

TREE DEMOGRAPHY PLOTS: A NEGLECTED RESOURCE FOR SYSTEMATIC AND CONSERVATION RESEARCH

*Peter Ashton*¹

ABSTRACT

The pantropical network of large tree demography plots coordinated by the Smithsonian's Center for Tropical Forest Science has now gone global, as part of the Smithsonian Institution Global Earth Observatories. Some four million tropical trees, representing about 10,000 species, are now tagged, provisionally identified and periodically recensused. Some 3,000 species are captured in the six plots within Malesia. These include species rarely collected and many that are now endangered. Easy location of trees for periodic examination for fertile material and detailed ecological data, together with seasoned in-country research teams, provide unique opportunities for research collaboration.

INTRODUCTION

All terrestrial life is dependent on the primary producers – which are plants. The diversity of life – biodiversity – is dependent on the diversity of plants. Plant diversity is in turn dependent, in part, on habitat diversity. In hyperdiverse ecosystems plant diversity mostly results from the struggle between plants which evolve ever more complex chemical and other species-specific defences, and their pathogens and predators which evolve ever more costly means to overcome them. The most hyperdiverse terrestrial ecosystems are some of the lowland rain forests of Malesia, and those of northern Borneo have recently been shown by rigorous quantitative comparison (Slik *et al.*, 2015) to be the most species-diverse in the world, even more so than the upper Amazon. But the forests are now mostly degraded by unmanaged logging, and are increasingly being converted to oil palm plantation. The plant taxonomists of Malesia therefore have a responsibility of global importance, because they alone have the knowledge required to explore and identify the remaining forests of Malesia which are of global importance for their species diversity, unique flora – and, by inference, dependent fauna.

If we fail, systematic research joins the field of palaeontology. How much government or charitable funding is invested in palaeontological research? Let's get real!

During the colonial era, there was a period during which some Malesian forests were managed for sustainable production of timber, in particular species for which demand was greatest. Most of their biodiversity was thereby conserved. Excepting some forests in Sabah, notably Deramakot Forest Reserve and the Mangkuwagu Community

1. Peter Ashton is Bullard Professor of Forestry Emeritus at Harvard University, Department of Organismic and Evolutionary Biology.

Address: 29 Windmill Road, Chiswick, London, W4 1RN, UK.

Email: pashton@oeb.harvard.edu

Forest Reserve, I am unaware of any active management still occurring in Malesia. The forest, with the complicity of politicians, has subsequently been co-opted by logging companies, who have also been given responsibility for its management. But it is not clear how much management they are doing, or can do, given that licences have been awarded for far shorter times than it takes to grow a tree. Again, Sabah is the praiseworthy exception.

The forests of Malesia have traditionally been the heritage of indigenous minorities who, in country too hilly or wet for irrigation, relied on it for swiddening land, water and the essential goods of life: building materials, medicines, food, cultural items, cord, fibre and so much more. It is these same indigenous minorities who had believed they owned the forest, respected it and sustained it as a spiritual inheritance.

Now, with few indigenous forests remaining unlogged, or unconverted to commodity crops, the economic role of the remaining indigenous forests is changing. The role of forests in the amelioration of weather, the maintenance of water supply and soil protection, and, of course, for their function as the major living carbon store aiding the arresting of climate change, is now, at last, starting to be recognised by policymakers. Nations of the region have both an unique opportunity and a global responsibility to conserve what still remains of the genetic heritage in their unparalleled regional biodiversity. It will continue to yield the chemistry for future cures, while the living and soils carbon mass can yet avert climatic catastrophe. With more of us living in cities, we are coming to realise how vital it is to conserve what remains of species which yield rare forest products, but also their overall biological diversity including wildlife.

THE VALUE OF LARGE PERMANENT PLOTS IN CONSERVATION SCIENCE, PLANNING AND POLICY

What future do biodiversity and our indigenous flora have if we do not succeed in conserving a representative sample? Conservation research depends on thorough taxonomic documentation, but equally on knowledge of species' natural history, especially habitat.

Plant collectors are often the only scientists to explore a forest, and have the knowledge to accurately document habitat and natural history. It is therefore plant scientists who are primarily responsible for guiding the conservation planner with advice arising from the knowledge gained from field observations.

We cannot do this alone. Patterns of both diversity and endemism vary on the local as well as the regional scale. They are correlated with the age of landscapes on the regional scale, but on the local scale correlate especially with soil, which in turn is correlated with geology and topography. In addition, islands are lower in species diversity, though they may be rich in endemism if they have existed in their current climate over geological time or by the presence of species with broad habitat tolerance to other habitats nearby. In one striking example, 15 0.6-ha plots set in dipterocarp forest on acid humult soils over rhyolite in Central Sarawak yielded a rich flora of humult specialists, some of

which have rarely been collected, including the rare endemic genus *Sarawakodendron* Ding Hou, but also several widespread taxa of the prevailing udult loam soils such as *Hopea dryobalanoides* Miq. Whereas many mammals survive or may actually increase in number following logging, successive logging leads to increasing levels of plant extinction. The first to go are the epiphytes but then, as the area of successional forest increases and old growth decreases, the old growth specialists, which comprise the majority of plant species' diversity, increasingly fail to compete and die out.

