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The ecology of the Asian dipterocarps

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The Dipterocarpaceae is the emblematic family of South-east Asian tropical rain forests and many of the seasonally dry forests of continental South and South-east Asia. Whilst dipterocarps are pantropical, with two sub-families Monotoideae and Pakaraimoideae found in Africa and South America (Maury-Lechon and Curtet 1998), Asian forests that can be dominated by dipterocarps occur from southern India throughout Malesia to New Guinea (Figures 1 and 2). In South-east Asia, the dominance of dipterocarps is evident in most mature forest communities, comprising around 20% of all trees (Slik et al. 2003) and a greater proportion of the larger forest trees; the majority are lowland species rarely found above 1200 m above sea level (Whitmore 1984). In the drier continental forests, dipterocarps make up a greater proportion of the trees but with reduced species diversity (Smitinand et al. 1980; Ashton 2014; Figure 2). Given this ecological predominance, advancing our knowledge of the ecology of dipterocarp species yields a better understanding of the forests of South and South-east Asia as a whole (Ashton 1988, 2014; Ghazoul 2016).

Dipterocarp trees are influential in the structure and function of Asian forests. They are amongst the tallest trees found in the tropics (Banin et al. 2012; Mongabay 2016a,b), making them important stores of above-ground carbon (Slik et al. 2013) and they are highly productive (Banin et al. 2014). These features, combined with their commercially favourable wood properties, clear straight boles and high stem density in accessible lowland forests meant they became widely exploited for timber in the twentieth century (Sodhi et al. 2004). Indeed, many of the earliest studies of dipterocarps were by silviculturalists (e.g. Brandis 1895; Foxworthy 1932; Symington 1943). The forests of South-east Asia have therefore been shaped by a long management and disturbance history, with slightly less than half of the original forest area now remaining (Stibig et al. 2014). Whilst logging has declined in some parts of Asia, agriculture and the fragmentation associated with land conversion, pose further threats to the ecological functioning of remaining forest stands (Wilcove et al. 2013). Nonetheless, in recent years there has been an increased commitment to restoring forest cover in tropical Asia and new scientific understanding is required to determine how this might be done successfully (Chazdon 2008; Kettle 2010; Tuck et al. 2016). Evidently, forest restoration in much of Asia will have to rely on successful establishment of dipterocarp communities facilitated by a deeper understanding of their ecology.

The Asian dipterocarps are found in India (Antin et al. 2016), Bangladesh, Nepal, Sri Lanka and the Andaman Islands, in the seasonal forests of Thailand (Disyatat et al. 2016), Cambodia (Kenzo et al. 2016b), Vietnam (Dong et al. 2016 a, b; Nguyen and Baker 2016), Myanmar, Laos and into southern China. These drier forests are more open, shorter and have markedly lower diversity (Figures 1 and 2). Dipterocarps are found across Malesia, throughout the Malay peninsula (Chong et al. 2016; Kenzo et al. 2016a; Ng et al. 2016; Yamada et al. 2016), Sumatra, Java, and in Borneo (Ang et al. 2016; Brearley et al. 2016; Dent and Burslem 2016; Nutt et al. 2016; Saner et al. 2016) they reach their highest species diversity (Figure 2). East of Wallace's line, in neighbouring Sulawesi, diversity decreases markedly and although dipterocarp ranges extend to New Guinea (Figure 2), dipterocarp species constitute a much smaller component of the forest canopy.

