

A VIEW FROM THE TREES

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ABSTRACT. — Plant species are highly niche-specific, and with short dispersal distances, therefore can survive effectively permanently in quite small areas if pollen and seed dispersers are conserved. Plant diversity is compromised by logging, even selective. Plant species diversity and endemism are broadly correlated with that of overall biodiversity, vertebrate diversity not. Biodiversity conservation therefore requires strict protection of sufficient small areas representative of all habitats, including principal soils, and policies to ensure connectivity of similar including secondary vegetation corridors between them and large conservation areas.

KEY WORDS. — plant diversity, overall biodiversity, rain forest, large versus small reserves, conservation priorities

INTRODUCTION

It was a surprise for me, yet a pleasure to be invited to contribute to this *festsschrift* in honour of our leading vertebrate biologist and field naturalist of Far Eastern tropical forests. And also, to receive that invitation from Singapore, because that city is most known to me on account of its prescient conservation of a slip of indigenous forest near its centre, the Bukit Timah Nature Reserve. That 163 ha slip contains a mere 67 ha of remaining ‘primary’, that is to say unlogged, forest. With that at Mukah Head, Penang, currently under legislation, it is the only formally conserved example of primary Coastal Hill Dipterocarp forest, a widespread forest type around the Sunda Islands, yet in existence.

Plant communities can survive in surprisingly small areas.

— One 2-ha plot within that forest, established by scientists from the National University of Singapore and the Center for Tropical Forest Science collaborative network of the Smithsonian Institution, includes 347 tree species of at least 1 cm diameter at breast height (Ercelawn, 1997; LaFrankie et al., 2005), while a recent census of canopy individuals revealed further new species records from Singapore. Nor is there strong evidence of climax species in decline, though the wild nutmegs (Myristicaceae), whose seeds are dispersed by hornbills and imperial pigeons now lost (though pied hornbills have recolonised Singapore and may visit), show some sign (seedling presence is undocumented). Squirrels do remain, while the cantankerous long-tailed macaque appears to have taken over the duties of others. A 52-ha plot in mixed dipterocarp forest on the coastal hills of the Lambir National Park, Sarawak, on heterogeneous topography and

geology, contains a staggering 1192 tree species, comparable to the richest forests of the neotropics. That represents more than half the tree species known from Lambir and about one quarter of the tree flora of northern Borneo (Ashton, 2005), itself the richest in the Old World. But here, hunting to extinction of many dispersers has led to worrying changes in tree demography (Harrison, 2011; Harrison et al., 2013).

Conservation policy is dominated by the opinions of vertebrate ecologists and naturalists, not surprisingly as vertebrates attract the most public and political interest. Vertebrates, particularly mammals and birds, require continuing sources of food, which must at least periodically be of sufficient quantity and quality to permit them to reproduce; while many require specific nesting sites. Although most vary in abundance with the productivity of the forest, there is little evidence for any consistent qualitative faunistic difference between lowland types of rain forest in perhumid Sundaland, the peat swamps excepted. Yet nearby mixed dipterocarp forests on different substrates and soils may consistently differ by one third of their species (Ashton, 1997). Of course, whereas vertebrates are motile, the only stages at which plants are motile are as pollen or seed, both of which are more or less restricted in rainforests: Whereas most animals require large areas for sustainment of stable breeding populations, it would appear that plants, even trees, can survive on much less (Ashton, 2010).

Plant communities are habitat-specific. — Trees not only provide the structure which animals inhabit and exploit. The unique combination of physical and chemical attributes by which each tree species defends itself provides the arena

in which other organisms, directly or indirectly, compete to exploit them. No rainforest vertebrate is dependent upon a single tree species for its sustenance or nesting site. Fig wasp species are the exception among arthropods, perhaps unique, that are dependent on single tree species, though others may be restricted to higher tree taxa or taxa sharing similar chemistry. Such appears to be the case also with mycorrhizal fungal symbionts. But the growing evidence of density-dependent patterns of juvenile mortality among populations of individual tree species' infers that there are species-specific predators, or more likely pathogens. At a general level, even soil fauna and saprophytic fungi differ between forest soils, in part on account of the litter chemistry resulting from their prevailing tree flora.

