becoming more commonly recognised as just Northwest Borneo in emerging geographical and biodiversity studies. In the reckoning of Ashton (1992, 2014), Northwest Borneo is an exceptional region of species richness, and it includes mainly western Kalimantan, Sarawak, Brunei, and southwest Sabah. Geographically, Sarawak, in the words of Hedda Morrison (1956), "faces Asia across the South China Sea". Through a pantropical network of plot censuses set up with the Centre for Tropical Forestry Science (CTFS) (Ashton, 2018), the tree flora of Sarawak (as exemplified by that in the Lambir CTFS plot) would be established as among the world's richest floras (Lee et al., 2002).

Within Sarawak, the Lupar River roughly traces a portion of the geological divide through to and beyond the Danau Lakes region of the upper Kapuas River in West Kalimantan. Although still in refinement, the Plate Tectonic model being used to explain the geological scenario around this Lupar Line (Fig. 1) increasingly finds support, if not corroboration (e.g., Mathew et al., 2016).

Of direct interest to this study is the biological relevance of the Lupar divide, emphasised by Ashton (1972), where two major regions can be defined: the portion west of the Lupar (Southwest Borneo, including West Sarawak), and that essentially north of the Lupar. Although several river valleys in Sarawak appear to restrict a number of dipterocarp species to either side, none approach the significance of the Lupar, which appears to confine 57 dipterocarps to either side (Ashton, 1977).

Southwest Borneo including West Sarawak

The part west of the Lupar Line (West Sarawak), together with West Kalimantan (and a bit of Central Kalimantan), form an exposed portion of ancient Sundaland geology, generally older than 80 Ma but with material even exceeding 300 Ma (Hazebroek & Abang Kashim, 2000; Tate, 2002). In this western region sometimes referred to as part of the Sunda Shield, the very long and complex history of uplift, erosion and subsidence of different portions, together with the intrusion of igneous rocks, has resulted in a rather heterogeneous landscape with diverse soils (Hutchison, 1989).

Greater Sarawak North of the Lupar

In contrast, the Greater Sarawak region north of the Lupar Line, including Brunei, west Sabah and adjacent parts of Kalimantan (Fig. 1), is formed by Late Cretaceous and Tertiary rocks younger than 80 Ma (Hazebroek & Abang Kashim, 2000).

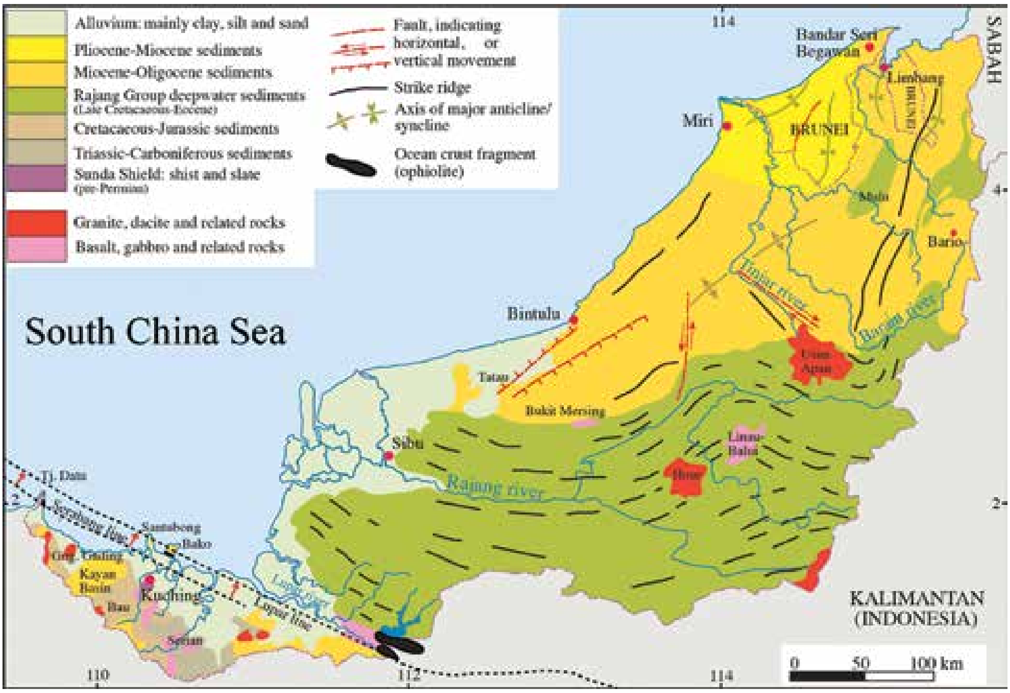


Fig. 1. The geology of Sarawak. Note the geological 'patchiness' of West Sarawak west of the Lupar line, in contrast with the area to the north of the Lupar which is covered by a large expanse of younger, more wide-ranging substrata of the Rajang Group deepwater sediments from the Late Cretaceous to Eocene, and Miocene-Oligocene sediments. Modified from Hazebroek & Abang Kashim (2000).

A substantial portion of these rocks belong to the Rajang Group sediments, and are derived from deep water deposition together with sediments derived from West Borneo, including the Schwaner Mountains, and form one of the world's largest ancient submarine fans (Hutchison, 1989). They are mainly harder sandstones interbedded with softer shale deposits, which constitute the extensive Belaga Formation (Haile, 1974) that underlies much of Central and North Sarawak. These are, in turn, overlain by younger sediments especially evident in North Sarawak.

This formation is thought to have been laid down as an oceanic plate progressively dipped beneath the continental plate margin of Sundaland (at the Lupar Line), causing the overlying strata to be crumpled into a crescent-shaped fold belt called an accretionary prism (Fig. 2, 3). This prism roughly defines what used to be referred to as the Northwest Borneo geosyncline. Tectonic models aside, the regions on both sides of the Lupar have very different geological origins.

Another probably significant event that followed was the major Late Eocene uplift (40 Ma) that began north of the Lupar and continued northwards into southwest Sabah, creating the high ranges forming Borneo's central mountainous spine (Hutchison, 1989). The erosion of this mountain chain produced progressively younger sediments (Oligocene-Miocene, 35−5 Ma), such as the Setap Shales overlain by the Belait, Miri and Lambir sandstone formations.

Within Greater Sarawak north of the Lupar Line are the Rajang and Baram, two of the largest rivers of Borneo. The drainage basins of these two rivers are characterised by deep and steep V-shaped valleys formed by actively incising rivers, and high elevation but low relief surfaces nested between ridges that are thought to represent relict parts of landscapes that were tectonically uplifted (Mathew et al., 2016). The geomorphology of this landscape suggests even more recent major tectonic activity (after 5 Ma) had taken place, which led to the uplift of the Interior Highlands and coastal areas of Sarawak, as well as active folding of the Rajang Group thrust belts (Mathew et al., 2016). This resultantly heterogeneous terrain could indeed have a role in supporting multiple different habitats for species.

Historical biogeographic influences

Endemics can be found in many different localities, where their distribution may be chiefly influenced by the type of substrate or vegetation, e.g., *Turpinia calciphila* J.T.Pereira occurring on the widely separated Bau and Mulu limestones, *Cotylelobium burckii* (F.Heim) F.Heim in widely separated *kerangas*, or *Shorea albida* Symington in widely separated peat swamp forests (Wong, 1998). The restriction of endemic taxa to regions with historically different origins, such as Southwest Borneo and Sarawak north of the Lupar, lend support to the idea that historical biogeography factors too can shape the distribution or accumulation of taxa of limited distribution.

Bornean taxa restricted to Southwest Borneo/West Sarawak may be divided into two broad categories (Table 1): those shared with the Malay Peninsula or Sumatra but not elsewhere in Borneo (the so-called ‘Sunda Shield taxa’), and others that are strictly endemic to only this part of Borneo. We provide examples gleaned from 17 families revised for the first five volumes of the *Tree Flora of Sabah and Sarawak* (Soepadmo et al., 1995−2004), the palms (Dransfield, 1972, 1992), as well as from two recent revisions of Bornean *Melastoma* L. and *Saurauia* Willd. (Wong, 2016, 2017). It is notable that some Southwestern Bornean endemics occur on a variety of substrates and geology and are not just restricted to any one, such as *Melastoma kuchingense* K.M.Wong or *Saurauia planchonii* Hook.f., suggesting they are indeed restricted to the region rather than by edaphic factors alone.

A second historical biogeographic influence is present in Sarawak, called the ‘Riau pocket’ (Corner 1960: ‘Riouw-pocket’). This refers to a degree of shared floristics among three main regions comprising (1) Southeast Sumatra, Riau and Lingga islands, Bangka, Billiton; (2) South and East Malay Peninsula; (3) Southwest Borneo and much of coastal Sarawak north of the Lupar. This was an area of substantial land and vegetation connectivity during the last Pleistocene low sea-level episodes (Voris, 2000) that could have facilitated a more continuous range for plant species across the region (Ashton, 1992, 1995, 2014; Wong, 1998, 2011). The fact that this flora has now been reduced to pockets at a time of intense human-mediated landscape changes is cause for concern for the survival of these species (Cannon et al., 2009).