We can identify the broad geographical terrestrial characteristics of a region and a locality under review, but for habitat characteristics we need the collaboration of ecologists. They in turn can correlate individual habitats, therefore individual floristic associations and species distributions, through soil to geology. With that evidence, habitats and their distinct floristic associations can be mapped from the geological maps that are universal throughout the Malesian region.

During research into dipterocarp systematics, and the Myrtaceae of Malaysian Borneo, I have been disappointed by the lack of precise information on habitat or field characteristics on herbarium labels. If any habitat data is included at all, it is most often a general summary of the habitats that were visited during a day of collecting. A single altitude is stated, even when a range of over 500 m may have been traversed, and topography is often just stated as 'hills', when ridges, slopes and valleys have been traversed. Scarcely is any reference to geology or soil made, except in conspicuous examples such as limestone karst when the adjacent habitat visited may then not be documented as different.

Soil characteristics, which can be key to the identification of leading forest floristic associations, can easily be detected: is the surface litter greyish or coppery-brown, respectively with little surface humus or distinctive tobacco-like raw humus matted with fine roots? Is the mineral soil beneath yellow-red or white, sticky with clay when squeezed in the hand and silty in the mouth, or is it sandy and gritty?

The conservation scientist, in order to identify priority sites for legislation, requires knowledge of locations of high species diversity, where endemics are concentrated, where species of exceptional importance (use, value to wildlife, evolutionary interest, rarity) are concentrated and the optimum (and minimum) area necessary to sustain genetically sustainable breeding populations (often estimated to be 200 reproductives among outbreeders).

This requires testing knowledge of floristic relationships with habitat, and is often derived from ecological plots whose establishment and census is time-consuming and expensive. But the process can be effectively achieved by reference to published plot data from elsewhere in the region. Species rarely, perhaps never, change their habitat specificity within one climate throughout their range (apparent differences in soil preference are often due to differences in terminology used by different collectors, not genuine differences in soils). In one striking example, it was predicted, when the Center for Tropical Forest Science (CTFS) plot near Trang in Peninsular Thailand was first censused, that a few species of the widespread sandy clay flora of Sunda mixed dipterocarp forest would

be recorded for the first time in its shortly seasonal climate. This proved to be the case when *Neoscortechinia kingii* Pax & K.Hoffm. (Euphorbiaceae), occurring on similar soils at both the Pasoh Forest Reserve in Peninsular Malaysia and Lambir Hills National Park in Borneo, was found to be present, and a first record for Thailand.

Fortunately, permanent forest plots large enough to record and analyse the local variation in floristic patterns that occur on one geological formation, and sometimes across the ecotone between two formations, and that are rigorously censused using a standard protocol, already exist both in the region and globally. This is thanks to an international partnership, the Center for Tropical Forest Science (CTFS) collaboration (Fig. 1). They are among the key permanent plots availed of in Baker *et al.*'s recent paper (2017), whose primary focus is on the neotropics.

These plots cannot survive without long-term collaboration with a national institution such as a university, forest or botanical research institute. This in turn requires the continued service of at least one permanent staff member able and willing to take responsibility for organising an initial survey and census, a five-yearly recensus, field technicians (botanical assistants) to carry out the work and funding at least for their wages.

CTFS is a collaboration of researchers and institutions dedicated to pursuing long-term forest research, with the objectives of understanding forest dynamics in order