The composition and diversity of the tree flora can therefore be seen to be a proxy for biodiversity overall. It will, to a substantial extent, vary in a parallel way while much of it may require similar areas for its sustainment in the short to medium term. Ultimately, of course and importantly, many tropical tree species depend on vertebrates for seed dispersal, and some for cross-pollination, therefore the large reserves upon which many vertebrates depend are also necessary. The underlying drivers, of patterns of tree species composition and diversity, are beginning to be understood in lowland Sunda forests. This is thanks in part to studies of small forestry plots in Malaysia, and now in part to the opportunities provided by the regional network of landscape-scale plots of the CTFS collaboration. In it, tree populations and whole forest samples are mapped, identified, measured and re-censused according to a rigorously applied standard procedure.

The tree species *composition* of our rainforests is influenced by both soil water economy and, more particularly, by soil nutrient levels (Potts et al., 2002). Soil water retention is influenced by soil clay content and friability, and by topography. Both are broadly correlated with soil nutrient levels, for nutrients are ultimately derived from clay; while drying of the soil surface impedes litter decomposition which leads to build-up of comminuted litter as acid-reacting raw humus, low in nutrient ions available for uptake by roots. Teasing apart of the relative influence of water and nutrients on tree performance, although amenable to pot experiment, is extraordinarily difficult to infer from empirical study in the forest. The incidence of periodic, usually ENSO-induced drought on selective mortality has as yet not been rigorously examined, although some species in low population densities have been found to increase in following years (Potts, 2003). The distinctive species composition of *kerangas* forest on low nutrient humic tropical podsoles has long been known (Whitmore, 1984; Richards, 1996). Its similarity to the flora of inner peat swamps implies that it is the similar low available nutrient and acidity of their raw humus surface soils that is the cause; although the increase of that similarity towards the peat dome, also subject, as is *kerangas*, to occasional exceptional drought implies that soil water conditions are also influential.

Species composition within upland rainforests is nevertheless closely correlated with total mineral soil nutrient levels,

with major ecotones between podsoles and zonal yellow-red soils, and within the latter between more strongly leached soils bearing surface raw humus, and those lacking it. The influence of soils nutrients has been found to override that of distance between forests—presumably caused by the random effect of limited seed dispersal, though forests restricted by an ancient river valley in Sarawak remain distinct, similar soils notwithstanding (Fig. 1; Potts et al., 2002).

The close correlation between tree species composition and soils results in a correlation of composition with geology at the landscape scale. This provides a crucial tool for biodiversity conservation planning: Areas of similar surface lithology share a similar tree flora, therefore by implication biodiversity, substantially so even to the scale of all Sundaland although regional differences do exist. The pattern of composition variation in relation to mineral soil nutrient levels is universal, even if the flora as a whole changes according to history, climate (notably rainfall seasonality), and other factors. There is growing evidence that a similar pattern exists in montane forests (Aiba et al., 1999, 2006). Importantly, areas of exceptional surface lithology identify areas of likely exceptional diversity composition. These areas, notably of karst limestone and ultramafics, may most often occur as small habitat islands, yet they retain distinctive floras rich in rare species.

But where are the forests *richest* in tree species diversity? In Asia, as in the neotropics, community (α), species diversity reaches its highest levels in wet lowland climates lacking an annual period in which rainfall falls below expected evapotranspiration (e.g., Condit et al., 2004). Within one climate, tree species α diversity is low on lowest nutrient peats and podsoles, steeply rises to a peak on relatively low nutrient yellow-red soils at the humic-non humic (humult versus udult) ecotone, then—counterintuitively—descends on soils of with increasing mineral soil nutrient levels. But highest nutrient soils support the highest vertebrate biomass and species diversity, especially in famine years.

David Tilman first proposed an explanation for a peaked pattern in plant species diversity (Tilman, 1982), which is consistent with what occurs in our lowland rainforests (Ashton, 1977). Relatively few species survive on low nutrient (or droughty) soils. More importantly, these offer insufficient independent variability in nutrients and water for competition to lead to much species' survival through niche differentiation. With increasing nutrient availability, the number of coexisting species populations therefore increases. The range of species' maximum growth rates also increases (Tilman, 1982; Ashton & Hall, 1992). As a result, the fastest growing species increasingly overgrow others and exclude light from them, decreasing the number of subcanopy species which can survive and thereby reducing α diversity.

