What's so special about Asian tropical forests?

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Tropical forests developed in isolation in five main areas during the Tertiary: Asia, New Guinea, Africa, Madagascar and the Neotropics. Asian forests share taxa with New Guinea and Africa, but there are also unique features. Most emphasis has been on the dominance of lowland moist forests by the Dipterocarpaceae, but the importance of the Fagaceae in lowland forests is also unique. Among the vertebrates, gibbons, tree shrews, forest rhinoceroses and lowland bears are unique to Asia, as is the diversity of squirrels, babblers and gliding vertebrates. Honeybees are shared with Africa, but only Asian forests support several coexisting species.

ENVIRONMENTS suitable for the growth of tropical forests occur in a broad band around the equator. In contrast to the boreal forest zone, however, which forms an almost continuous band around the northern hemisphere, tropical forest environments occur as isolated areas that are separated from each other by marine or desert barriers. Some of these barriers are relatively permeable and/or relatively recent, but the complex geological history of the tropical land masses has maintained the isolation of five major tropical forest regions (and several additional minor ones) from each other for tens of millions of years[1]. In effect, these five regions – Asia, Africa, New Guinea, Madagascar and the Neotropics – can be seen as five, more or less independent, evolutionary responses to the tropical forest environment[1,2]. The objective of this paper is to identify the unique ecological features of one of these regions – tropical Asia.

Tropical Asia as a biogeographical region

Most major biogeographical regions coincide, more or less, with continents, each with a stable geological core that has existed for hundreds of millions of years. Tropical Asia, however, is not a continent, but more like a hastily assembled and rather ill-fitting jig-saw puzzle, made from pieces rifted off the margins of the southern supercontinent of Gondwana between 350 and 130 million years ago. These continental fragments drifted northwards and were progressively amalgamated to form modern tropical Asia. By the end of the Cretaceous, 65 million years ago, the

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core of tropical East Asia had been formed, but the largest Gondwanic fragment, India, was still heading north, at 21 cm/year. The timing of India's collision with Eurasia is uncertain: the most widely accepted date is 55 million years ago, but others have argued for a much later date of only 34 million years ago[3]. Tropical Asia is thus considerably younger, at least in its current configuration, than most of the other tropical biogeographical regions.

Fossil evidence shows that each fragment carried its own characteristic flora and fauna when it separated from Gondwana. As far as we know, however, no modern lineages are old enough to have travelled north on the major fragments that make up the east of the region, although it is possible that one or more of the micro-continental fragments that accreted onto eastern Sulawesi from the Miocene to Pleistocene were above sea-level long enough to have acted as rafts or stepping-stones for plants and animals of Australian affinity[4]. The contribution of India's Gondwanic heritage to the modern biota of the region is still debated. Divergence times derived from dated molecular phylogenies do not always fit the current fragmentation timetable, implying either transoceanic dispersal or terrestrial connections that persisted longer than current geological models assume[5], but there are also examples, particularly among the freshwater fish and amphibians, where the phylogenies are consistent with our current understanding of the geological history[6]. It must also be remembered that the end-Cretaceous (K/T) global extinction episode occurred while India was in motion and the volcanic eruptions that formed the Deccan Traps flooded half of modern India with lava at the same time.

It might be expected that tropical Asia's complex tectonic origins, its broad land border with the rest of Eurasia, and its rather vague eastern limits would have reduced the biogeographical distinctiveness of the region. Not so. It is true that plant- and animal-biogeographers have usually drawn different boundaries to the region, with the botanists often including New Guinea and the western Pacific, while the zoogeographic region stops at Wallace's Line[7], but the common core of the region shows a high degree of similarity at the generic and family levels in both the flora and fauna. This is particularly true of the closed forest communities, which are the subject of this paper. Lowland rainforests as far apart as Sinharaja, Sri Lanka (6°N,80°E), Xishuangbanna, China (22°N,102°E), and Lambir Hills, Sarawak (4°N,114°E) would not look out of place adjacent to each other, but are very different from rainforests in similar climates in New Guinea or Africa.