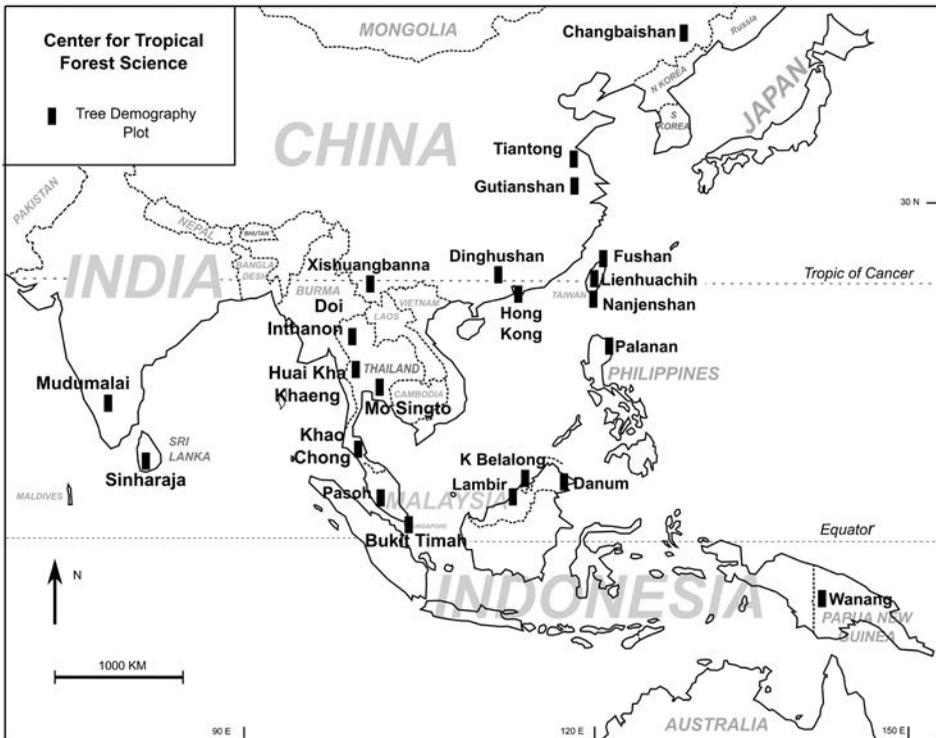


Fig. 1 CTFS plots in Asia (plots are present in every country in Malaysia but for the largest, Indonesia) (from Ashton, 2014).

to understand how tree species diversity is maintained over time, how to use this understanding to define the necessary protocols for managing nature preserves, to develop optimal silvicultural methods for sustainable production of goods (especially timber) and to understand the impact of harvesting goods on maintenance of biodiversity. Today several plots of the CTFS network are also being monitored for rigorous recording of the impact of climate change on terrestrial ecosystems.

HOW CAN CONSERVATION BIOLOGISTS AND SYSTEMATISTS TAKE
ADVANTAGE OF THE OPPORTUNITIES PRESENTED BY CTFS PLOTS?

In most cases, plots are large enough to include individuals of about half the local tree flora, and about one-quarter of the regional flora. For example, the Forest Research Institute Malaysia's (FRIM) Pasoh CTFS plot includes 817 species, whereas the tree flora of Peninsular Malaysia as a whole includes c. 3,100 species. The Sarawak Forest Department's Lambir CTFS plot includes c. 1,200 species, whereas the tree flora of Sabah and Sarawak includes c. 4,500 species (Lee *et al.*, 2002). The Lambir plot is exceptionally rich because its soils are diverse, including sandstone and a shale (clay) geological formation supporting separate tree communities, and the ecotone between them.

Plots, both permanent and temporary, small as well as large, have been furnished with soil analyses at a greater level of detail than elsewhere in the tropics, and particularly in northern Borneo (Ashton, 2014). Data from these plots show that the range of community and species can be clearly characterised in relation to soil and topography (Figs 2 & 3). These plots are large enough to describe how the species and their communities vary across part of the landscape. As examples, Potts *et al.* (2002), reporting on the relationship of tree flora, geography and soils in 105 0.6-ha plots laid out across Sarawak, showed that the soil's nutrient variation was as influential as geographical distribution of both tree flora as a whole, and on the range and site specificity of congeneric taxa.

For example, *Dryobalanops aromatica* C.F.Gaertn., concentrated through the Sunda region on the expanded Riau Pocket province (Corner, 1954; Ashton, 2014), is confined in Sarawak to those plots on humult yellow sands north-west of the Lupar Fault, whereas *Dryobalanops lanceolata* Burck, endemic to Borneo, occurs throughout Sarawak on udult loams. But the two species co-occur within the Lambir 52-ha plot, where their habitats hardly overlap: whereas *D. aromatica* hugs the humult sandy clay loams of ridge and dip slope of habitat 1 in Fig. 2, *D. lanceolata* is confined to the clay loams and slopes over underlying shale, represented by habitat 2. Of two infraspecific taxa within *Shorea macroptera* Dyer, subspecies *baillonii* (F.Heim) P.S.Ashton is found on shallowly humult sandy clay soils in the plots and confined to the north-west, while subspecies *macropterifolia* P.S.Ashton occurring on quite similar udult clay loams is found in north-east Borneo, with ranges overlapping in the Baram drainage in north-east Sarawak: the 52-ha CTFS plot at Lambir Hills National Park revealed that the subspecies can co-occur in the same landscape, albeit predominantly on differing soils.