This pattern is therefore partly caused by variation in forest dynamics and canopy structure. Variation in dynamics, therefore canopy structure and subcanopy light climate, is also caused by prevailing causes of disturbance: Wind, landslip, drought, and lightning each create gaps in the

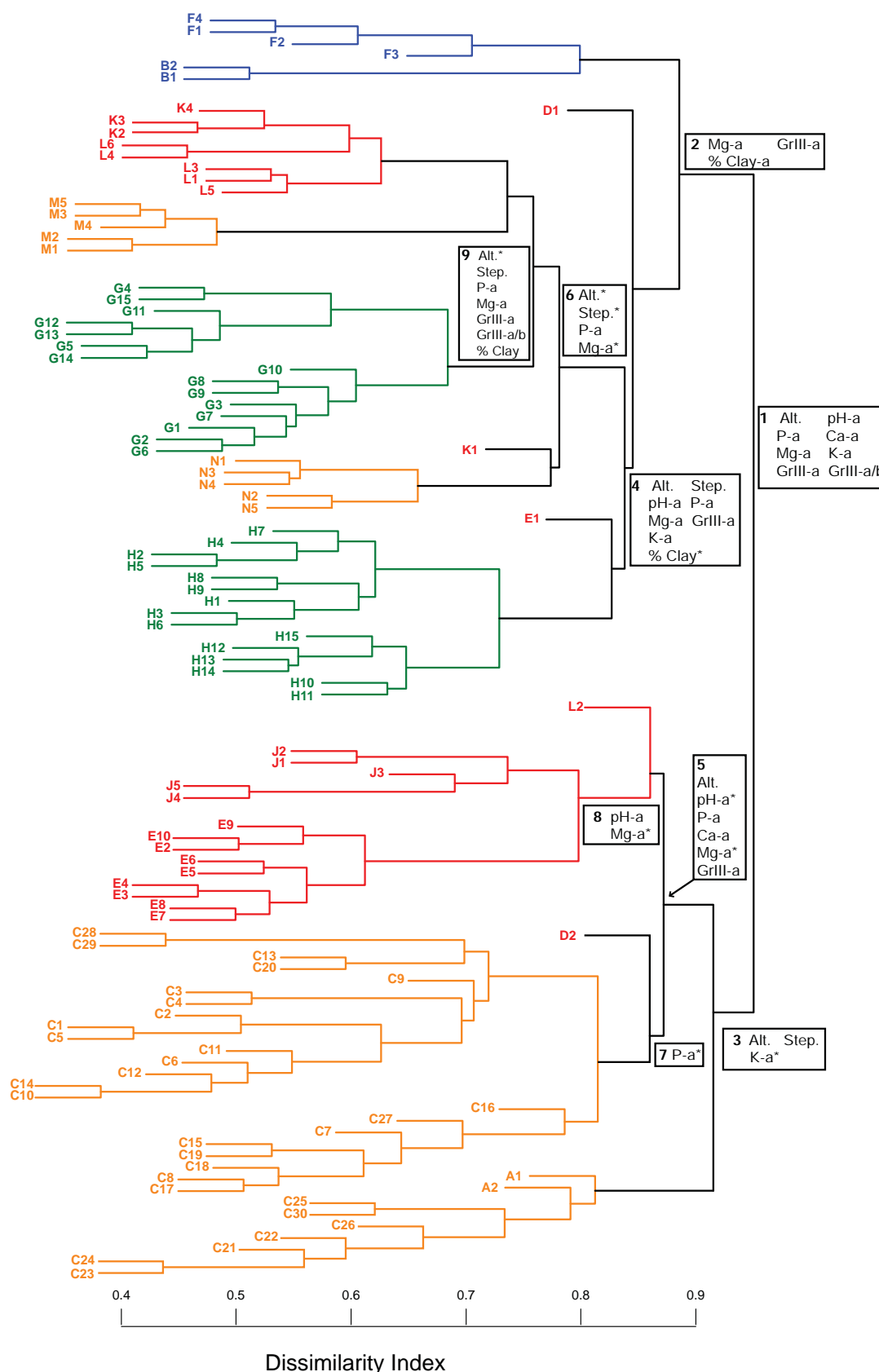


Fig. 1. Classification dendrogram of 105, 0.6 ha, Sarawak plots in mixed dipterocarp forest. Correlated topography (step=steep), and soils mean HCl-extractable Group III elements (Fe, Al), and nutrient ions at 20–30 cm indicated: colours indicate geographical locations within Sarawak: blue, south-west; green, west central; yellow, east central; red, north-east (see fig. 3.9). With the exception of plots from sites west of the Lupar river (B and F), the dendrogram classifies sites by habitat rather than geography, though plots tend to remain grouped within their sites. Sites: A1, base of Hose Mountains, Ulu Mujong, Balleh; A2, Carapa Pila, Ulu Mujong; B, Gng Santubong; C, Bt Mersing, Anap; D, Ulu Dapoi, Tinjar; E, Bok Tisam forest, lower Tinjar; F, Bako N.P., G, By Iju, Arip, Balingian; H, Bt Raya, Kapit, Rejang; J, Ulu Bakong, Tinjar; K, Lambir N.P., north slope; L, Lambir N.P., south slope; M, Nyabau forest, Bintulu; N, Segam forest, Bintulu (after Potts et al., 2002).

canopy of differing severity and size. Landslips alone remove both juveniles and seed, offering a *tabula rasa* for regeneration by immigrant seed dispersal. Wind-throw excludes more established regeneration through sudden descent of obliterating litter than do drought and lightning following which leaves, twigs, then branches and trunks fall in sequence, resulting in greater juvenile survivorship. Topography and degree of soil aeration (and therefore rooting depth), influence the relative frequency of differing causes of canopy mortality. Prevailing frequency, extent, and mode of canopy mortality therefore vary consistently with soils and topography, at both local and landscape scale and in correlation with both species composition and diversity. Joseph Connell, in studies of tidal zonation and coral reefs, proposed an explanatory *intermediate disturbance hypothesis* which, again, is consistent with patterns observed in our rainforests (Connell, 1971).

Forests in which rooting is deep and maximum growth rates high have a relatively continuous and dense canopy. In the Sunda region, this canopy is high above the ground, a nearly continuous phalanx of emergent dipterocarps. Gaps may be of varying size, but relatively few in number. The seedling light environment is one of deep shade occasionally pierced by patches of sunlight. All tree guilds, pioneers, successional and climax species, understorey