The relationship among Riau pocket regions is amply demonstrated by the

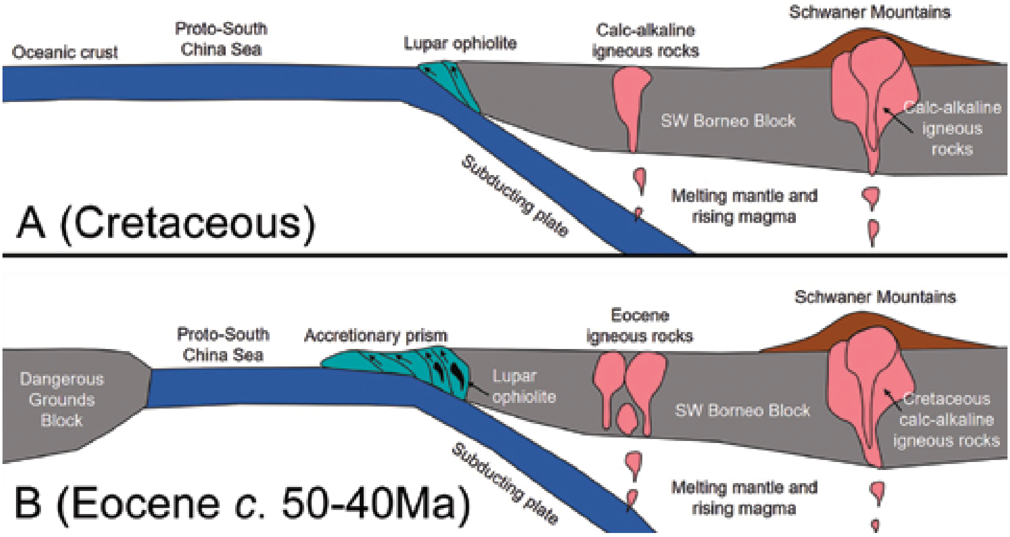


Fig. 2. Schematic cross-sectional representation of accretionary orogenic processes in Southwest Borneo from the Cretaceous to the Early Tertiary (Paleocene to Eocene). **A.** The subduction of the Proto-South China Sea under the Southwest Borneo Block was initiated during the Cretaceous. **B.** In the Eocene, continued subduction led to the generation of calc-alkaline igneous rocks along the Kuching Zone (between the Lupar line and the Schwaner Mountains), as well as the build-up of the accretionary prism and ophiolites at the Lupar line. Modified from Wang et al. (2016).

phylogeographic analyses of the dipterocarp *Shorea leprosula* Miq. of Ohtani et al. (2013), which show that, although there is a clear genetic differentiation between Borneo and the Malay Peninsula/Sumatra region, Southwest Borneo populations included an admixture of the genetic lineages that probably arose during the mid-Pleistocene when better land and forest connectivity had allowed a predominantly west-to-east migration.

'Above' the Lupar divide

Northeast Sarawak

Northeast Sarawak is well known for its peat swamp complexes and limestone formations. The key limestone areas occur as the Subis and Melinau formations, which are of much younger age than the Carboniferous-Permian or Jurassic-Cretaceous limestones in Southwest Sarawak.

With the different plant family examples examined from the *Tree Flora*, no strict endemics were noted for the Melinau limestone (Mt Api in Mulu National Park);

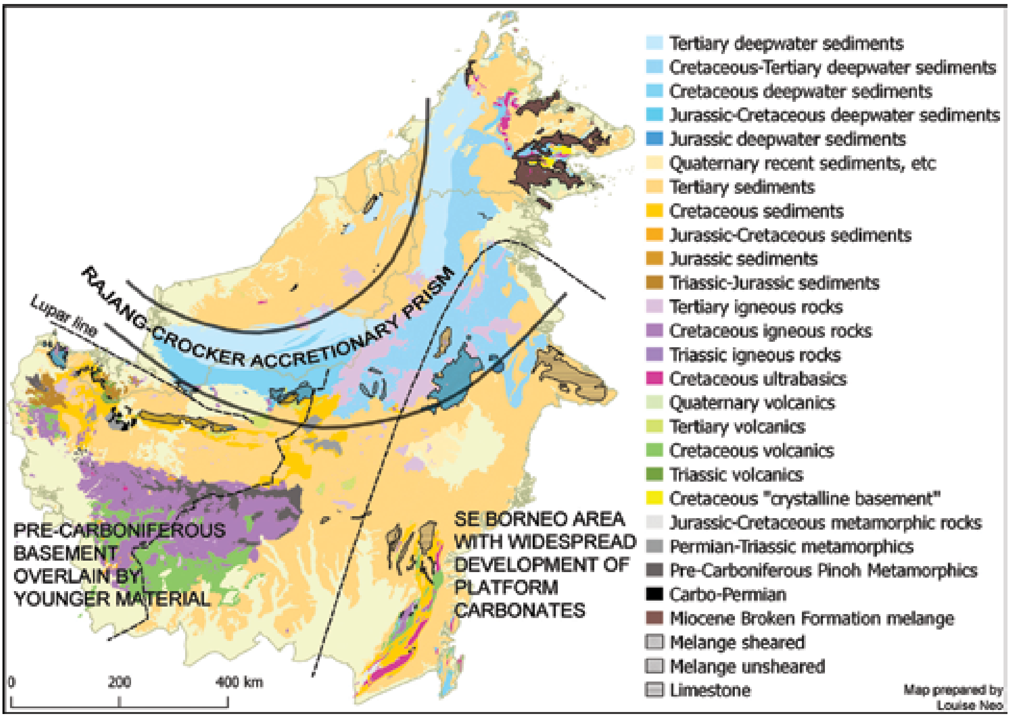


Fig. 3. The geology of Borneo and the ages of different sediments and strata. The Rajang-Crocker accretionary prism is defined in the area immediately north of the Lupar line, through Sarawak into Southwest Sabah and Northeast Kalimantan. Credit: L. Neo, adapted from Tate (2001).

this Flora emphasises tree life forms. However, revisions of groups of smaller plant stature, such as *Melastoma* or *Saurauia*, do yield restricted endemics, which reflects the nature of the substrate (skeletal soils on limestone) and the ability of these plants to subsist only in this environment. It is expected that there should be many more examples among other herbaceous plant groups, such as begonias and gingers.

Middle Sarawak

North of the Lupar and away from the extreme or habitat-island environments of the peat swamps, limestones, dacites (e.g., Usun Apau, Hose Mountains) and basaltic outcrops (e.g., Linau Balui plateau), the most significant environment of this 'Middle Sarawak' portion comprises the mixed dipterocarp forests established on substrates of the Rajang Group or younger. This, of course, is the mainstay of the timber industry and deserves special attention.

Here, in this comparatively vast region, the endemics include some widespread taxa but in general very rare taxa predominate (Tables 2, 3; Fig. 4). Among smaller plants, the endemism may be even more markedly narrow, or of very small scattered populations: examples are provided by many aroids (e.g., Wong & Boyce, 2015, 2016; Wong et al., 2017).

Table 1. Examples of species restricted to West Sarawak or Southwest Borneo. Genera indicated in bold are endemic not only to this region but also to Borneo.

West Sarawak / Southwest Borneo specialties
'SUNDA SHIELD': Shared with Malay Peninsula and/or Sumatra but not elsewhere in Borneo:
Johannesteijsmannia altifrons H.E.Moore (W Sarawak, Malay Peninsula, N Sumatra) (Arecaceae)
Dacryodes rubiginosa (A.W.Benn.) H.J.Lam (Burseraceae)
Glyptopetalum quadrangulare Prain ex King, *Lophopetalum pachyphyllum* King (Celastraceae)
Shorea dasyphylla Foxw., *S. dealbata* Foxw., *S. falcifera* Dyer ex Brandis, *S. resinosa* Foxw. (Dipterocarpaceae)
Olea brachiata (Lour.) Merr. (Oleaceae)
Madhuca erythrophylla (King & Gamble) H.J.Lam (Sapotaceae)
Endemic to West Sarawak / Southwest Borneo:
Saurauia bentuangensis K.M.Wong, *S. kuchingensis* K.M.Wong, *S. nooteboomii* K.M.Wong, *S. planchonii* Hook.f., *S. ridleyi* Merr. (Actinidiaceae)
Alangium circulare B.C.Stone & Kochummen (Alangiaceae)
Melanochyla axillaris Ridl., *M. borneensis* (Ridl.) Ding Hou, *M. scalarinervis* Kochummen, *Parishia dinghouiana* Kochummen (Anacardiaceae)
Anisophyllea rhomboidea Baill. (Anisophylleaceae)
Calamus conjugatus Furtado, *C. crassifolius* J.Dransf., *C. poensis* Becc., *C. pygmaeus* Becc., *C. sabalensis* J.Dransf., etc. (Arecaceae)
Haplolobus beccarii Husson, *H. inaequifolius* Kochummen (Burseraceae)
Dryobalanops fusca Slooten, *Shorea alutacea* P.S.Ashton, *S. bakoensis* P.S.Ashton, *S. lunduensis* P.S.Ashton, 10 others (Dipterocarpaceae)
Erythroxylum sarawakanum R.C.K.Chung (Erythroxylaceae)
Fagraea havilandii K.M.Wong & Sugau (Gentianaceae)
Melastoma kuchingense K.M.Wong (Melastomataceae)

Table 1. Continuation.