These differences between regions have a variety of origins, which cannot always be distinguished[2]. The simplest explanation is that they reflect differences between regions in the physical environment. Given the vast range of environments present in tropical Asia, it is hard to believe that they are all different from elsewhere, but differences in the predominant environments – climates or soil types, for example – could, over evolutionary time, influence the composition of the species pool from which local communities are assembled. One environmental feature that might qualify as an Asian speciality is the strong influence of the El Niño-Southern Oscillation (ENSO) and, in the west of the region, the Indian Ocean Dipole (IOD), on interannual variation in rainfall. ENSO influences climates across the tropics, but the effects appear to be both stronger and more widespread in tropical Asia than elsewhere[8–10]. If, as has been suggested, both the ENSO system and the otherwise everwet climates of the Sunda region have been in place since the early Miocene collision between the Australian and Asian plates[11], then there have been 20 million years for the regional biota to adapt. The alternative to environmental explanations of Asian uniqueness is that the differences largely reflect the biogeographic history of the region: the bridges and barriers that allowed some taxa to disperse to or from tropical Asia and others not to, and the past environmental changes that favoured the proliferation of certain taxa and the elimination of others.

Vascular plants

Dipterocarp dominance

The extraordinary combination of diversity and dominance by the family Dipterocarpaceae in the canopy of lowland rainforests inevitably comes top of any list of the botanical specialities of tropical Asia. There is no equivalent elsewhere in the tropics of a single, highly diverse, family dominating the large-tree component of forests over such large areas. Monodominance at the family level is elsewhere synonymous with dominance by one or a few species, a situation that occurs in Asian lowland dipterocarp forests only on extreme soils (e.g. the *Shorea albida* peat swamp forests of Borneo) or near their latitudinal margins (e.g. the *Shorea chinensis* forests in Xishuangbanna, SE China). At the other extreme, the 52 ha research plot at Lambir, Sarawak, supports 88 species of dipterocarp trees[12].

Rainforest dipterocarps have been the focus of a great deal of research effort, but we are still unable to answer some fundamental questions, such as: how and why did this pantropical family come to dominate lowland rainforest canopies in tropical Asia? And, what are the consequences of this dominance for other organisms? Some major features of rainforest dipterocarp biology appear to form a package of interacting traits that may give the family a competitive edge over other tree taxa, including their great height, their large, wind-dispersed seeds, their habit of synchronous mast-fruiting at irregular multi-year intervals[13,14], and, perhaps, their ectomycorrhizal condition[15]. But even in the rainforest there are subcanopy dipterocarps, wingless fruits and annual fruiting, while other key ecological characters, such as pollination[16], are so diverse as to defy generalization. There are many ways to be a rainforest dipterocarp.

Some of the consequences of dipterocarp dominance are clear. Dipterocarp leaves appear, in general, to be ignored by leaf-eating canopy vertebrates and this may contribute to the generally low biomass of folivorous vertebrates in tropical Asian forests. Furthermore, the fact that such a large proportion of the forest biomass produces flowers and fruits only at irregular, multi-year intervals must depress the average population densities of numerous flower- and seed-dependent species, in addition to the major seed predators that this strategy is apparently targeted at. But it is by no means only dipterocarps that mass flower and mast fruit: so do a huge range of non-dipterocarp species, from canopy trees to climbers, shrubs, herbs and epiphytes. Have these species somehow become 'entrained' by the phenology of the dipterocarps, or have the similar pressures produced the same answer independently in many species? Is the community-level supra-annual reproductive phenology, and all its downstream impacts on other rainforest organisms, a consequence of dipterocarp dominance or something that would have developed anyway in this physical environment, perhaps as a consequence of the pervasive influence of ENSO?