and emergent, are poor in species, while the ‘main canopy’ comprising those species which fill the interstices between the dipterocarps and Caesalpiniaceae, uniquely ectotrophic mycorrhizal families which comprise the Far Eastern truly emergent canopy, are particularly poor (Ashton, 2008). Where these forests of friable clay upland soils extend to seasonal riparian swamps, and the soil is periodically waterlogged so rooting shallow, the tree flora differs little from that on similar soils but the forest, being wind-prone, is mostly successional and it is the pioneers which dominate and overall species richness is even lower. At the opposite edaphic extreme, on freely draining podsols in which the sole source of nutrients (other than those stored in the raw humus) is rainwater, root systems form a densely intertwined mat in the surface organic horizon. The forest, drought-prone, is short, with few if any emergents, while wind-throw is rare and gaps small. The pioneer guild is absent, and the emergent represented at best by a handful of species. The canopy consists of genera which occupy the main canopy in forests with a well developed emergent stratum, and is continuous; but leaves are small, often held at an angle to sunlight, allowing penetration of diffuse but rather uniform light to the understorey. The main canopy guild is most species-diverse, albeit still relatively poor.

It is the forest on intermediate soils which experiences the greatest diversity of gap sizes, and at intermediate frequencies. Light conditions near the floor are most diverse, and the emergent canopy clumped, allowing space between for a rich main canopy tree flora. All guilds are more species-diverse in these forests than in others, providing another explanation for the peak in species richness at intermediate forest structural and dynamic, as well as nutrient soil levels (Fig. 2).

The high species α diversity of all tree guilds in these forests is also consistent with predictions from island biogeography theory: In forests with the most secure rooting, the mature canopy is an ocean within which pioneer and successional stages form an archipelago of islands whose mean size is small, therefore species diversity low. On floodplains, and landslip-prone slopes, it is successional stages and species guilds which occupy the ocean, and the mature forest and climax species which are reduced to isolated islands, poorest in species. But in forests of intermediate rooting security, there is greater connectedness between successional islands; all guilds approach a more equal area and each reaches its maximum diversity, although it is the main canopy guild which is most diverse in our forests, and the pioneer the least.