West Sarawak / Southwest Borneo specialties
Schuurmansiella *angustifolia* (Hook.f.) Hallier f. (Ochnaceae)
Chionanthus havilandii Kiew, *C. polycephalus* Kiew, *C. rugosus* Kiew (Oleaceae)
Sarcotheca macrophylla Blume (Oxalidaceae)
Lepisanthes ramiflora (Radlk.) Leenh., *Nephelium compressum* Radlk., *N. havilandii* Leenh. (Sapindaceae)
Madhuca primoplagensis Vink, *M. sarawakensis* (Pierre ex Dubard) H.J.Lam, *Palaquium ferrugineum* Pierre ex Dubard, *P. multiflorum* Pierre ex Dubard (Sapotaceae)
Aetoxylon *sympetalum* (Steenis & Domke) Airy Shaw, *Gonystylus augescens* Ridl., *G. pendulus* Airy Shaw (Thymelaeaceae)
+ many others. . . Including *Aulandra beccarii* (Pierre ex Dubard) P.Royen (Sapotaceae) documented only along the Lupar River!

The ‘generalised’ lowland mixed dipterocarp forests: more than meets the eye

Are these mixed dipterocarp forests at all ‘generalised’? There are certainly some features in common among areas with such forests. However, the tall stature, very high species richness, preponderance of canopy dipterocarps, abundance of species that are endemic or occurring at low frequencies, presence of series of co-occurring congeners (Fig. 5 and 6), and paucity of very nutrient-rich soils may be about the only common characteristics. The huge range of within-forest environmental clines as well as the dynamic processes that shape species diversity maintenance have been much expounded by tropical biologists (Whitmore, 1984; Richards, 1996; Wright, 2002; Losos & Leigh, 2005; Ashton, 2014).

Maintenance of species diversity: eco-physiology and the niche

A key approach has been to consider how a large number of species can co-exist at small spatial scales, especially in hyper-diverse communities. In applying the competitive exclusion principle, where competition should exclude all except one superior competitor, mechanisms that reduce competition will enhance diversity. This can happen through reduced competitive encounters (e.g., through reduced population densities: Connell, 1978; Brown & Whitmore, 1992; Coomes & Grubb, 1998; Lewis

Table 2. Examples of tree species restricted to Sarawak north of the Lupar Line.

Endemics or near-endemics of Southwest Sabah – Brunei – Sarawak
Common/ widespread:
Crypteronia elegans J.T.Pereira & K.M.Wong (Penaeaceae/ 'Crypteroniaceae')
Gonystylus calophylloides Airy Shaw, *G. spectabilis* Airy Shaw (Thymelaeaceae)
Rare:
Drimycarpus maximus Kochummen (Kapit), *Melanochyla semecarpoides* Ding Hou (Kapit), *Semecarpus cupularis* Kochummen (Kapit), *Swintonia sarawakana* Kochummen (Kapit) (Anacardiaceae)
Shorea woodii P.S.Ashton (Belaga, Kapit) (Dipterocarpaceae)
Fagraea dulitensis K.M.Wong & Sugau (Marudi), *F. floribunda* K.M.Wong & Sugau (Bintulu, Mukah) (Gentianaceae/ 'Loganiaceae')
Heliciopsis mahmudii (P.Chai) R.C.K.Chung (Bintulu, Song) (Proteaceae)
Payena grandistipula J.T.Pereira, *P. kapitensis* J.T.Pereira (Belaga) (Sapotaceae)
Gonystylus costalis Airy Shaw (Belaga, Kapit), *G. decipiens* Airy Shaw (Belaga), *G. eximius* Airy Shaw (Kapit), *G. nobilis* Airy Shaw (Bintulu) (Thymelaeaceae)
'Brunei area' (+ Lambir/ Miri/ Mulu N.P.):
Mangifera khoonmengiana Kochummen (Anacardiaceae)
Crypteronia glabriflora J.T.Pereira & K.M.Wong (Penaeaceae/ 'Crypteroniaceae')
Picrophloeus rugulosus (K.M.Wong & Sugau) K.M.Wong (Gentianaceae/ 'Loganiaceae')

& Tanner, 2000); or via species equivalence (ecologically equivalent species) obtained though common descent (Federov, 1966; Van Steenis, 1969), convergent evolution (Hubbell & Foster, 1986), or with slow population dynamics (Huston, 1994).

The degree of niche partitioning among congeners can be at a very fine level. Davies et al. (1998) demonstrated the differences among 11 *Macaranga* Thouars species in the Lambir Hills by soil texture and crown illumination class, and showed their different relative positions (= niches) occupied with respect to maximum height, stems in high-light levels and frequency on sand-rich soil. The net photosynthetic

Table 3. *Melastoma* (Melastomataceae) and *Saurauia* (Actinidiaceae) species (recently revised) restricted to Sarawak north of the Lupar Line.

Endemics or near-endemics of Southwest Sabah – Brunei – Sarawak
Common/ widespread:
Melastoma beccarianum Cogn., *M. linusii* K.M.Wong, *M. oresbium* K.M.Wong
Saurauia ashtonii K.M.Wong, *S. myrmecoidea* Merr.
Rare:
Melastoma iliasii K.M.Wong (Kapit), *M. incisum* K.M.Wong (Kapit), *M. oreophilum* K.M.Wong (Kapit), *M. picklesii* K.M.Wong (Marudi), *M. praetermissum* K.M.Wong (Kapit), *M. pulongtauense* K.M.Wong (Limbang), *M. runiae* K.M.Wong (Kapit), *M. sibatii* K.M.Wong (Marudi), *M. yahudii* K.M.Wong (Belaga, Kapit), *M. yiianthum* K.M.Wong (Belaga)
Saurauia brevicymula K.M.Wong (Kapit), *S. chaiana* K.M.Wong (Belaga, Kapit), *S. hiranohottae* K.M.Wong (Bintulu), *S. hosei* Merr. (Marudi), *S. iliasii* K.M.Wong (Tatau, Kapit), *S. jugahii* K.M.Wong (Mukah), *S. latifolia* K.M.Wong (Marudi, Tatau), *S. minutiflora* K.M.Wong (Belaga), *S. othmanii* K.M.Wong (Kapit, Belaga, Tatau, Lawas), *S. rantaijawae* K.M.Wong (Kapit, Lubok Antu, Song), *S. runiae* K.M.Wong (Kapit), *S. subnuda* K.M.Wong (Song), *S. subsessilifolia* Kamariah ex K.M.Wong (Kapit), *S. urophylla* K.M.Wong (Kapit)
'*Brunei area' (+ Lambir/ Miri/ Mulu National Park):*
Melastoma ashtonii K.M.Wong, *M. botryanthum* K.M.Wong
Saurauia bruneiensis Kamariah
Melinau limestone (Mt Api in Mulu National Park):
Melastoma impressinervium K.M.Wong
Saurauia calcicola K.M.Wong, *S. montiflagrans* K.M.Wong

rates at light saturation for nine *Macaranga* species in three light environments was also demonstrably variable (Davies et al., 1998). Such niche partitioning through differential use of a number of resource gradients has been derived from theory as expounded by Pianka (1976) through a simplified example with just two gradients (Fig. 7). Therefore, resource utilisation and partitioning within the rain forest environment can indeed be rather fine. In fact, the variability or partitioning in growth requirements and characteristics can already be seen from a coarser scale as shown by Turner (2001) (Fig. 8). So within the forest matrix there seems to be intrinsically no limit to combinatorial niches along different resource gradients. The interaction of niche quality and availability with different population attributes (e.g., population size and fecundity) defines the circumstances for local responses and selection pressure.