The dipterocarps also dominate in vast areas of dry deciduous dipterocarp forest in continental Southeast Asia and the sal forest (*Shorea robusta*) of northern India, Nepal and Bangladesh. The trait package that may help the family in lowland rainforest is of no apparent use here, where drought, fire and poor soils are the main challenges, and it is not obvious what shared aspect of 'dipterocarpness' gives the family an edge in such a different environment.

Fagaceae

Peter Ashton first pointed out the many similarities between the Fagaceae and the dipterocarps and stated that the complementary altitudinal distribution of the families in tropical Asia was 'suggestive of interfamilial competitive exclusion'[13]. Note, however, that there are also many Fagaceae growing alongside dipterocarps in the lowlands, with 21 species in the Lambir plot and 15 at Pasoh[12]. Both families are ectomycorrhizal, both have large, poorly dispersed, one-seeded fruits, and both have desiccation-sensitive (recalcitrant), non-dormant seeds. Both mast, although not, apparently, in the same years. Both families thin out to the east of Wallace's Line, but the Fagaceae

have also not made it to southern India or Sri Lanka, while a few clades have been spectacularly successful north of the tropics. Ashton further suggested that the absence of the Fagaceae from Sri Lanka explains the dominance of lower montane forest there by dipterocarps[17]. The Fagaceae are also often well represented in the dry deciduous dipterocarp forest in Thailand[18]. Here the balance between the two families is controlled by fire frequency, rather than altitude, with fires favouring the dipterocarps and fire-protection favouring the Fagaceae.

The idea of competition between families is not as unlikely as it may at first seem. Other widespread and successful clades of plants and animals each seem to occupy a distinct volume of niche space, allowing them to coexist in a variety of different species assemblages if this space is otherwise unoccupied[19,20], but potentially leading to competitive exclusion where two or more clades which evolved in isolation need the same niche space. If, as currently seems likely, the Dipterocarpaceae had a tropical, Gondwanic origin, while the Fagaceae had a subtropical or warm-temperate northern origin[11,21,22], then the families could have had complementary tropical Asian distributions from their first meeting in the mid Eocene, with a subsequent blurring of boundaries as each family expanded into specific unoccupied niches.

Other angiosperms

Many genera that are often thought of as Asian specialities, such as *Syzygium*, *Pandanus*, *Calamus*, and the many climbing Annonaceae (e.g. *Artobotrys*, *Desmos*, *Fissistigma*, *Uvaria*), are in fact widespread in the Palaeotropics, from Africa to New Guinea and beyond. The Dipterocarpaceae and Fagaceae are exceptions because of the difficulties both families have in crossing marine or other non-forest barriers. Restricted dispersal may also explain another floristic example: the ant-*Macarangas*. The 280 or so species in the genus *Macaranga* are widespread in the Palaeotropics, but the 30 species that form obligate defensive mutualisms with ants (*Crematogaster* or *Camponotus*) are restricted to the everwet regions of Peninsula Malaysia, Borneo and Sumatra, where they are abundant[23]. Similar habitats occur in many parts of the Palaeotropics, but the successful spread of an ant-dependent *Macaranga* species requires at least two seeds, because the genus is dioecious, and the ant mutualist, which must limit the ability of these species to cross barriers.

Sapling dominance in the forest understorey

Dan Janzen first pointed out a striking structural peculiarity of tropical Asian rainforests, that the understorey is dominated by sterile saplings of canopy trees, in contrast to the diversity of small trees that flower and fruit in the understorey of Neotropical forests[24]. This distinction

holds up with the larger pantropical dataset now available[25]. The generality of these conclusions still need testing at additional sites in Asia and elsewhere, but the pattern is so strong that it cannot be entirely an artefact of the choice of sites for comparison. There is no obvious explanation for this pattern, but the consequences in terms of reduced flower and fruit resources in the understorey are clearly seen in the lack of understorey specialist frugivores in tropical Asian forests[26].