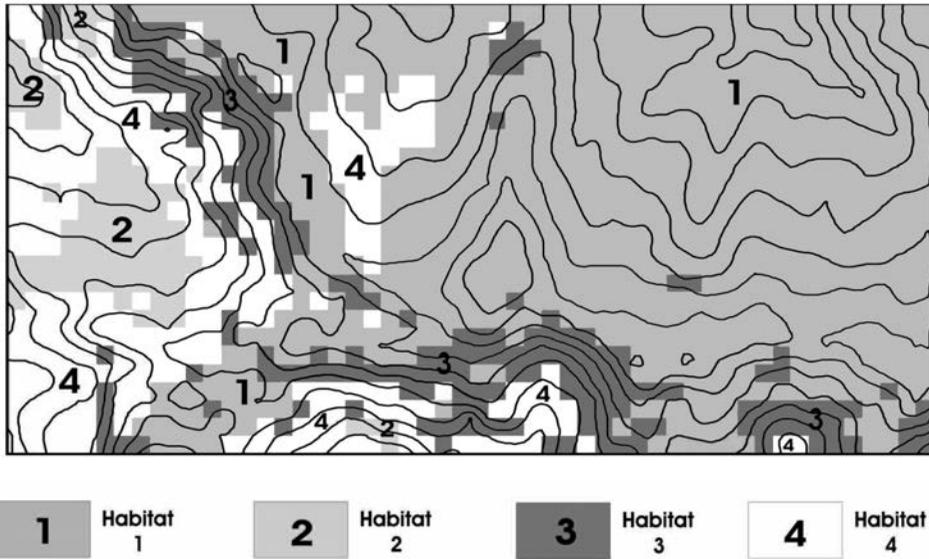


Fig. 2 Floristically correlated main habitat types within the 52-ha CTFS plot at Lambir Hills National Park. 1: Humic sandy clay loams on dip slope; 2: Clay loam ('clay loam'); 3: Yellow humult sandy soil along ridges ('sandy loam'); 4: Silty clay loam ('fine loam'), mainly on dip slopes (from Ashton, 2014).

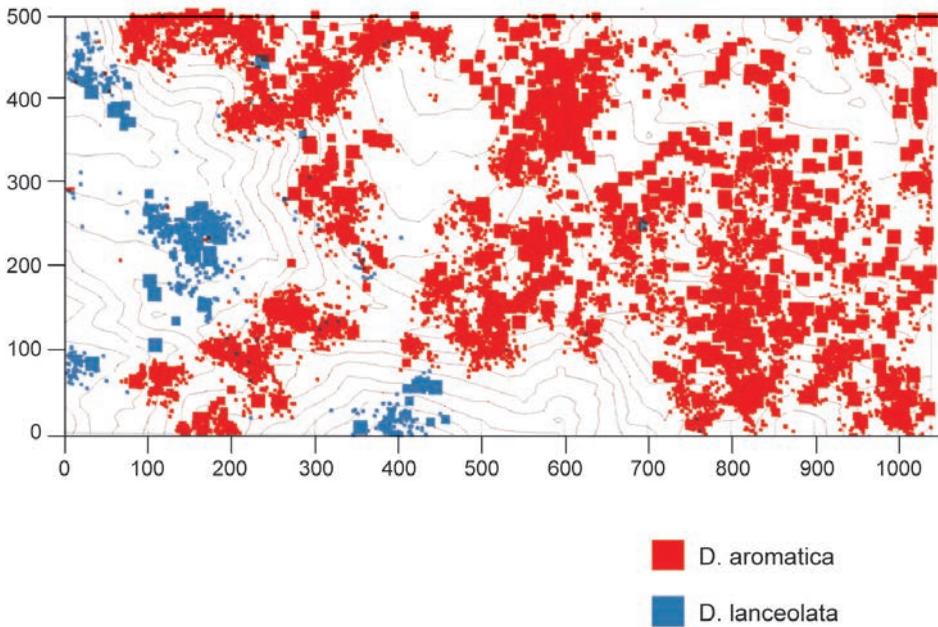


Fig. 3 Distribution of two *Dryobalanops* species in the 52-ha CTFS plot at Lambir Hills National Park. *D. lanceolata* Burck (blue), *D. aromatica* C.F.Gaertn. (red). Symbols indicate diameter classes (from Ashton, 2014).

Such examples illustrate how well-documented plots that have details of surface geology and topography provide vital data to conservation researchers who can extrapolate such data in the identification and mapping of potentially critical areas for conservation. Further, because these CTFS plots can be subdivided into a grid of smaller plots, species alpha diversity, that is diversity within a community and uniform habitat, can be mapped across the sampled landscape, while gamma diversity, that is the total diversity among the sum of communities sampled, can also be estimated. Fisher's alpha, which is independent of sample density or area, is the appropriate diversity measure (Fig. 4).