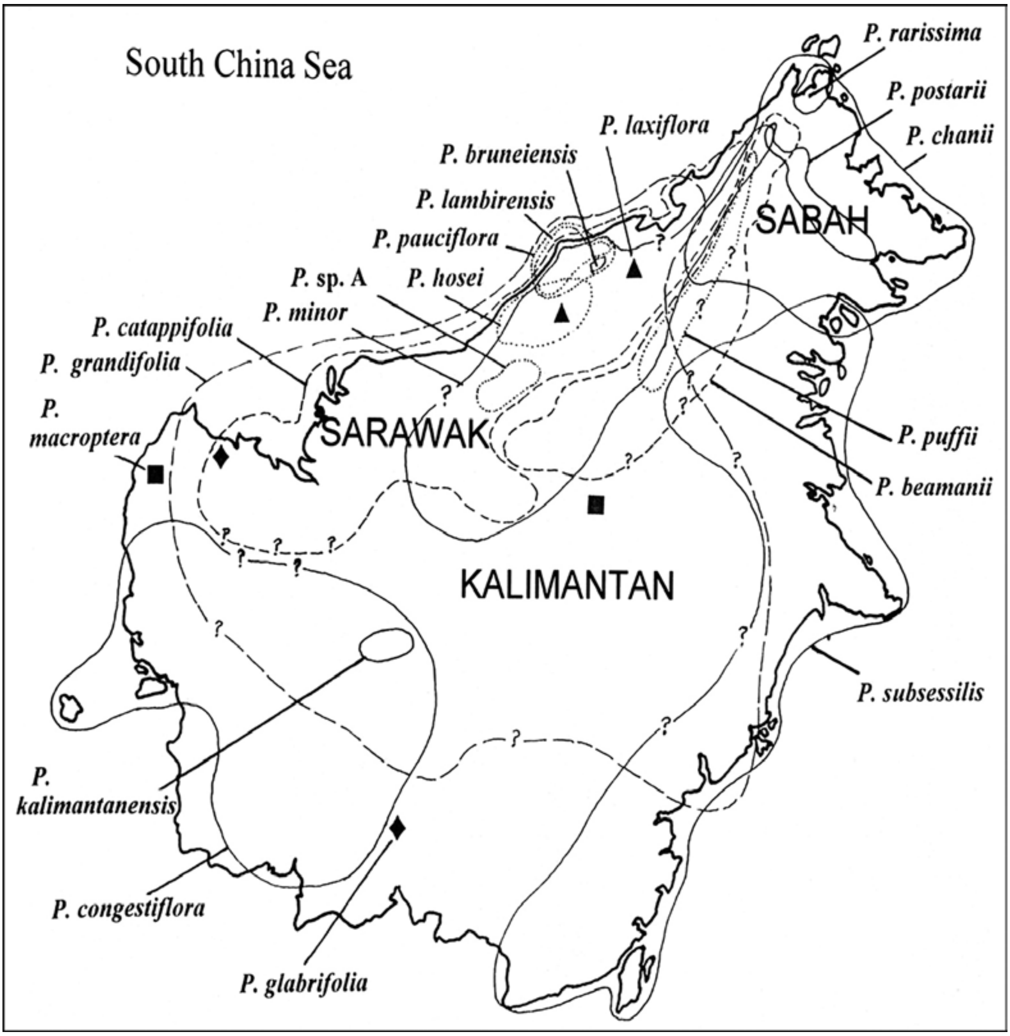
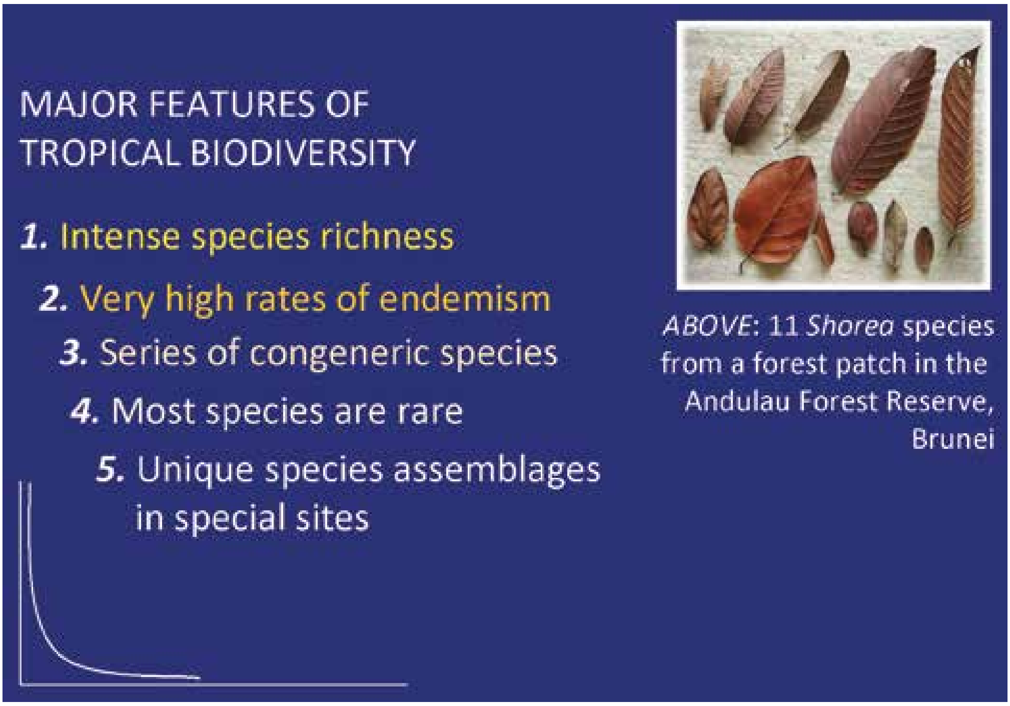


Fig. 4. Distribution of 19 species of *Porterandia* endemic to Borneo, showing the variation in range sizes among species, from widespread to restricted. Very rare species known from only a few scattered localities (e.g., *Porterandia glabrifolia* Ridl., *P. laxiflora* Zahid, *P. macroptera* (Miq.) Tirveng.) are indicated by symbols rather than a delineated range. Figure reproduced from Zahid & Wong (2010).

Population genetic processes: polyploidy

> *. . .it is unreasonable to suppose that species are not still extending their ranges, or indeed succumbing to those that are. Also, species are still in the making, and the frustrating variation patterns of certain tree species, for example, may mirror just this.*
>
> – D.J. Mabberley (1992: 265)



MAJOR FEATURES OF TROPICAL BIODIVERSITY

1. Intense species richness
2. Very high rates of endemism
3. Series of congeneric species
4. Most species are rare
5. Unique species assemblages in special sites

ABOVE: 11 *Shorea* species from a forest patch in the Andulau Forest Reserve, Brunei

Fig. 5. Five major features of tropical biodiversity. The inset shows 11 co-occurring species of *Shorea* at a single lowland site. The graph on the lower left corner is a typical reverse-J trace when number of species (vertical axis) is plotted against frequency in lowland rainforest plots, indicating most species are rare by frequency. (Image: K.M.Wong).

Another area which we know very little about is the population genetics of rainforest plants. Some investigations are throwing light on genetic processes, including how pollen flow (Ng et al., 2006) and seed dispersal (Foster & Sork, 1997) affect genetic differentiation, and the possible influences of life history and ecological traits on levels of genetic diversity (Hamrick et al., 1992; Lee et al., 2002; Noreen & Webb, 2013). Whereas selective logging may not significantly reduce the genetic diversity of some canopy tree species (Ang et al., 2017), it appears to do so in a number of cases, where inbreeding with a reduced number of individuals may be a potential outcome (*Shorea megistophylla* P.S.Ashton: Murawski et al., 1994; *Dryobalanops aromatica* C.F.Gaertn.: Lee, 2000). In any case, there is a dearth of such work with smaller rainforest plants.

Polyploidy is a significant mechanism of speciation in plants (Ramsey & Schemske, 1998; Soltis, 2005). Rainforest canopy species (e.g., *Hopea* Roxb., Clyde et al., 2002) or understorey species (e.g., *Saurauia*, Soejarto, 1969, 1970; He et al., 2005) can be polyploid. Many invasive plants in the tropics could also be polyploids (Pandit et al., 2006). The dynamic nature of polyploid genomes provides possibilities for a range of alterations in gene content, number, arrangement and expression that can generate a range of phenotypic expressions within the polyploid population (Stebbins,

Fig. 6. Five *Anisophyllea* R.Br. ex Sabine species, including two forms of *A. disticha* (Jack) Baill. (left, upper: hairy and glabrescent forms) that can be easily seen on Mt Serapi, Sarawak. The others: *A.* cf. *disticha*, with discolorous leaf surfaces (left, lower); *A. rhomboidea* Baill. (centre, left); *A. ferruginea* Ding Hou (centre right); *A. beccariana* Baill. (right). (Photo: K.M. Wong).

1940; Scarpino et al., 2014; Soltis et al., 2014). Meyers & Levin (2006) have likened polyploidy among plants to a simple ratcheting progression that moves ever onward, and which does not require evolutionary advantages. So the bewildering variation in morphology among the derivatives of a generic lineage is not unexpected in a genus with a paleopolyploid origin, such as *Saurauia* (Wong, 2017). In this genus, a high prevalence of aberrant chromosomal behaviour has been noted in some species studied and abnormal pollen development and some degree of functional dioecy have also been observed (He et al., 2005). Although there has been no or little study of the genetic characteristics of a single lineage in line with a modern revision of a complex genus, 'difficult' taxonomy indicated by bewildering morphological variation would typically seem to indicate complex genetic backgrounds. This is reminiscent of recently demonstrated phylogenetic reticulation within the Bambusinae, the largest and most complex of all tropical Southeast Asian bamboo subtribes involving polyploids with ancient introgression as well as current hybridisation, both within and between genera (Goh et al., 2013). In the super-speciose genus *Piper* L. (Piperaceae), most New World species are diploids with 2n = 26 whereas Old World species include many polyploids (2n = 52 or higher) (Jose & Sharma, 1985; Samuel et al., 1986).