The family-level dominance of the dipterocarps in the forests of South and South-east Asia has long fascinated ecologists; the closest tropical ecological equivalent are the stands of Caesalpinioideae subfamily of the Leguminosae found in west Africa and South America (Henkel 2003; Peh et al. 2011; Newbery et al. 2013). Dipterocarps have a number of ecological characteristics that all likely contribute, in some way, to their dominance, which play out at various points during their life cycle (Figure 3). These include their non-pioneering yet often fast-growing lifestyle (Thomas and Bazzaz 1999; Banin et al. 2014), mast fruiting (Ashton et al. 1988; Brearley et al. 2007; Numata et al. 2013), wind-dispersed winged fruits (Suzuki and Ashton 1996; Smith et al. 2015) and symbiotic ectomycorrhizal associations (Brearley 2011, 2012) (Figure 3). Under conditions relatively free from exogenous disturbance, these family-wide traits and underlying mechanisms could help dipterocarps gain a competitive advantage and lead to their ecosystem dominance. Nonetheless, species within the family are certainly not equal and there is clear variation in growth rates, wood density, maximum tree size, leaf form, pollinators, seed size, dispersal distance, germination rates, and niche breadth including edaphically- and irradiance-mediated habitat specialisation (Ashton 1964, 1982, 2014; Gunatilleke et al. 1997; Thomas and Bazzaz 1999; Marod et al. 2004; Russo et al. 2005; Philipson et al. 2012; O'Brien et al. 2013; Born et al. 2014; Smith et al. 2015; Ghazoul 2016). Indeed, this functional variation and exploitation of different environmental niches is one explanation for the maintenance of high dipterocarp diversity, of over 500 species, in the tropical forests of Asia.

The key to understanding the ecology of the Asian dipterocarps lies in improving our knowledge of the ecological processes at various scales, and the life-cycle stage(s) at which these operate (Figure 3). This special issue compiles new research relating to these key processes, across the majority of the Asian dipterocarps' range. Ultimately, through understanding how dipterocarp species reproduce, establish, function, and become organised in space and time, we can better interpret the impacts of environmental change on the functioning, survival and evolution of these communities and judge the effectiveness of management interventions. Here, we briefly outline the key messages of the papers contained in this special issue and conclude by placing the new understanding in the context of the future for Asian forests.

Genetics and reproduction

We have a reasonable picture of the broader branches of the dipterocarp phylogeny with three subfamilies (Dipterocarpoideae, Monotoidae and Pakaraimoidae) and two tribes (Dipterocarpeae and Shoreae) in the former subfamily (Dayanandan et al. 1999; Gamage et al. 2006). This is confirmed by Ng et al. (2016) using two marker regions (*rpo*B and *trn*L). However, the 'twigs' of the tree, particularly within *Shorea* and closely related clades, still need attention – part of this lack of clarity is likely due to historical hybridisation events. Hybridisation between dipterocarp species is known (e.g. Kamiya et al. 2011) and may be one of the causes of high species diversity in this family. Kenzo et al. (2016a) examined a population of hybrid seedlings in Singapore and showed how their growth and survival rates are comparable to their parent species. However, the proportion of hybrids was greater at the seedling stage than the adult stage and they suggested that this might be due to increasing forest disturbance. At the population level, Ang et al. (2016) report that whilst naturally occurring seedlings of two dipterocarp species did not have lower genetic diversity in logged forest compared to unlogged forest, genetic variation within enrichment-planted seedlings was lower in monocultures compared to mixed-species plantings, presumably through post-planting mortality processes, which warrants further research. A possible mechanism for this was demonstrated by Nutt et al. (2016) who found *Parashorea tomentella* seedlings with greater heterozygosity had a greater survival rate, as did those with larger seeds, although neither seedling growth nor germination rate were influenced by heterozygosity. Ng et al. (2016) further fill a gap by providing new data on genome sizes for over 100 species of dipterocarps. Genome sizes were found to be consistently small (< 0.8 picograms in all cases). Because of the high nutrient demand for nucleic acids, it has been suggested that infertile soils, as found in much of South-east Asia (e.g. Banin et al. 2015), will lead to small genome sizes (Kang et al. 2015) supported by the data of Ng et al. (2016). However, there is still work to be done to determine the evolutionary importance and ecological correlates of genome size variation in dipterocarps and Ng et al. (2016) provides the starting point for this.