As can be seen from Fig. 4 there is a clear relationship between species diversity, soil and topography, even at this quite small scale within the landscape. Soil sampling and analysis reveal that diversity correlates with nutrient concentrations. But instead of an increase of diversity with increase in soil fertility, diversity has a peaked distribution in relation to fertility, and this peak is nearer the low rather than the high nutrient end of the fertility gradient (Fig. 5). This is a worldwide property of closed canopy plant communities. But there is a large scatter in plot diversity beneath the peak, which is due to subplots stationed within secondary vegetation beneath canopy gaps. On low-nutrient soils, recent canopy gaps may contain lower diversity than mature-phase closed canopy

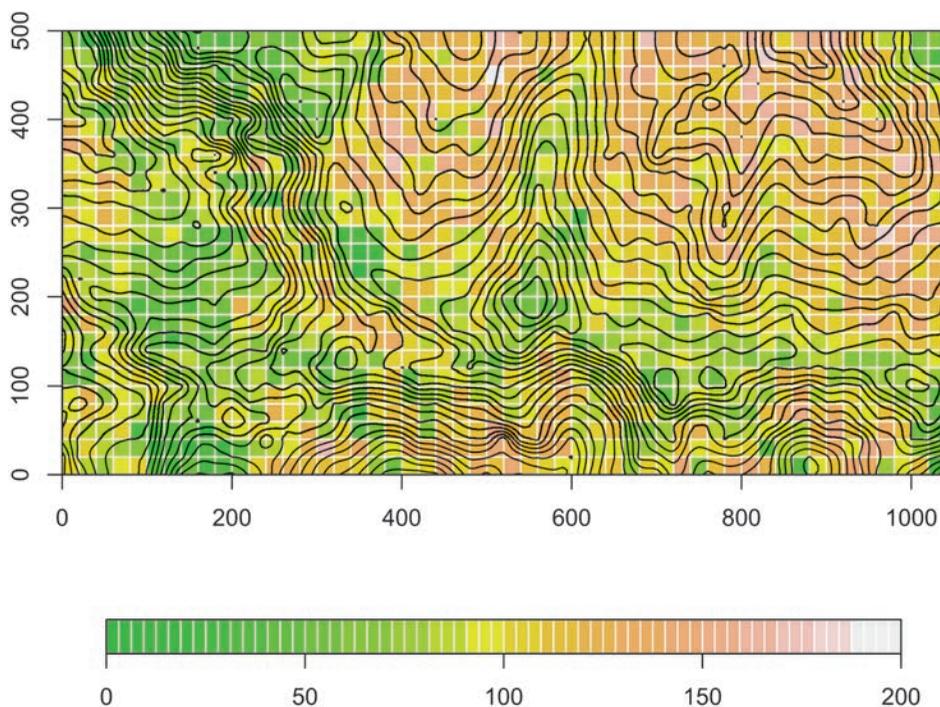


Fig. 4 Species diversity (Fisher's alpha) mapped in 20-m² plots in the 52-ha CTFS plot at Lambir Hills National Park, for all trees equal or greater than 1 cm in diameter (from Hall in Ashton, 2014).