Invertebrates

Honeybees

Many invertebrate groups disperse over barriers even more easily than plants, so again the Asian specialities are taxa with exceptionally poor dispersal. New honeybee colonies, for example, are founded by swarms, which must make their dispersal across barriers less easy than for most other hymenoptera (ants and wasps), where a single fertilized female can found a new colony. Tropical Asian forests support up to four species of honeybee (Apidae, Apini, *Apis*), out of a regional total of ten or more species, while other tropical regions have either one native species (Africa), or had none at all until their recent introduction (Neotropics and New Guinea). Honeybees are ecologically important because of the ability of a single worker bee to recruit huge numbers of its sisters to newly discovered floral resources. Tropical Asian plants must either use honeybees as pollinators or exclude them from their flowers, as many species do[16]. The consequences for pollination biology in the Asian tropics are unclear, but the dominance of *Apis* bees on many large floral resources may help explain the relatively low diversity of other bees in the Asian tropics. On the positive side, the tolerance of at least some *Apis* species to habitat fragmentation and deforestation may enhance the resilience of pollination to human impacts in tropical Asia[16].

Termites

Termites also appear to disperse poorly, probably because colony foundation, unlike in the ants, requires a sexual pair. Termites that feed inside dead wood are an exception, since a whole colony can be carried inside floating wood. The soil-feeding species – tropical analogues of the earthworms that feed on humified substrates – are particularly poorly dispersed and this niche is dominated by different clades in different parts of the tropics. It has been suggested that the apparently much lower energy flow through termites in Borneo than Africa may be a consequence of the low diversity of soil-feeding termites in tropical Asia[27], but it is not known if other decomposer organisms compensate for this difference.

Mammals

Endemic orders and families

Non-flying mammals disperse poorly or not at all across marine barriers, but 24 million years of land connections to Africa have ensured that all but the most forest-dependent orders and families are shared. The forest-dependent mammalian orders Dermoptera (colugos) and Scandentia (tree shrews), each with a single family, are not only endemic to tropical Asian forests, but an increasing amount of evidence suggests that they together form a clade 'Sundatheria', which is sister to the primates[28]. Fossil evidence shows that the Dermoptera are an ancient group that occurred in Thailand, Myanmar and as far west as modern Pakistan in the Oligocene[29]. Three other forest-dependent mammalian families are also endemic: the gibbons (Hylobatidae), the tarsiers (Tarsiidae) and the Asian linsangs (Prionodontidae), until recently misplaced among the civets[30]. Out of these five endemic families, the gibbons are probably of greatest ecological significance, as arguably the best seed dispersal agents among all mammals, consuming large quantities of fruit, swallowing most seeds, and defecating them intact over their large home ranges. A study in Borneo found that >90% of seeds were dispersed >100 m from the parent plant[31].

Megaherbivores

It has recently been suggested that the diversity and abundance of large herbivores (>5 kg) in the Asian and African tropics has put their ecosystems on very different 'evolutionary trajectories' from the Neotropics and that this helps explain many other differences in their floras, faunas and ecological interactions[32]. These authors particularly highlight the ecological role of the very largest herbivores, which are immune to predators as adults and attained high biomass densities before they were hunted by humans. Asia and Africa have similar-sized forest elephants, but only Asia has forest rhinoceroses, the Sumatran (*Dicerorhinus sumatrensis*; 800–1000 kg) and Javan (*Rhinoceros sondaicus*; 1500–2000 kg). Both have been hunted for millennia and are now on the verge of extinction, but there are enough historical accounts to show that they lived at high densities where they were not persecuted[33]. In historical times, most forest areas in tropical and subtropical Asia supported elephants and most forests in the east of the region also had one or two rhinoceros species. It is too late to investigate the ecological impacts of forest rhinoceroses at natural densities, but there is anecdotal evidence for a significant impact on forest dynamics through their browsing activity, as well as a role in seed dispersal[26,32,33].