Dispersal and predation

Mast fruiting is hypothesised to be competitively advantageous to trees by satiating seed predators (Janzen 1974). Chong et al. (2016) studied the fates of seeds following a masting event at a fragmented site in Singapore to examine how human impacts on the forest might influence reproduction. Overall, they found that longtailed macaques were the dominant pre-dispersal seed predators whereas insects dominated predation post-dispersal. Vertebrate post-dispersal predation was more comparable to that of a logged forest than an intact forest in a previous study (Curran and Webb 2000), indicating possible changes in seed predation patterns associated with forest disturbance. Notably, Chong et al. (2016) identified a large proportion of non-viable seeds, which could be attributed to lower rates of out-crossing in a disturbed and fragmented landscape. Maintaining seed viability could become increasingly important for future dipterocarp communities, since it has also been established that successful reproduction may be lower in 'minor' masting events (Maycock et al. 2005) that appear to be increasing in frequency.

Leaf and stem traits

We are still learning how seedling ecophysiology drives species co-existence in dipterocarp communities, for example through the growth and survival strategies of light-demanding versus shade tolerant dipterocarps under resource-limited environmental conditions. Saner et al. (2016) observed six dipterocarp species and grouped the seedlings into light-demanding species that increased their growth rates after a simulated gap opening in contrast to shade tolerant species that showed a greater relative increase in non-structural carbohydrates. Although the role of non-structural carbohydrates in light adaptation is not well understood, it was found that enhanced non-structural carbohydrates were related to increased dipterocarp seedling drought survival in an earlier study (O'Brien et al. 2014). Kenzo et al. (2016b) looked at leaf traits of two common dipterocarps in dry deciduous dipterocarp forest in Cambodia and found strong relationships with height in the canopy. Canopy leaves had the fastest rate of photosynthesis - comparable to those in evergreen forests - despite a dry, hot and bright environment. These were maintained by thick leaves with a high nitrogen content and minimal stomatal limitation even in the early dry season. There were also clear seasonal differences with photosynthesis being faster in the wet season as stomata could remain open due to less water stress and, in general, the two species showed similar patterns in leaf ecophysiological traits, indicating their convergent adaptation to a highly seasonal environment. In contrast, Dent and Burslem (2016) showed differing leaf traits among saplings of nine dipterocarp species in a tropical forest of Malaysian Borneo that had soil-specific edaphic preferences. Seedlings specialised to more nutrient-poor sandy soil had strategies for nutrient and water conservation such as lower foliar nitrogen and phosphorus concentrations, reduced stomatal density and less negative $\delta^{13}C$, whereas those species specialised to more nutrient-rich clay soils generally had traits with a broader range of values (particularly for leaf mass per area and leaf lifespan). This has implications for the high diversity of dipterocarps seen across Borneo as high alpha diversity on nutrient-rich soils may be driven by a wider range of growth strategies (see also Coomes et al. 2009) and the considerable edaphic variation leads to high beta diversity across the island. Dong et al. (2016a) examined the ecophysiology of *Hopea odorata* within artificial gaps in an *Acacia* plantation in a silvicultural restoration experiment in Vietnam. They showed optimal physiological traits and growth towards the centre of the gaps where irradiance was greatest; this species demonstrated high phenotypic plasticity and rapid growth under high light conditions indicating that it could be a good candidate for initial forest restoration. In follow-up research, Dong et al. (2016b) showed that these seedlings achieved such growth rates through a greater light-use efficiency, obtained by changes in crown structure under the higher irradiance conditions. There was, however, competition for water when growing near the gap edge and closer to the *Acacia* nurse crop, suggesting consideration should be given to the choice of nurse crops to minimise competitive interactions in restoration plantings (Dong et al. 2016a). These studies indicate how information on species-level functioning can provide insights for applied conservation and forest management, as well as fundamental ecological understanding of factors influencing community assembly and diversity.