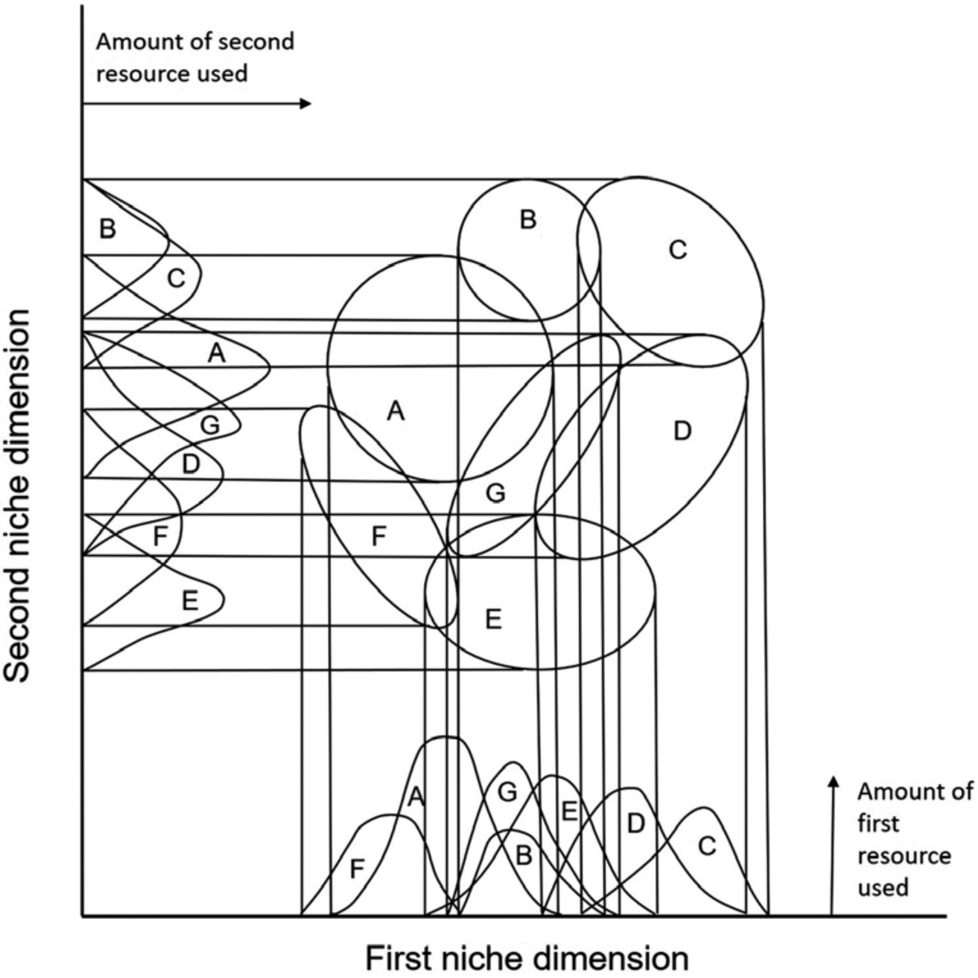


Fig. 7. Resource utilisation of seven species along two niche dimensions. Note that pairs of species with substantial or complete overlap along one dimension can avoid competition by niche separation along another dimension (e.g., B & E). Redrawn from Pianka (1976).

It seems likely that the more speciose, predominantly understorey, plant genera of tropical rain forests could have had similarly (or typically) complex diversification histories. It would appear to be similar in *Begonia* L. (c. 1,550 species, Hughes, 2008), another super-speciose tropical genus where high polyploidy and aneuploidy are important (Oginowa & Peng, 2002). For *Begonia*, it seems likely that reproductive barriers are strong among populations weakly connected by gene flow, promoting allopatric speciation (DeWitte et al., 2011; Twyford et al., 2015). There should be similar instances within families like the Gesneriaceae (Moeller & Kiehn, 2003) or genera like *Hedyotis* L., *Ixora* L. or *Psychotria* L. (Rubiaceae).

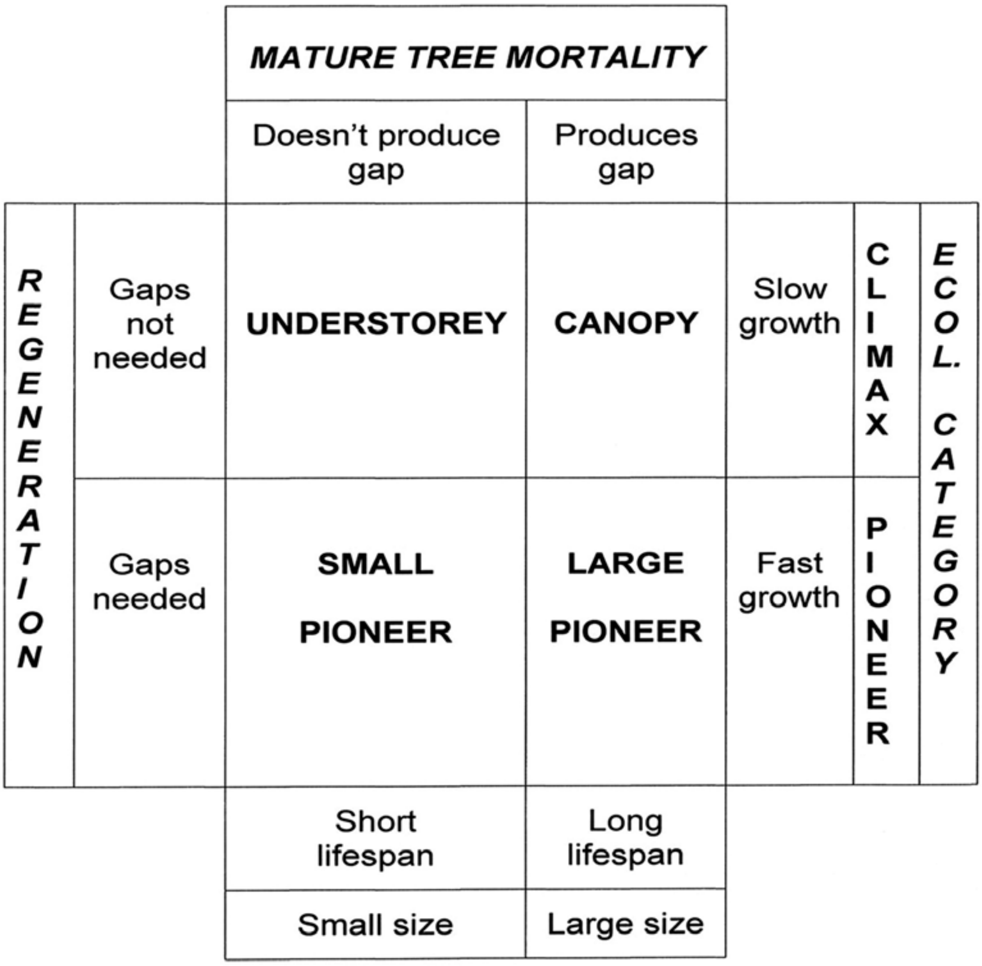


Fig. 8. Two-way classification of tropical rainforest tree species based on size at maturity and the pioneer-climax axis. Redrawn from Turner (2001).

In some other cases, such as *Melastoma*, cytology is poorly known, even though generally, the incidence of polyploidy in the family seems high (Renner, 2006). Our morphological reanalysis of this genus for Borneo (Wong, 2015, 2016) indicated the highly likely occurrence of hybridisation between or among species, as has been demonstrated by molecular methods elsewhere in Asia (Dai et al., 2012; Liu et al., 2014). Indeed, there is now molecular demonstration of bidirectional introgression between *Melastoma malabathricum* L. and *M. beccarianum* Cogn. from Sarawak (Wu et al., 2019). Incomplete reproductive isolation following rapid diversification, such as possible in the case of *Melastoma* (Renner & Meyer, 2001), as well as shared pollinators and overlapping distribution (Wu et al., 2019), should also be important factors.

Expectedly, smaller seed mass concomitant with high selfing rates, such as in the canopy dipterocarp *Neobalanocarpus heimii* (King) P.S.Ashton, ties in with lower survival of selfed progeny from seeds to established seedlings, indicating inbreeding depression (Naito et al., 2005). But are the products of genetic diversification arrived at through self-fertilisation processes in polyploid lineages advantageous in any way for survival and selection, or are they simply also an evolutionary dead-end (Takebayashi & Morrell, 2001)? A comparative study of the dipterocarps *Shorea leprosula* (diploid, predominantly outcrossed) and *S. ovalis* (Korth.) Blume subsp. *sericea* (Dyer) P.S.Ashton (autotetraploid, apomictic) in the same forest in Peninsular Malaysia by Ng et al. (2004) displayed relatively high levels of genetic diversity in the tetraploid, where each locus may accommodate up to four different alleles. There could be benefits through a history of greater random retention of heterogeneous loci, and high diversity levels could be maintained through apomictic reproduction. In other words, contexts are to some degree determined by the way various characteristics are combined in different species.

An interesting study on Barro Colorado Island by Lasso et al. (2011) indicated significant genetic differentiation among five species of self-compatible *Piper* that have localised highly dense populations. They suggested that high levels of genetic diversity could have been sustained by limited seed and pollen dispersal, clonal spread, as well as selfing. Is this support for the contentions of Baker (1959) and Fedorov (1966), where inbreeding and genetic drift could lead to population differentiation and sympatric speciation that produces the typically low frequencies of tropical rainforest trees? Dick et al. (2008) noted that tropical trees had higher levels of population differentiation than temperate trees, possibly owed also to their higher levels of inbreeding, in spite of the fact that most trees studied that maintain high levels of genetic diversity are predominantly outcrossed with extensive gene flow. Do introgressive hybridisation and polyploidy have fundamental roles too? From their studies with understorey *Psychotria* species, Theim et al. (2014) also suggest that fleshy-fruited understorey species should experience dispersal limitation (and restricted gene flow) as their avian dispersers have more sedentary habits, resulting in population differentiation at local scales and allopatric speciation.