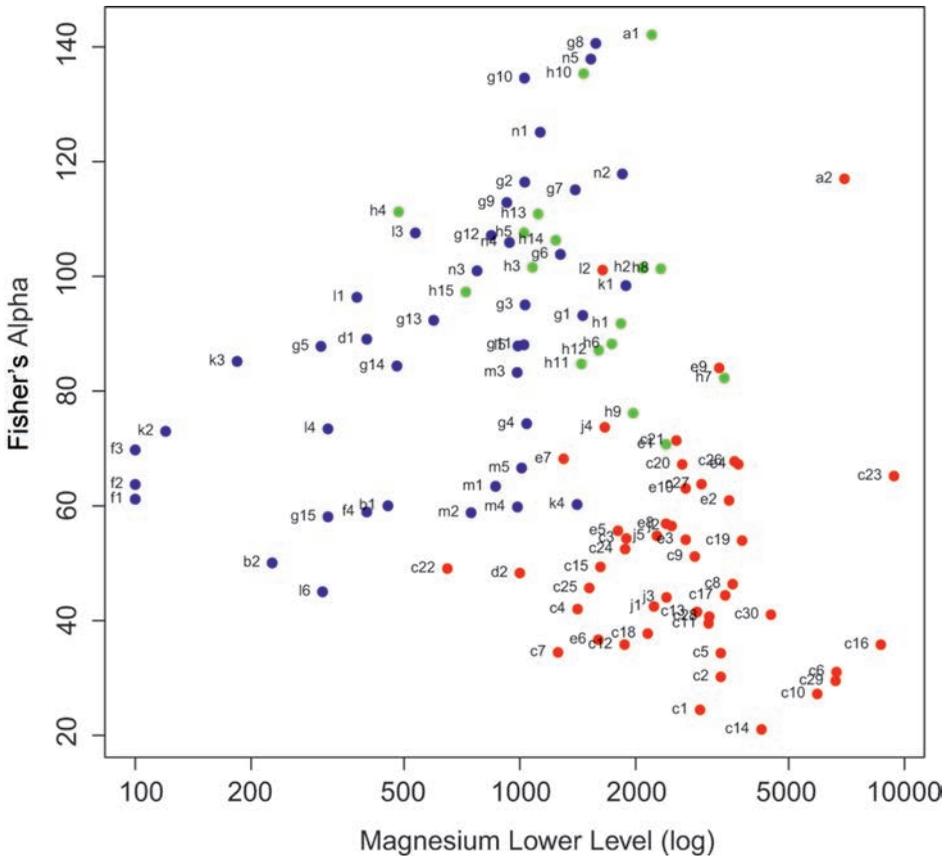


Fig. 5 Species diversity in relation to mineral soil magnesium concentration (70–80 cm depth) in 105 0.6-ha plots in mixed dipterocarp forest, scattered throughout Sarawak. Blue dots: plots on humult (raw humus-bearing) sandy soils; red dots: plots on udult (raw humus-free) clay soils; green dots: plots on intermediate soils (from Hall in Ashton, 2014).

but, on high-nutrient soils, gaps may have the highest diversity. That is because, on high-nutrient soils, a few fast-growing species come to dominate the canopy, suppressing diversity both in the canopy and beneath.

Each soil type supports a distinct tree flora. In north-west Borneo, only one third of the dipterocarp forest tree flora has a generalised distribution, occurring on both udult clay and humult sandy yellow-red soils. These local patterns of floristic composition and species diversity, being correlated with variation in soil nutrients, also correlate at a broader scale with geology. The Malesian land masses predominantly consist of rocks yielding clay-rich udult soils, which provide continuity for migration. Although there is endemism specific to all soil types, it is least on the clay soils where the most widespread species occur, as is found in the regional distribution of Brunei's clay soil dipterocarps (Fig. 6).

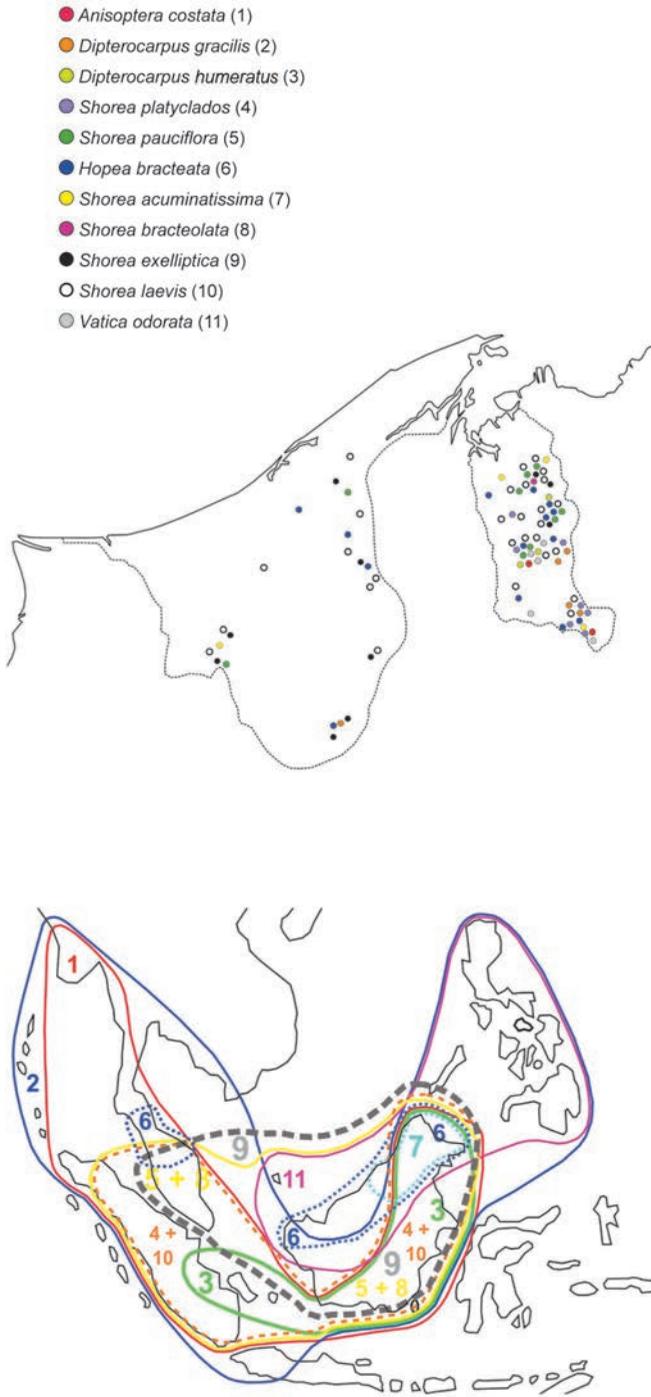


Fig. 6 Distribution of Brunei dipterocarps of adult clay soils within Brunei Darussalam (above). Regional ranges of the same species (below) (from Ashton, 2014).