Mycorrhizas and soil processes

Dipterocarps have long been known to be ectomycorrhizal (Singh 1966) with ectomycorrhizas often credited as promoting faster growth rates and the high species diversity and dominance of the family. Brearley et al. (2016) combined four independent studies that manipulated connection to an ectomycorrhizal hyphal network and found very little supporting evidence that this network influenced seedling growth or survival over the short term. They hypothesised this was due to low host specificity of ectomycorrhizal fungi meaning that there would be little chance for adult trees to exclusively support kin through a hyphal network and it would not, therefore, provide an adaptive benefit. However, they did not actually examine the ectomycorrhizal fungi found in their study system, as did Disyatat et al. (2016); the latter looked at fungal diversity and composition in a dry dipterocarp forest fragment and a dipterocarp plantation in Thailand. They found lower ectomycorrhizal richness in the plantation and differences in ectomycorrhizal species composition between wet and dry seasons elucidating a previously overlooked temporal dimension to dipterocarp-associated ectomycorrhizal communities. Their traditional molecular research methods can be complemented in the future by using next generation sequencing for improving our understanding of tropical soil microbial processes (Peay et al. 2015; Thomas et al. 2015) and their links with their respective above-ground communities.

Structure and composition

Monitoring forest structure and composition has become increasingly important with a need to accurately and efficiently quantify carbon stocks and fluxes in association with REDD+ (Reducing Emissions from Deforestation and forest Degradation) policies (Miles and Kapos 2008). Changes in community composition may also alter the ability of a forest to sequester and store carbon. Thuy and Baker (2016) present a study on the dry dipterocarp forests of Vietnam based on numerous small sampling plots where four dipterocarp species made up about 80% of the trees. In terms of regeneration, the seedling composition in each plot was not always representative of the canopy composition and *Shorea siamensis* appeared to have poor regeneration capacity that is likely to lead to a changing species composition over time. Temporal forest dynamics were also explored by Antin et al. (2016) who used direct observations of diameter growth over a 21-year period in the Western Ghats of India, combined with allometric projections of height and crown dimensions to predict dynamics of the two dominant dipterocarps *Dipterocarpus indicus* and *Vateria indica*. They found that *Vateria indica* was a faster growing species in all dimensions in the majority of situations suggesting that it was increasing in dominance in the forest, possibly from some past disturbance. Yamada et al. (2016) examined the impacts of logging on five common dipterocarp species at Pasoh Forest Reserve in Peninsular Malaysia. An influence of past logging on tree growth or mortality was not detected, but there was still a signature on patterns of recruitment that was an order of magnitude lower in logged forest, with the caveats that the study was based on only a single plot of each forest type and the logged plot may also have been impacted by edge effects. These studies indicate the need for monitoring a variety of structural parameters (horizontal and vertical), dynamic processes (growth, mortality and recruitment) and community members (adults, saplings and seedlings) to understand changes and predict the future of dipterocarp assemblages.

Disturbance and fragmentation

Forest disturbance and fragmentation are prevalent in the forests of South-east Asia (Sodhi et al. 2004; Wilcove et al. 2013) and understanding the impacts of these human-driven processes on dipterocarp-dominated forests is thus pressing. Numerous studies noted above addressed some aspects of forest disturbance or fragmentation. Ang et al. (2016) showed how logging had minimal impacts on seedling genetic diversity and Yamada et al. (2016) also found that logging did not impact tree growth rates or mortality but did influence recruitment. A number of studies used the small Bukit Timah Nature Reserve and surrounding secondary forest as examples of fragmented forest within an urbanised matrix (Corlett 1992) that may represent an extreme fate of dipterocarp forests in the future. Chong et al. (2016) indicated that fragmentation and disturbance might affect patterns of dipterocarp reproduction and successful seed dispersal and germination and Kenzo et al. (2016a) suggested that fragmentation may increase rates of hybridisaton. In a dry dipterocarp forest, Disyatat et al. (2016) further demonstrated that fragmentation can influence patterns of ectomycorrhizal fungal diversity. Varying results indicate both that different stages of the dipterocarp life cycle may be differentially affected by disturbance and fragmentation, and that the degree of disturbance and the environmental setting also play a role in determining tangible effects on dipterocarp communities.