Plant community diversity is affected by logging. — It would be tempting to suggest that selective logging, by increasing the diversity and frequency of gaps especially in those with densest timber stands, might actually increase their species diversity; but it is the opposite, for several reasons. First, the only source of *additional* species at landscape scale is from exotic immigrants such as plantation species, or through speciation which, for trees, takes millions of years. Second, because the dynamic and structural, notably canopy characteristics within individual forest habitats have been stable ever since the last climate change, 10,000 years ago or often beyond, any change in them will bring about changes in area which will, even if the first felling cycle is carefully executed, inevitably lead to decline in the species diversity of those guilds which experience a decline in area and connectedness. In most rainforest communities these are the climax canopy guilds, which in Asian primary rainforests are the most diverse. Thirdly, silviculturists have striven to shorten the length of the felling cycle, essential if discount rates on the growing timber stand are not to overtake anticipated returns. The old Malayan Uniform shelterwood system had a felling cycle realistically estimated at 70 years, too long on financial criteria and favouring successional light hardwood species against both climax heavy hardwoods and pioneers. The current selective systems, based on a minimum felling diameter, reduce the cycle—optimistically—to about 40 years. That results in felling individuals of many climax species before they have started to reproduce, or have reproduced sufficiently to sustain their populations.

Species-diverse rainforests are particularly rich in ‘rare’ species, that is, those in exceptionally low population densities. No evidence has yet arisen to imply that any suffer Allee effects, that is, reduced fertility resulting from restricted cross-pollination. Unlike vertebrates and most animals, most rainforest trees bear bisexual flowers and are at least partially self-compatible. Many subcanopy genera nevertheless are dioecious, that is their individuals are unisexual; but many of these (and others) have been found to produce embryos asexually, therefore genetically identical to the mother tree (through apomixis by adventive embryony). Decline in population densities consequent on logging may not therefore be initially detectable, but will inevitably reduce genetic diversity therefore competitiveness.

SUMMARY

Rainforest tree community composition and richness, and therefore by inference that of overall biodiversity, differ in important respects from those attributes that must guide conservation planning:

- They are highly habitat-specific.
- They can be sustained, in the medium term in relatively small areas, but in the long will require connection to areas sufficiently large to sustain populations of dispersing vertebrates.
- Nevertheless, vertebrates are crucial for seed dispersal of many species and are hunted to extinction, or fail to survive famine years, in small reserves while pollinators and other motile organisms are also subject to increased likelihood of rapid extinction.

- Tree species diversity, their relative abundance, and the genetic structure of populations of most are negatively affected by logging.

Criteria for conservation of vertebrate fauna therefore provide an inadequate basis for biodiversity conservation. But solutions are feasible, although it is not a moment too soon to implement them!

TOWARDS AN OPTIMAL CONSERVATION POLICY

We are already in the bottleneck of a global extinction event on an unprecedented scale in the palaeontological record: The most biodiverse rainforests in the Old World are in the Sunda lowlands, on those very yellow-red zonal soils favoured by