The species concentrate where shale and clay geology predominates, in the eastern enclave of Temburong, in patches in the Ladan hills to the east and in the Labi hills in the west of the western Belait-Tutong enclave. A few occur on the clay alluvium of central Belait. Most of these species range beyond Borneo with some reaching to the seasonal Far Eastern forests, and one in the Philippines whose dipterocarp flora is highly endemic. Sandstone geological formations occur as islands in a region dominated by clay rocks. Humult sandy yellow-red soils dominate on sandstones, but also on other siliceous rocks, especially granite, in drought-prone habitats including coastal hills and high ridges. These habitats together are insufficient to provide continuous corridors for migration within the current Malesian land masses, or indeed during periods when sea levels were lower and west Malesia formed a continuous land mass. At this point the great river Proto-Mekong and its mostly clay valley alluvium, which would have been dominated by clay soils, would have continued to restrict migration routes between the islands of humult sandy yellow-red soils. The result is higher endemism and narrower overall ranges for the species of sandy soil (Fig. 7). This distinct range pattern was first noticed in Peninsular Malaysia and the Riau Archipelago after which it was named the Riau Pocket by Corner (1954). More recent collecting has shown this pattern to be more widespread, especially in Borneo, while plot studies have provided the data which support the ecological reason for these shared restricted ranges.

Within Brunei Darussalam these species are restricted in the eastern Temburong enclave to the northern Biang range, with one species in montane forest in the far south. However, they are best represented in the sandstone areas of the western enclave, especially the coastal Miocene-Pliocene sandstones whose soft rocks yield deep soils bearing among the richest endemic flora of all lowland Malesia. Within Malesia these species are heavily concentrated in north-west Borneo, with a few in the coastal hills

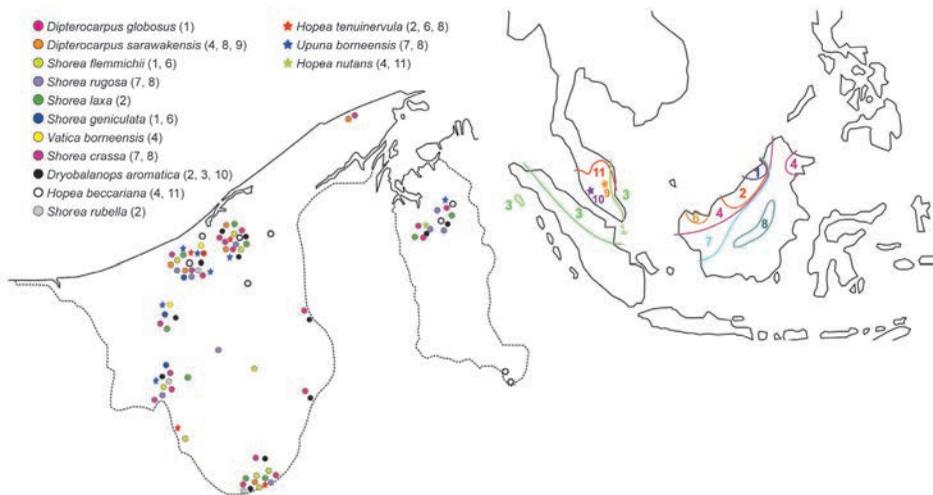


Fig. 7 Distribution of dipterocarp species of mixed dipterocarp forests on humult sandy yellow-red soils (from Ashton, 2014).

and along granite ridges in Peninsular Malaysia. Individual species can be found in the coastal hills of eastern Sumatra and the sandstone hills at the southern foot of the central Borneo uplands. This area is now separated from the sea by peat swamps, but bordered the Java Sea in the early Holocene when sea levels were somewhat higher (Ashton, 2014).

SUMMARY CONCLUSION

It is clear that tagged large tree demography plots serve to locate individuals of rare and rarely flowering species and can provide information on habit, demography and reproductive characteristics. These data are essential for conservation science and planning. Data on soil, geology and other habitat characteristics of target species, floristic communities and centres of species diversity help us interpret geographical ranges and predict other likely locations.

THE VALUE OF LARGE PERMANENT PLOTS IN SYSTEMATIC RESEARCH: WHAT IS A SPECIES IN HYPERDIVERSE RAIN FOREST?