Moving forward: applying autecological knowledge of dipterocarps to forest change, regeneration and restoration

The tropical forest biome is undergoing unprecedented environmental changes, including climatic, biogeochemical, fragmentation and extraction disturbances (Malhi et al. 2014). Particular challenges in South-east Asia include possible increasing frequency and/or intensity of El Niño-associated droughts and fires (e.g. Huijnen et al. 2016) and associated tree mortality (Slik 2004; Ngo et al. 2016) along with the widespread forest conversion to agriculture, forest fragmentation and associated edge effects and isolation effects. These landscape-level changes can alter forest biomass dynamics (Chaplin-Cramer et al. 2015), seedling performance (Yeong et al. 2016) and successful reproduction (Chong et al. 2016). Timber extraction has been extensive in the past, and long-lived taxa, such as the dipterocarps, may have a 'disturbance memory' of such perturbations, transcending generations and lasting decades or hundreds of years (e.g. Yamada et al. 2016). Understanding the fundamental ecology of this important taxon, and the processes that underpin the structure and function of dipterocarp communities will help us identify the ways in which Asian forests may be affected now and into the future.

Forest restoration is on the agenda in many Asian countries, with initiatives proposed or underway, for example, in Sabah, Malaysia (The Star 2015) and in India (Business Standard 2015). This is a welcome development and represents a distinct opportunity. Contributions to this special issue have demonstrated that successful regeneration and restoration programmes may require an understanding of the entire life cycle of target species and communities (see also Kettle 2010). Seed viability and seedling survival are affected by genetics of parent trees and their landscape context, in both natural regeneration and enrichment planting situations (Ang et al. 2016; Chong et al. 2016; Nutt et al. 2016; Kenzo 2016a). Seedling physiology, performance and competition in given environmental settings (Dent and Burslem 2016; Dong et al. 2016 a, b, Saner et al. 2016) and changes in communities over time through mortality and recruitment processes ultimately shape the future communities (Ang et al. 2016; Antin et al. 2016; Nguyen and Baker 2016). Perturbations to other biotic components (e.g. fungi, fauna) in these forest systems will also interact to affect rehabilitation of dipterocarp communities (Chong et al. 2016; Disyatat et al. 2016).

We acknowledge the challenge in knowledge transfer between those who pursue fundamental research on the ecology of dipterocarps and those involved in applied forest management. However, we hope that this special issue demonstrates how bridges between fundamental research and applied questions can be crossed and that the contributions within direct us to a new domain of confidence and a more comprehensive understanding of the ecology of the Asian dipterocarps.

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Figure 1: Dipterocarp-dominated forest types in South and South-east Asia including some of the study sites in this special issue. Dry dipterocarp forest in Kratie province (Cambodia) in the (a) wet season and (b) dry season; (c) Lowland evergreen rain forest at Gunung Mulu, Sarawak, northern Borneo; (d) Heath forest (also known as *kerangas*) at Barito Ulu, central Borneo; (e) Bukit Timah, a fragment of dipterocarp forest in Singapore; (f) canopy walkway at Pasoh Forest Reserve, Peninsular Malaysia; (g) Uppangala in the Western Ghats of India; (h) Danum Valley in Sabah, northern Borneo; (i) forest in Murung Raya regency, central Borneo showing traversing logging road. Photos by Tanaka Kenzo (a, b, e), Lindsay Banin (c), Francis Brearley (d, f, i), Jimmy Le Bec (g) and Ch'ien Lee (h).

Figure 2: Map of South and South-east Asia depicting mean annual precipitation across the region (from WORLDCLIM; Hijmans et al. 2005) with region-specific species richness values for members of the Dipterocarpaceae. Species richness data come from Ashton (1982) for Peninsular Malaysia, Sumatra, Java, Borneo, The Philippines, Sulawesi and New Guinea, Jacobs (1981) for Sri Lanka, Thailand, Cambodia and Vietnam and Li et al. (2000) for Chin). Photos by Aswandi (Sumatra), Shangwen Xia (China), Thuy Nguyen Thi (Vietnam) and Liam Trethowan (Sulawesi).

Figure 3: Key stages of the dipterocarp life cycle (inner circle) and the linkages with fundamental environmental processes (symbols on outer circle) that are discussed in this special issue. Note that the ecological processes cannot be linked to a single life cycle stage, but represent the approximate scale at which the process operates and/or the starting point for interaction among stages and processes through the life cycle. © Diogo Guerra.