105 MDF Plots in Sarawak : Diversity and Soil Nutrients

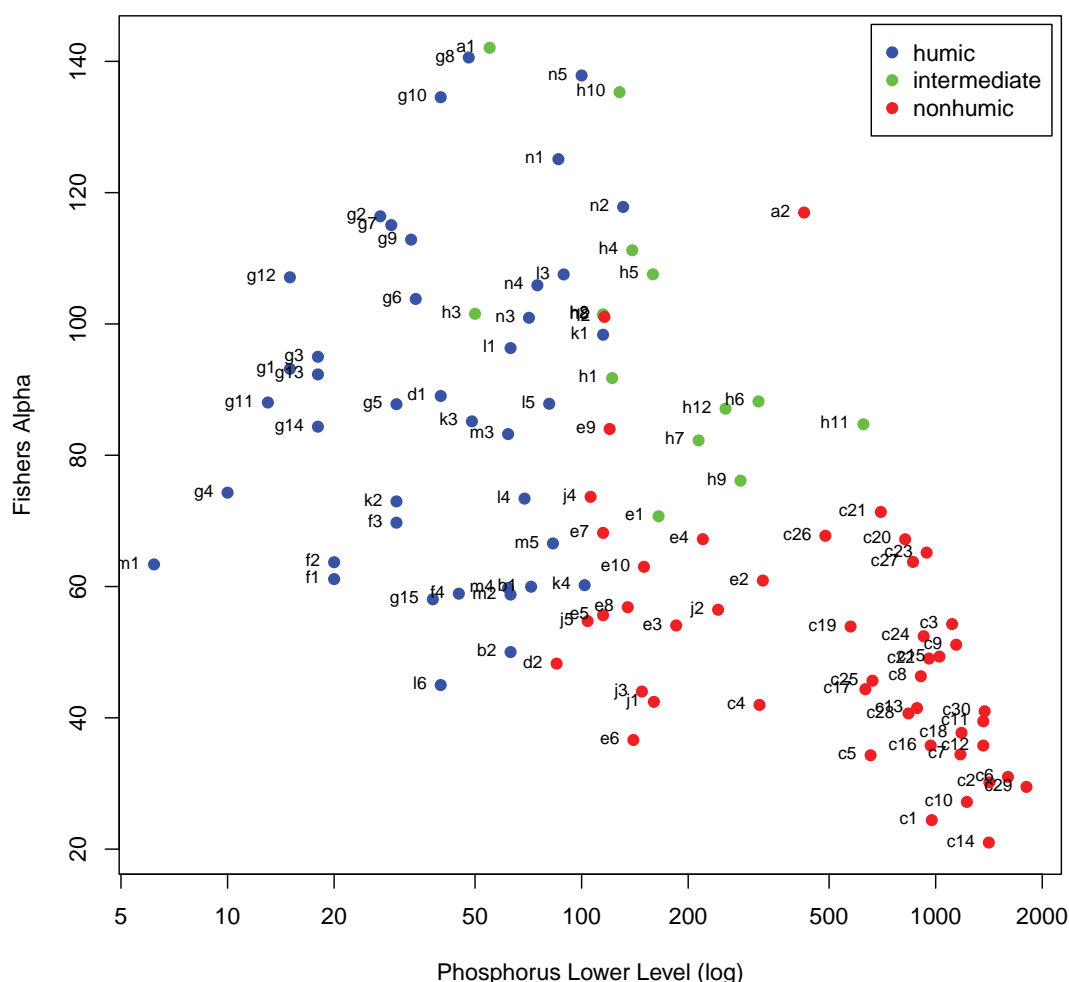


Fig. 2. The relationship between species diversity (Fisher's α) in 105, 0.6 ha Sarawak plots (trees >9.7 cm dbh) and total conc. HCl extractable phosphorus in the mineral soil at 70–80 cm. The decline at high nutrient concentrations is correlated with increasing stand basal area and emergent canopy density (see text). Although maximum α values show a peaked distribution along the nutrient gradient, there is much variation beneath them which is due to variation through gap succession within the communities. The lowest values correlate both with landslips, and with mature stands where emergents can be locally densely clumped in all communities (P. Hall).

oil palm, and formerly rubber plantations. The forests among the richest in endemic species, on the coastal hills and sandy soils, have with few exceptions been degraded by logging. Especially, the raw humus soil surface, seed-bed for their specialised flora, has been eroded by vehicles, exposure and sometimes fire. Following deforestation and cultivation, these soils suffer irreversible leaching, and a different flora succeeds on them, witness regeneration adjacent to Bukit Timah, and in the Singapore reservoir catchments (Shono et al., 2006). Only patches of lowland mixed dipterocarp forests now remain, in national parks and research forests, and in some Peninsular Malaysian Virgin Jungle Reserves. These latter were established 50 years ago on an Indian Forest Service precedent, to act as control to monitor the success of silvicultural prescriptions. Now, they act as an invaluable, albeit only partially representative, network of sanctuaries imbedded in surviving production forest reserves. What priorities must we adopt from the limited options remaining?

How big is big enough? — As a rule of thumb, 200 reproductive individuals sufficiently close to interbreed should be sufficient to maintain genetic diversity. The large plots of the CTFS network aim to capture at least 200 individuals of at least half the species within them. In this they succeed, but the vast majority of these are pre-reproductive juveniles. To capture that number of reproductives, at least 500 ha would be required. But only the commoner rainforest tree species likely attain that in nature! The majority of species which are confined to habitats that form ecological islands—and these include some of our most biodiverse forests such as those of the Lambir and Andulau coastal hills of northwest Borneo—must survive for many generations in far smaller populations. The minimum viable size for tree populations is therefore small, and Bukit Timah acts as an impressive testimony, although time and further research may prove otherwise. But larger is clearly to be preferred.