The paleopolyploid background of angiosperms may not be immediately apparent unless lineages are sufficiently understood. Recent analyses of genomic data reveal that large-scale reorganisation of genomes can take place through the diploidisation process involving DNA and gene loss, as well as chromosome reconfiguration (e.g., through fusion and fission), so that diploidisation following polyploidisation may be important in the run up to lineage diversification (Dodsworth et al., 2016). It has been argued that diploidisation could be important for evolutionary persistence and diversification over intermediate timescales of tens of millions of years (Dodsworth et al., 2016).

Does conventional taxonomy matter? Bamboos, *Saurauia* and the syngameon

> *It cannot be expected that a rigid hierarchical system, demanded by nomenclature (or nomenclaturists), should encompass organisms absolutely, if we believe in evolution at all.*
>
> – D.J. Mabberley (1992: 115)

Taxonomic considerations change as we learn more about the biology of groups. Wallace (1865) had been pragmatic himself: "...when the difference between two forms inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only, I have considered such forms to be species. When, however, the individuals of each locality vary among themselves, so as to cause the differences between the two forms to become inconsiderable... I class one of the forms as a variety of the other". When the taxonomy of a group like the Bambusinae referred to earlier is taken into consideration, the difficulty of even defining the main genera – *Bambusa* Schreb., *Dendrocalamus* Nees and *Gigantochloa* Kurz ex Munro – by selected morphological features, considered against the intergeneric introgressions that have been rife in that group, become understandable. But what do we do in terms of our need for handles to everyday recognition of genera and species?

The syngameon concept (Lotsy, 1925; Grant, 1981; Mallet, 2003), referring to a complex of genetically related species that can occasionally be inter-fertile, applies well to the generation of new forms. As observed by Givnish (2010), it "bridges the roles of adaptive radiation, hybridisation, and subsequent selection for reproductive reinforcement". The syngameon concept may also be a useful one in viewing the complex radiations and diversity within such speciose genera as *Aglaia* Lour., *Piper*, *Psychotria* (subgenus *Psychotria*) and *Saurauia*. However, there can be variation that seemingly refutes such causes. Morphologically, variation that cannot be put down to definite causes such as hybridisation may be given over to the concept of the ochlospecies (Cronk, 1998; White, 1998), which, as enigmatic as it sounds, White (1998) described as a "very variable species, whose variation, though partly correlated with ecology and geography, is of such a complex pattern that it cannot be satisfactorily accommodated within a formal classification". Are ochlospecies products of highly reticulated phylogenies, whether among subtypes or fully speciated entities?

In light of this, Pannell (1992) has understandably stated in her revision of 105 species of *Aglaia* (in which polyploid series also occurs): "The term complex is applied to species with a more extensive, complicated and reticulate pattern of variation, in which the extremes appear at first sight to belong to distinct species. It may prove possible to divide some of these species into two or more subspecies based on partial discontinuities in their variation, probably correlated with different geographical distributions or ecological conditions. Such infraspecific categories are difficult to define in *Aglaia* from existing herbarium material. . ."

However, with regard to *Syzygium* Gaertn. in Borneo (more than 200 species), Ashton (2011) stated “Though the commoner species exhibit much variation, the generally constant distinctions between *Syzygium* species implies that their hybrids seldom survive in nature”. Does the variation making up the “commoner species” have syngameon-like characteristics? This remains to be tested. In a group like *Ficus* L. (some 30-plus species in Borneo), with an extent of dioecy and reasonably specific fig-wasp pollination (that can bridge long distances), it is perhaps understandable that Berg & Corner (2005) state: “Material that could be regarded as hybrids with a clear mixture of parental characters [has] not been encountered. The few specimens showing (one or two) characteristic features of co-occurring species might be products of hybridisation. *Ficus* species can hybridise, as has been demonstrated... Evidence for the occurrence of first and later generation hybrids in *Ficus* populations in the Krakatau Islands has been provided (Parish et al., 2003).” Natural hybrids have been demonstrated among co-occurring *Shorea* Roxb. ex C.F.Gaertn., which have pollinators in common (Kamiya et al., 2011), but survival beyond the F1 generation may be critical for understanding of survivorship and evolution among such co-occurring congeners (Ashton, 2014 and *in litt.*, 2017).

Indeed, as Paterson et al. (2008) remarked, the unresolved question of how species may be composed of genetically polymorphic populations of individuals, or of phenotypically plastic but genetically similar individuals, may not be “an either-or question but a quantitative one”.

Sarawak’s forest understorey: some illumination, much darkness

Grenier et al. (2016) emphasise that, although adaptive plasticity increases individual fitness, it is relevant to consider the costs of such plasticity. For many herbs, perhaps some shrubs, and certainly not a few lianas, the preservation of the clone through proliferation and maintenance of ramets would seem to be an important strategy in keeping a baseline diversity. In the case of woody plants, cauliflory would fit into an understorey strategy, if there were one (Wong, 2017). What is an ‘understorey strategy’?

Wallace (1878) suggested that pollinators in the relatively dark forest understorey would find flowers borne on stems much more easily than those in the canopy. Others pondering bats as pollinators (Van der Pijl, 1957; Marshall, 1983) also suggested these animals were more likely to visit flowers that were relatively uncluttered by foliage. Some considering primate habits (Janson, 1983; Howe, 1986) have argued that fruits were more easily accessible if borne on sturdier trunks and branches instead of flimsy shoots in the canopy. On the other hand, many cauliflorous plants also flower and fruit in the canopy (Warren et al., 1997) and, in the understorey, there seems mostly not to be just one species or group of pollinators with a single efficacy involved per plant species (Momose et al., 1998). An astute four-year study in the lowland dipterocarp forests of Sarawak by Sakai et al. (1999) showed that understorey taxa flower more frequently, and more often out of mast years, than canopy species, suggesting sustained levels of fecundity.

There are possible selective advantages inherent to cauliflory. The understorey is a comparatively even environment where a larger range of potential pollinators or dispersers, including some incidental ones, can be found. Perhaps floral innovations require less investments as they need not be particularly hardy or borne on especially sturdy axes, as in the variable environment of the crown periphery. But perhaps owing to the very nature of cauliflory, intermittent to continuous (or near-continuous) flowering confers some distinct advantage (Wong, 2017). Chen et al. (2014) have pointed out that when long-lived trees in a syngameon are inter-fertile, they benefit from increased heterozygosity including the capture of advantageous alleles. Also, occasional reproductive failures may even out, if long-lived individuals flower and fruit more frequently (Calvo & Horvitz, 1990; Ashman et al., 2004), a consequence of cauliflory.

Certainly in *Saurauia* as well as in *Ficus* (Wong, 2017), cauliflorous axes continue to develop new or higher-order lateral axes (albeit in a highly condensed state) that give rise to ensuing episodes of flowering (Fig. 9). This ensures intermittent to even continuous flowering from the initiation of the cauliflorous meristem, and the cauliflorous bosses on such stems or trunks become bigger and more noticeable. The condensation of axes on stems and branches implies smaller reproductive investment, compared to the seasonal development of new reproductive flushes in the canopy, where meristems and development must adapt to the more extreme fluctuations of the external environment and, therefore, more frequently attune to an annual or supra-annual frequency. Furthermore, the understorey flowering habit may be more common in smaller plants than for canopy-sized trees, as resource requirements for each reproductive episode may be lower with cauliflory (Wong, 2017).

Although a more frequent flowering may be expected to promote gene flow and so even out any extreme variation, it may also increase the possibilities for odd genetic combinations or morphological expression against a background of polyploidy or reticulate inheritance. This appears possible for *Saurauia* and perhaps other large groups with a complex genetic history (Wong, 2017).

> *We simply do not know if recombinational speciation is moderately common in certain groups or exceedingly rare in all taxa, little more than an evolutionary curiosity. It is remarkable that we cannot yet answer this question. The matter of how often new species arise by the fusion of old ones is not, after all, some arcane issue, but one that is central to our view of the origin of species – and one that can only be readily resolved by experiment.*
>
> — J.A. Coyne & H.A. Orr (2004)

Slow progression of science

Even though taxonomy is unevenly treated among taxonomists themselves, overall it is an undeniably slow science. Taxonomy sets out the premises for interpreting taxa and hypotheses of relationships, which can be tested; but first the taxonomic sorting, frequently based on morphology alone, needs to be completed. Students carry out detailed work and in many cases attempt to relate their perceived taxonomy to other areas of investigation. However, the more practical and wiser choices are to revise smaller genera or groups for a thesis, in a project that is their imperative to finish. Prolonged crafting of a baseline taxonomy, such as required in highly speciose or complicated groups, can only be effectively carried out as longer-term projects by researchers with stable positions and who are able to justify some of these studies in a diversity of topics they may handle. Thus we often see many taxonomists working past their retirement to complete their work. Even so, some of this taxonomic effort may even fizzle out.

The recent (re-)scrutiny of cases that we have been involved with, including the Burseraceae (Seah & Wong, unpublished), Fagaceae (Arora, Neo, Tan & Wong, unpublished) and Loganiaceae/ Gentianaceae (Wong & Sugau, 1996; Sugumaran & Wong, 2012, 2014), has shown that a number of "widespread species" have turned out to be simply mixtures, the components of which can be characterised by suites of both vegetative and reproductive characteristics previously undiagnosed. Whether the earlier impressions were in response to taxonomic resolve in handling large groups expediently or were simply due to extremely broad taxonomic concepts, or otherwise, remains uncertain. Also, when groups are large and their taxonomic revision is slow in completing, opportunities for complementary work in phylogenetics or lineage studies could be difficult to organise, be unappealing or not realised. The corollary is that our perceptions of the tropical rain forest may not be sufficiently shaped by better understanding the processes operative for many groups, especially those of the lower forest strata, and in particular the understorey.