The large tree demography plots of the CTFS collaboration provide samples of about half of a local flora. Plants representing the ontogenetic changes of the whole life history are present in all but those with populations of the least density and, as they are tagged and easily accessible, they are ideal for observation and description, and for research on reproductive biology and breeding systems. The thousands of individuals thus permanently tagged are initially identified by characters which are often underused by herbarium taxonomists: bark morphology and colour, exudates and inner bark character and, most reliably, fallen leaf. All species are represented by leafy twig vouchers in field herbaria. There is no tree species within one forest or its region which cannot be first identified by the characters offered by its fallen leaf, though corroboration by collection of fertile material, whenever available, is ultimately definitive. Compared with the neotropics, the tree flora of our region is well known, and only a few species new to science will be discovered from the plots (Baker *et al.*, 2017). However, coordination in the attainment of consistent identifications across the regional network is still in its infancy, and could stimulate the strengthening of regional research collaboration which can yield much important new science.

The occurrence of series of species within a single genus sharing the same community is well known, for example among eastern American red oaks, or temperate chalk grassland hawkweeds, but the sheer number of such genera within individual hyperdiverse tropical rain forests is unique. This poses questions of what these entities, often differing in apparently trivial, non-adaptive characters, really are. This is a crucial issue for the monographer and those researching the early stages of diversification and evolution.

Genera in many families contribute such series of species sharing the same habitat in species-diverse forests (including some temperate forests). These species may share

almost identical flowers and fruits, and differ in apparently trivial characters of leaf or tomentum, but which are often remarkably consistent. Some species manifest morphologically distinct forms, which might prove to merit separate species status, especially on exceptional substrates including ultramafics, and on rhyolite as in the 15 0.4-ha plots in the Ulu Arip, Balingian (now sadly degraded) which, on the evidence of ecological vouchers (now in the Harvard herbaria), include several rare entities. Yet morphologically intermediate populations which might indicate introgressive hybridisation appear to be rare. Kamiya *et al.* (2011), using molecular evidence, found abundant hybrid seedlings among the four co-occurring red meranti (*Shorea* section *Mutica*) species in and around the Bukit Timah forest CTFS plot, Singapore. However, there were few reproductively mature hybrid trees – and almost all were F_1 generation!

A central question arises for both systematists and ecologists: are hybrids less fit because they suffer some (internal) genetic malfunction? Or because they are less competitive than their parent species? If it is the latter then how can it be that the species' juveniles are so consistently more competitive than those of their hybrids? Large demographic plots provide the arena in which this question can be resolved.

In North America, red oaks (*Quercus* subgenus *Erythrobalanus* Trel.) dominated the canopy of the vast temperate broad-leaf forest that stretched down the east coast, virtually all of which was felled for agriculture over the last two centuries. Within local landscapes, up to five of these species may co-occur in overlapping sequence from ridge to valley alluvium. Regenerating after the land was left to fallow after farmers migrated west to better soils, or into industry 150 years ago, many of the first trees proved to be hybrids. But these declined in number as the new forest matured – presumably because hybrid individuals proved less fit. Continued timber harvesting may be expected to gradually increase the proportion of hybrid trees that persist. What then will the fate of our co-occurring red meranti and other congeneric species series be in continuously logged tropical rain forests?

Another question for systematists and ecologists to consider, and one for which large tree demography plots provide ideal research sites, is why adventive embryony (apomixis through asexual seed formation) is so widespread among biodiverse tropical rain forest tree species?

Temperate apomictic plant species (both herbs and trees) are mostly pioneer species. Rapid colonisation by seedlings, which are all equally highly pre-adapted to these open sites free of competitors, is obviously advantageous. These temperate apomictic taxa form allopatric congeneric series but readily hybridise where ranges overlap, forming swarms of 'microspecies'. Tropical trees are plants of the mature phase in the dynamic cycle of old-growth forests, and apparently rarely hybridise (or hybrids rarely reproduce). Apomixis results in seedlings genetically identical to the mother tree – that is, swarms of genetically identical seedlings. How can that be advantageous in the highly competitive environment of a species-rich tropical rain forest? The CTFS plots provide the numbered and censused population samples, of co-occurring congeneric and other species and await study by systematists.

WHY ARE SO MANY PLOTS CONCENTRATED IN A FEW REGIONS?

The answer is simple: absence of institutions and secure employment for long-term research. But now, with so many emerging universities throughout Malesia, large tree demography plots, established in remaining securely managed primary forest refuges, give superb opportunities for integrated ecological, systematic and evolutionary biological instruction and research. From the research perspective alone, suitable sites for plots are still awaited in a majority of habitats, notably ecological islands of kerangas, and limestone karst, ophiolite (ultramafic), rhyolite (acid volcanic) and basalt (base-rich) substrates, and lower and upper montane forests. And representation of major forest regions, namely Sumatra, Wallacea and New Guinea, where one lowland plot is already established in Papua, could yield important novel biogeographic information on the history and evolution of both communities and taxa, besides providing the basis for a scientifically rigorous plan for long-term biodiversity conservation. And who knows? Research in such secure scientific refuges could even point a way to restoration and sustainable management of degraded forests by their rightful owners, the local inhabitants.

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