It is worth noting that both elephants and rhinoceroses occurred in Pleistocene Luzon, elephants in Sulawesi, and elephant-like stegodons at sites from southern China to eastern Indonesia, showing that an earlier wave of extinctions – possibly associated with the arrival of hominids – eliminated megaherbivores from regions that have been without large vertebrates ever since[33]. There were also megaherbivores in the late Pleistocene Neotropics, although their occurrence in closed forests is still debated[32].

Squirrels

Tropical Asian forests have a greater local diversity of squirrels – in terms of species, morphology and ecology – than anywhere else in the world. Tropical Asian squirrels represent three major clades: a nocturnal flying clade (e.g. *Hylopetes, Iomys, Petaurista*); a diurnal clade of Oriental tree (e.g. *Callosciurus*) and ground squirrels (e.g. *Lariscus, Rhinosciurus*); and the diurnal giant squirrels in the genus *Ratufa*[34]. In lowland dipterocarp forests in Southeast Asia, up to 11 diurnal squirrels (including two *Ratufa* spp.) can coexist[35]. There is no reliable data for the diversity of coexisting flying squirrels, but the maximum is certainly more than three and may be as high as five or six (personal observations). A typical squirrel community spans a weight range of at least 50–2000 g, inhabits strata from the ground to the upper canopy, includes specialist feeders on seeds, fruits, insects or leaves, and is active round the clock. This diversity of squirrels may explain the very low diversity of small primates in tropical Asian forests, compared with Africa, Madagascar or the Neotropics[2], although small primates are mostly insectivorous while few squirrels are. More convincing, perhaps, is the inverse correlation between the diversities of squirrels and that other group of muscular-jawed seed predators, the parrots, with the Neotropics and New Guinea richest in parrots and poorest in squirrels[1].

Bears

Only Asia has widespread tropical lowland bears, although a single species, the spectacled bear (*Tremarctos ornatus*) occupies montane forests in South America and occasionally occurs in the lowlands[2]. Three bear species more or less partitioned the Asian tropics in historical times, although their distributions have now been greatly reduced. The sloth bear (*Ursus ursinus*) occupied Sri Lanka and most of the Indian subcontinent, except deserts and high mountains. The sun bear (*Ursus malayanus*) occupied most of Southeast Asia, from southwest China south to Sumatra and Borneo. The Asiatic black bear (*U. thibetanus*) occupied forests in southern China and a belt across the Himalayan ranges west to Pakistan. The range of this species had a broad overlap with the sun bear in continental Southeast Asia and a narrower one with the sloth bear in northern India, with all three species apparently coexisting in parts of eastern India. The ecological consequences of having lowland bears are unclear. All

three species appear to feed largely on varying proportions of fruit, other plant material, and invertebrates.

Carnivores

A striking feature of Asian tropical forest communities is the high diversity of sympatric mammalian carnivores. The Oriental Region supports a total of 80 species in the order Carnivora[36], and the most intact lowland forests have 15–25 species, with the greatest diversities at Southeast Asian sites with extensive closed-canopy forest[37,38]. Different forest sites support up to six sympatric cats, six civets (plus *Prionodon*), three mongooses, eight mustelids (including otters), two canids and two bears[37–43]. These numbers compare with estimates for the Neotropics ranging from <18 in western Amazonia (although 15 is the maximum actually recorded) and <15 in Central America[44], and even lower numbers in African forests, which have no dogs or bears and only two cats[2]. The tiger is the world's largest tropical forest carnivore and the only one for which prey weighing >100 kg is a regular part of the diet.

Birds

Endemic families

Three monogeneric families of birds are, as currently constituted, endemic to this region: the ioras (Aegithinidae), the fairy-bluebirds (Irenidae) and the leafbirds (Chloropseidae). None of these are of major ecological significance, although the fairy bluebirds are highly frugivorous and the leafbirds take both fruit and nectar[16,26]. Several groups of birds, including the pittas, pheasants, babblers and flowerpeckers, are more diverse in tropical Asian forests than elsewhere.