Few big or many small reserves? — The very large conservation areas, such as are advocated by vertebrate ecologists for the Heart of Borneo project, suit all of us for they include landscape-scale habitat diversity, large breeding populations, and well-conserved disperser populations. But they suffer two crucial disadvantages: They rarely include some of the habitats richest in endemics and sometimes in overall species diversity, notably the coastal hills, and lowland ultramafics and karst limestone; and these habitats are either confined to ecological islands in nature or confined now by forest conversion and urbanisation. These are not alternatives: *Both* must be conserved; remaining habitat islands are the most critically endangered now. The model of the Virgin Jungle Reserves (VJRs) urgently needs extension (Potts et al., 2007).

Separate conservation and production forests, or conservation set-asides within production forests? — The Heart of Borneo and other similar conservation programmes accept that logging within their designated areas is inevitable. Acceptance of logging in the past, or inability to prevent it, led to the demise of the Philippine park network, is leading to extensive degradation in that at Indonesia, especially in

the lowlands as at Kutei and Gunung Palung National Parks, and has made serious inroads into the lowland forests of Similajau and Gunung Gading National Parks in Sarawak. Logging within areas legislated for plant, especially tree species conservation will prove disastrous for the future of biodiversity. But national park networks can never be sufficient to conserve all habitats, all communities. Given an alternative of setting aside inviolate VJRs outside or within production forest reserves, those within are clearly preferable on ecological grounds. That is because surrounding production forest can sustain disperser populations and act as a source for immigration of species lost by chance, while the destructive impact of changes in local climate and other disturbance along the margins is avoided. Further, the setting aside of VJRs in production forests is the economically optimal alternative (Potts & Vincent, 2007, 2008).

Connectivity. — Conservation of forest corridors between conservation areas, particularly if small, facilitates movement of motile organisms and enhances the size of their breeding populations. It therefore assists the sustainment of dispersers. But it has no other short-term impact on the fate of sessile organisms. Further, the practical options for maintaining such corridors are effectively mostly restricted to riparian forests, where they serve the additional function of stabilising river banks. But riparian forests represent a limited range of habitats and forest communities, mostly of quite low species diversity.

The problem of hunting. — Hunting of wildlife, often to local extinction, by concession employees and others who take advantage of easier access within concessions, and lack of control within national parks, is proving disastrous for the medium term survival tree species as much as the wildlife itself. The only viable solution is to gain the participation of the communities involved in hunting wildlife also in its conservation. That requires that they remain major beneficiaries. Community participation in the ecotourism industry has been promoted in India and elsewhere, but offers limited benefits, especially in remote parks and where wildlife is—as so often—difficult for the inexperienced observer to see. Investment should also be made in providing both incentive and training, leading to conservation of wildlife both for the forest and the community, with well-regulated hunting licenses and seasons. Local leadership is essential.

The living dead. — Lillian Chua, Saw Leng Guan and their colleagues at the Forest Research Institute Malaysia, Kepong, several years ago initiated a scheme to identify isolated forest stands of exceptional conservation importance, and to conserve them by negotiation with their owners. Dipterocarps, being the best known of trees and generally easy to identify in the field, were used as proxy for overall endemism. Search for surviving populations, even individuals, of exceptionally local species led to notable success, both in locating other rare species that shared the same habitat and persuading owners to retain the forest patches involved. Similar initiatives have now been taken up in Sarawak under Julia Sang of the Forestry Corporation, and Yayan Wahyu Kusuma at Kebun Raya Indonesia. Both have achieved remarkable results,

relocating small numbers of all species sought; and many species in the case of Sang, whose Sarawak forests were the richest of all in dipterocarps and many other families. But these residual pockets are often no more than geriatric units, of individuals hardly representing breeding populations, set in an environment hostile to their regeneration: what Janzen has called the living dead. The priority must be to revisit during mast years, collect seeds for botanic gardens, and disperse to these internationally. That is their only hope.

Towards the optimal solution. — No conservation plan for a forest will succeed without the participation and support of the local community, a project in which local NGOs can play a pivotal and continuing role. But the forest or parks service must remain enthusiastic participants.

- A continuing involvement of nature societies, and interested volunteers and professionals, is invaluable provided they are sensitive to local interests and retain the support of the community.
- Both big and small conservation areas have essential roles to play, not one or the other.
- National parks and nature reserves should never be logged.
- Inviolable ‘virgin jungle reserves’ within production forests, small but optimally 200–500 hectares and including the diversity of habitats, must be an essential goal of regional conservation plans.
- The protection of riparian fringes, which serve as corridors for wildlife, is insufficiently enforced.

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