Much mystery remains and science continues to add bit by bit to the emerging understanding of nature. Those in science sometimes make contact with conservation because obviously some results are of direct use to conservation management. In a changing world, what can we do to promote conservation awareness and a better regard for non-drastic alterations to the forest environment?

The importance of accounts accessible to a general readership deserves some priority. Whether this should also be the initiative of an individual scientist or solely the responsibility of the organisations concerned for forest resources, is debatable, but some measure of interaction should be beneficial. Given Borneo's intense biodiversity and spectacular natural places, both the scope and the accomplishments to be made are indeed immense. We suggest that well-illustrated accounts of this biological richness, and its significance through a natural history perspective, will be as critical as the slowly advancing frontiers of the scientific platform on which our understanding will depend. Science is always a little late; consider the progression of knowledge about

Fig. 9. Examples of cauliflory in the forest understorey, seen in *Saurauia* and *Baccaurea* Lour. species. Arrow in C indicates the woody protrusion formed through repeated development of multiple or side shoots of higher order in the highly condensed lateral flowering system of *Saurauia agamae* Merr. (Photos: A, P. Miun; B, K.M. Wong; C, S. Bosuang).

diseases and illnesses before we learn better health management, and how it could be better despite great losses in the past. So it is with nature and our environment. Let us not forget the importance of works like *National Parks of Sarawak* (Hazebroek & Abang Kashim, 2000), which is not only about the existing Parks of Sarawak, but inherently about *how many more* areas there are to be conserved, especially in the highly special Middle Sarawak. Of late, more natural history accounts of Borneo have begun appearing, with a growing participation. The natural history perspective should be a very important one, totally complementary to the scientific endeavour.

Reconciliation at the beginning of the end?

Finally, as a small illustration, we can look at the distribution of *Saurauia* species now documented for Sarawak. The spread of rare species throughout the mainstay of the Northwest Borneo biodiversity hotspot is indeed impressive, but what will ultimately be the fate of the other numerous species?

Of the 85 species of *Saurauia* now known from Borneo, 38 occur in Sarawak (Wong, 2017). One of the authors of the present contribution (LN) mapped the occurrences of *Saurauia* species in Sarawak based only on herbarium specimen records (Fig. 10). From this, six main distribution patterns can be identified. The first is a restriction of three species to west Sarawak, west of the Lupar Line; 13 species are only found in Middle Sarawak, between the area east of the Lupar Line and west of the Baram river and Brunei; and six species are only found in northeast Sarawak, around and to the east of the Baram river and the Brunei area. A further three species are found throughout Sarawak; six species are primarily found in Sabah but their distribution ranges extend into Sarawak; and seven species are simply widespread and occur throughout Borneo.

As observed with the dipterocarps (Ashton, 1977), the Lupar river is also a relevant barrier for *Saurauia*, restricting three species to its west, while 25 species are only found east of it. Seven species do not seem to occur west of the Suai-Sibuti drainage, the ostensible Pleistocene valley of the Baram river (but these include species mostly only known from Brunei, as well as point endemics of Mulu National Park), and at least three species which are otherwise widespread in Sarawak are not yet known to occur east of the Baram river. In the case of other Sarawak rivers and valleys that could be important dispersal barriers (Ashton, 1972), the *Saurauia* species apparently restricted to them are still too poorly known and under-collected for any meaningful conclusions to be drawn.

The distribution of *Saurauia* in Sarawak clearly indicates that the contiguous lowland rainforests of Middle Sarawak are invaluable for harbouring the main bulk of species diversity, even as rarer habitat types or geology (such as the isolated granitic outcrops within the sedimentary geology of West Sarawak, or the limestone areas of Bau and Melinau), or biogeographically significant areas such as West Sarawak west of the Lupar river, may be where local endemics are restricted. The degradation of these lowland rainforests, therefore, affects the majority of species, especially those which are particularly vulnerable owing to extreme rarity, and which often have remained so poorly-known.

Data from Gaveau et al. (2016) show the extents and time periods at which the forest cover of Sarawak has been altered by logging, conversion to plantations or the construction of dams (Fig. 11). Large tracts of the forests of Middle Sarawak have been heavily logged, with most of the logging having taken place after 1973 (Gaveau et al. 2014). It is unknown what long-term consequences there may be of the opening up of the canopy and the edge effects created by logging roads, on the diversity of forest understorey plants such as *Saurauia.* The sufficiency of the coverage and connectivity of the current network of protected areas in Sarawak can be partly evaluated by estimating the number of *Saurauia* species represented or potentially not represented within them (Fig. 12). Most of the 38 species found in Sarawak are covered in at least one gazetted protected area (defined as having at least one specimen record from a site), but there are five species which are represented only in proposed (not yet gazetted) protected areas, and a further six species which are not represented in any protected areas at all. All but one of these latter 11 species are endemic to Sarawak, and seven of these are only known from Middle Sarawak. Clearly, the current system of protected areas may seem inadequate for safeguarding these rarest of species. Moreover, five

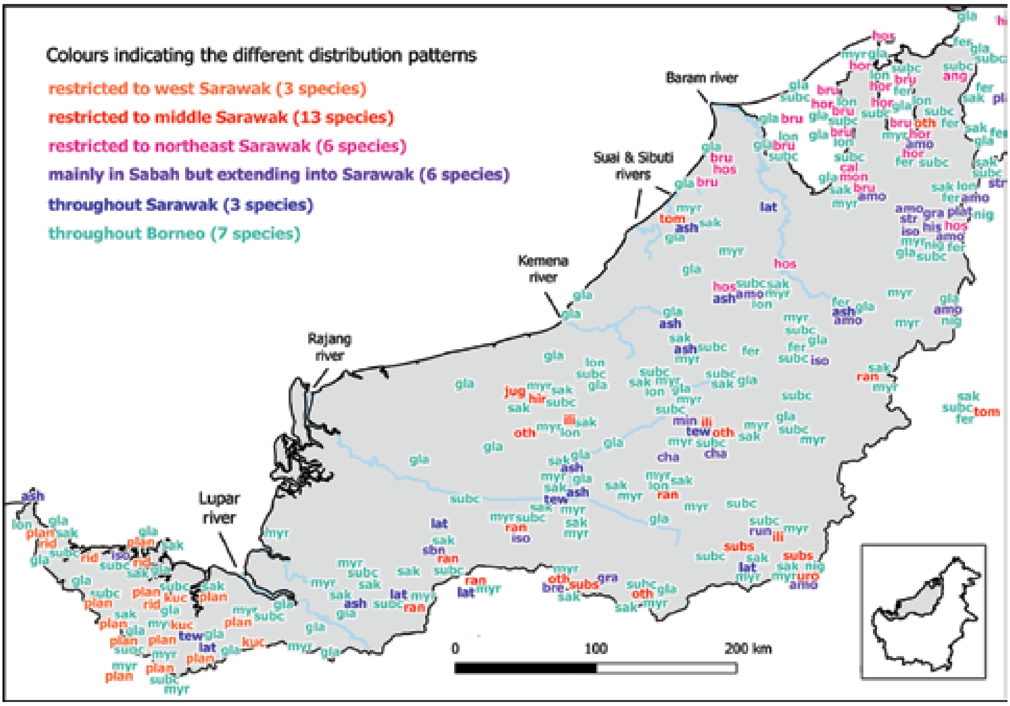


Fig. 10. Distribution of *Saurauia* species in Sarawak (the inset map shows Sarawak's position on the island of Borneo). Thick blue lines represent the main river systems of Sarawak. *Saurauia* species are represented by 3–4 letter-long abbreviations of their names and are coloured according to their main distribution patterns. Species occurrences are plotted from manually-georeferenced herbarium specimen records documented in Wong (2017). Note that each plotted occurrence can represent more than one collection. (Image: L. Neo).