Babblers

The last 10 years have seen the removal of numerous misplaced taxa from this group and the addition of many others[45]. Birds that have a reasonable claim to the title 'true babbler' are now split between several, more or less closely related clades, in which they associate with white-eyes (*Zosterops*), warblers (*Sylvia*) and other birds that were not previously considered to be babblers. There are still many questions to be sorted out before a new classification can be finalized, but the end result will surely include 1–3 related groups which reach their maximum morphological and species diversity in the forests of tropical and subtropical Asia. Of the babblers in the broadest sense, only *Zosterops* reaches New Guinea and the Pacific and there are relatively few species in African forests. In much of tropical Asia, the babblers are the most diverse group of forest birds, but we know very little about their ecology or how so many species can coexist. Although usually considered as insectivores, their role in seed dispersal in the understorey and subcanopy layer has probably been underestimated because they feed so inconspicuously, yet most babbler droppings contain some seed[26].

Flowerpeckers and mistletoes

Most of the 44 species of flowerpeckers (Dicaeidae) are confined to tropical Asia, but five occur in New Guinea and one in Australia. Flowerpeckers are the smallest frugivores in the region and some species have a relationship with hemi-parasitic mistletoes (Loranthaceae and Viscaceae) which is uniquely close. Not only are flowerpeckers the major effective seed dispersal agents for mistletoes in tropical Asia, depositing seeds on branches of the right diameter for establishment[46], but some species are also involved in their pollination[16,47,48]. Such specialized relationships are uncommon in pollination and extremely rare in seed dispersal, so the combination of the two is particularly unusual.

Other vertebrates

Gliders

One of the most bizarre and inexplicable features of tropical Asian forests is the independent evolution of gliding forms in at least six groups of vertebrates[2]. These include the flying squirrels and colugos, both mentioned above, and gliding lizards (*Draco* spp.), geckos (*Ptychozoon* spp.), snakes (*Chrysopelea* spp.) and frogs (*Rhacophorus* spp.). All six groups are represented, some with multiple species, in some Southeast Asian forests, while four groups (squirrels, snakes, lizards and frogs) are present even in the outlying rainforests of the Western Ghats. No other tropical forest in the world has more than 1–2 groups of gliders. There have been several attempts at explaining this striking pattern, including hypotheses that attribute it to the exceptional height of tropical Asian forests and/or a relative deficiency in the lianas that connect tree crowns in other tropical forests[2]. Perhaps the most convincing hypothesis attributes the diversity of gliders to a general deficiency in the food supply as a result of dipterocarp dominance and the supra-annual cycles of flowering and fruiting, which has in turn selected for energy-efficient travel.

Conclusions

Do these examples of Asian tropical forest uniqueness reflect simply an accumulation of biogeographical accidents

or is there a single, underlying, explanation? The complex geological history of the region, described at the beginning, does not provide a simple historical explanation for Asian uniqueness, although the biotic interchanges following the collision of the Asian and Australian plates may have contributed to the region's exceptional phyletic diversity[11]. Taxa have arrived – or failed to arrive – in tropical Asia by multiple routes and at multiple times since the late Cretaceous[11,21]. The strong influence of ENSO cycles is a plausible – if untestable – environmental explanation for many unique features of Asian tropical forests, but we still know too little about the antiquity of Holocene-like ENSO conditions to understand their possible impact over evolutionary time scales. The situation is not hopeless, however. Improved dating of major geological events, a better fossil record, new proxies for palaeoenvironmental conditions, and the use of dated molecular phylogenies are replacing speculative story-telling by testable hypotheses in many areas of biogeography. Understanding the biogeographical history of tropical Asia may be particularly difficult, because of its complexity, but it is not inherently impossible.

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