The abbreviations represent the species as follows: 'amo' = *S. amoena* Stapf; 'ang' = *S. angustipetala* Kamariah ex K.M.Wong; 'ash' = *S. ashtonii* K.M.Wong; 'bre' = *S. brevicymula* K.M.Wong; 'bru' = *S. bruneiensis* Kamariah; 'cal' = *S. calcicola* K.M.Wong; 'cha' = *S. chaiana* K.M.Wong; 'fer' = *S. ferox* Korth.; 'gla' = *S. glabra* Merr.; 'gra' = *S. graciliflora* Kamariah ex K.M.Wong; 'hir' = *S. hiranohottae* K.M.Wong; 'his' = *S. hispidicalyx* Kamariah ex K.M.Wong; 'hor' = *S. horrida* Hook.f.; 'hos' = *S. hosei* Merr.; 'ili' = *S. iliasii* K.M.Wong; 'iso' = *S. isosepala* Kamariah ex K.M.Wong; 'jug' = *S. jugahii* K.M.Wong; 'kuc' = S. *kuchingensis* K.M.Wong; 'lat' = *S. latifolia* K.M.Wong; 'lon' = *S. longipetiolata* Merr.; 'min' = *S. minutiflora* K.M.Wong; 'mon' = *S. montiflagrans* K.M.Wong; 'myr' = *S. myrmecoidea* Merr.; 'nig' = *S. nigrescens* Korth.; 'oth' = *S. othmanii* K.M.Wong; 'plan' = *S. planchonii* Hook.f.; 'plat' = S. *platyphylla* Merr.; 'ran' = *S. rantaijawae* K.M.Wong; 'rid' = *S. ridleyi* Merr.; 'run' = *S. runiae* K.M.Wong; 'sak' = *S. sakoembangensis* Korth.; 'str' = *S. strigosa* Kamariah ex K.M.Wong; 'subc' = *S. subcordata* Korth.; 'subn' = *S. subnuda* K.M.Wong; 'subs' = *S. subsessilifolia* Kamariah ex K.M.Wong; 'tew' = *S. tewensis* Korth.; 'tom' = *S. tomentocalyx* Kamariah ex K.M.Wong; 'uro'= *S. urophylla* K.M.Wong.

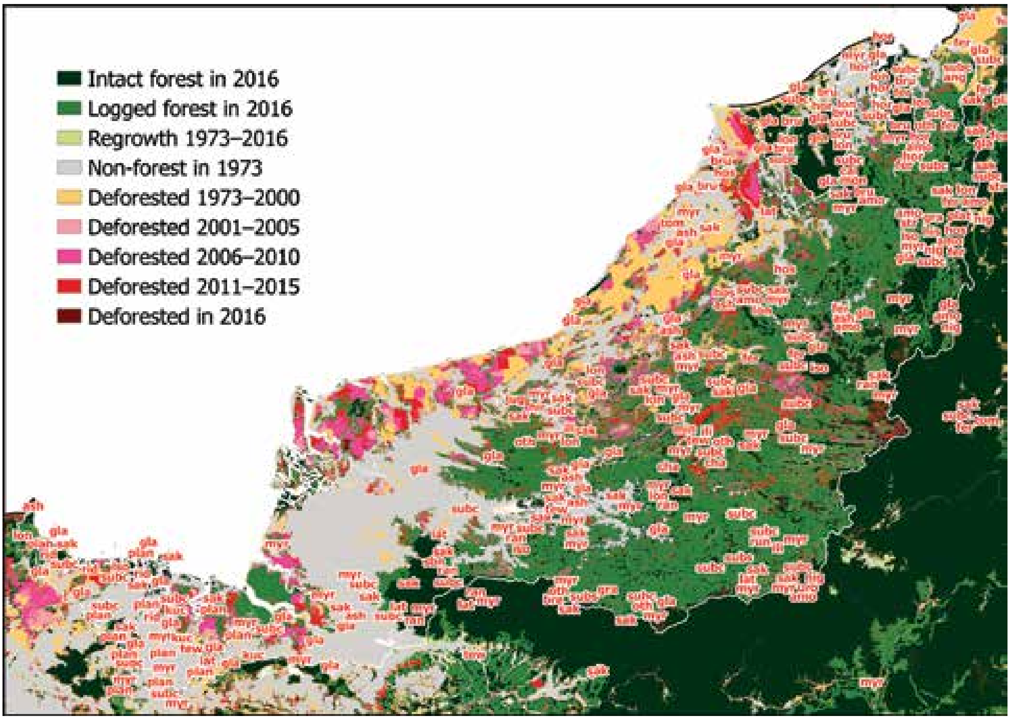


Fig. 11. *Saurauia* species in Sarawak mapped against forest cover in Borneo in 2016. For degraded and non-intact forest, the time periods in which forest degradation or deforestation occurred are also shown. Data for forest cover and deforestation in Borneo from Gaveau et al. (2016) and the Center for International Forestry Research (CIFOR); species codes as in Fig. 10. (Image: L. Neo).

of these 11 species are only known from areas that today are non-forested or logged forest (Fig. 11, Table 4).

Whether the distribution patterns shown for *Saurauia* species reflect those of other plant groups, such as similarly large, speciose genera like *Lithocarpus* Blume (Fagaceae), *Syzygium* (Myrtaceae), *Shorea* (Dipterocarpaceae) etc., remains to be demonstrated. Also of interest are areas where endemic taxa are concentrated, since these could be refugial areas where relict taxa are persisting (paleoendemics), or areas of speciation where newly-arisen taxa are restricted because they have not yet dispersed beyond (neoendemics). An ongoing study of endemic genera and the centres of their distribution in Borneo should inform where such special areas of biodiversity might be, and provide additional corroboration of the biogeographical significance of Northwest Borneo and the once-mighty ecosystems of Middle Sarawak.

Ultimately, science is not responsible for the rapid changes that have taken, or are taking, place in the forest landscape. In many cases, it is clear that irrevocable damage could have been done to Borneo's forests (Brown, 2018) (Fig. 13). Important questions, such as the extent of illicit logging, the incidence of incursions into protected area boundaries, and the protection of once-disturbed areas, must be urgently addressed.

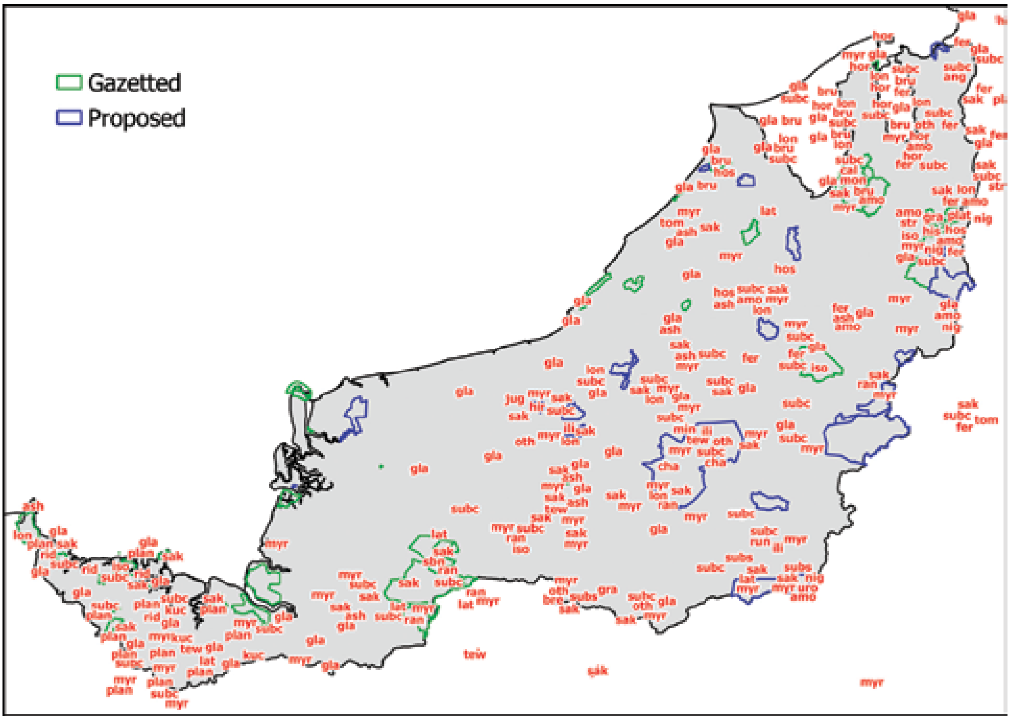


Fig. 12. *Saurauia* species in Sarawak mapped against gazetted and proposed protected areas in Sarawak. Protected areas are as of 2015 and are adapted from the Global Forest Watch (2019) which used data and maps from the Sarawak Forestry Department and Sarawak Forestry Corporation; species codes as in Fig. 10. (Image: L. Neo).

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Table 4. *Saurauia* species not represented in any protected areas or represented only in 'proposed' protected areas. The forest cover types (according to Gaveau et al., 2016) that the species are presently known from are also given.

Species	**Status in Sarawak**	**Occurrences in'proposed' protected areas**	**Occurrences in forest cover types**
S. angustipetala	Endemic		Deforested from 1973–2000
S. brevicymula	Endemic		Intact forest in 2016
S. chaiana	Endemic	Proposed Hose-Laga National Park	Intact forest in 2016, Logged forest in 2016
S. hiranohottae	Endemic	Proposed Bukit Kana National Park	Logged forest in 2016
S. horrida	Non-endemic		Intact forest in 2016
S. iliasii	Endemic	Proposed Bukit Mersing National Park, Proposed Hose-Laga National Park	Non forest in 1973, Intact forest in 2016
S. jugahii	Endemic		Logged forest in 2016
S. kuchingensis	Endemic		Non forest in 1973
S. othmanii	Endemic	Proposed Hose-Laga National Park	Intact forest in 2016, Logged forest in 2016
S. subsessilifolia	Endemic		Logged forest in 2016
S. urophylla	Endemic	Proposed Baleh National Park	Intact forest in 2016

Fig. 13. Aerial view of logging roads and heavily impacted vegetation in an area of 'Middle Sarawak', where, instead of effective precautions to maintain a semblance of forest structure, there is a resultant 'total illumination' (and drying out) of the forest understorey. (Photo: Haji Mohamed Abdul Majid).

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