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The ecology of the Asian dipterocarps

Francis Q. Brearley ¹, Lindsay F. Banin ² & Philippe Saner ³

1) School of Science and the Environment, Manchester Metropolitan University, Manchester, UK; 2) Centre for Ecology and Hydrology, Bush Estate, Penicuik, Scotland, UK; 3) Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland

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

33 exploited for timber in the twentieth century (Sodhi et al. 2004). Indeed, many of
34 the earliest studies of dipterocarps were by silviculturalists (e.g. Brandis 1895;
35 Foxworthy 1932; Symington 1943). The forests of South-east Asia have therefore
36 been shaped by a long management and disturbance history, with slightly less than
37 half of the original forest area now remaining (Stibig et al. 2014). Whilst logging has
38 declined in some parts of Asia, agriculture and the fragmentation associated with
39 land conversion, pose further threats to the ecological functioning of remaining
40 forest stands (Wilcove et al. 2013). Nonetheless, in recent years there has been an
41 increased commitment to restoring forest cover in tropical Asia and new scientific
42 understanding is required to determine how this might be done successfully
43 (Chazdon 2008; Kettle 2010; Tuck et al. 2016). Evidently, forest restoration in much
44 of Asia will have to rely on successful establishment of dipterocarp communities
45 facilitated by a deeper understanding of their ecology.

46

47 The Asian dipterocarps are found in India (Antin et al. 2016), Bangladesh,
48 Nepal, Sri Lanka and the Andaman Islands, in the seasonal forests of Thailand
49 (Disyatat et al. 2016), Cambodia (Kenzo et al. 2016b), Vietnam (Dong et al. 2016 a,
50 b; Nguyen and Baker 2016), Myanmar, Laos and into southern China. These drier
51 forests are more open, shorter and have markedly lower diversity (Figures 1 and 2).
52 Dipterocarps are found across Malesia, throughout the Malay peninsula (Chong et
53 al. 2016; Kenzo et al. 2016a; Ng et al. 2016; Yamada et al. 2016), Sumatra, Java, and
54 in Borneo (Ang et al. 2016; Brearley et al. 2016; Dent and Burslem 2016; Nutt et al.
55 2016; Saner et al. 2016) they reach their highest species diversity (Figure 2). East
56 of Wallace's line, in neighbouring Sulawesi, diversity decreases markedly and
57 although dipterocarp ranges extend to New Guinea (Figure 2), dipterocarp species
58 constitute a much smaller component of the forest canopy.

59

60 The family-level dominance of the dipterocarps in the forests of South and
61 South-east Asia has long fascinated ecologists; the closest tropical ecological
62 equivalent are the stands of Caesalpinioideae subfamily of the Leguminosae found
63 in west Africa and South America (Henkel 2003; Peh et al. 2011; Newbery et al.
64 2013). Dipterocarps have a number of ecological characteristics that all likely
65 contribute, in some way, to their dominance, which play out at various points during

66 their life cycle (Figure 3). These include their non-pioneering yet often fast-growing
67 lifestyle (Thomas and Bazzaz 1999; Banin et al. 2014), mast fruiting (Ashton et al.
68 1988; Brearley et al. 2007; Numata et al. 2013), wind-dispersed winged fruits
69 (Suzuki and Ashton 1996; Smith et al. 2015) and symbiotic ectomycorrhizal
70 associations (Brearley 2011, 2012) (Figure 3). Under conditions relatively free from
71 exogenous disturbance, these family-wide traits and underlying mechanisms could
72 help dipterocarps gain a competitive advantage and lead to their ecosystem
73 dominance. Nonetheless, species within the family are certainly not equal and there
74 is clear variation in growth rates, wood density, maximum tree size, leaf form,
75 pollinators, seed size, dispersal distance, germination rates, and niche breadth
76 including edaphically- and irradiance-mediated habitat specialisation (Ashton
77 1964, 1982, 2014; Gunatilleke et al. 1997; Thomas and Bazzaz 1999; Marod et al.
78 2004; Russo et al. 2005; Philipson et al. 2012; O'Brien et al. 2013; Born et al. 2014;
79 Smith et al. 2015; Ghazoul 2016). Indeed, this functional variation and exploitation
80 of different environmental niches is one explanation for the maintenance of high
81 dipterocarp diversity, of over 500 species, in the tropical forests of Asia.

82

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

94

95 ***Genetics and reproduction***

96 We have a reasonable picture of the broader branches of the dipterocarp phylogeny
97 with three subfamilies (Dipterocarpoideae, Monotoideae and Pakaraimoidae) and
98 two tribes (Dipterocarpeae and Shoreae) in the former subfamily (Dayanandan et

99 al. 1999; Gamage et al. 2006). This is confirmed by Ng et al. (2016) using two marker
100 regions (*rpoB* and *trnL*). However, the ‘twigs’ of the tree, particularly within *Shorea*
101 and closely related clades, still need attention – part of this lack of clarity is likely
102 due to historical hybridisation events. Hybridisation between dipterocarp species
103 is known (e.g. Kamiya et al. 2011) and may be one of the causes of high species
104 diversity in this family. Kenzo et al. (2016a) examined a population of hybrid
105 seedlings in Singapore and showed how their growth and survival rates are
106 comparable to their parent species. However, the proportion of hybrids was greater
107 at the seedling stage than the adult stage and they suggested that this might be due
108 to increasing forest disturbance. At the population level, Ang et al. (2016) report
109 that whilst naturally occurring seedlings of two dipterocarp species did not have
110 lower genetic diversity in logged forest compared to unlogged forest, genetic
111 variation within enrichment-planted seedlings was lower in monocultures
112 compared to mixed-species plantings, presumably through post-planting mortality
113 processes, which warrants further research. A possible mechanism for this was
114 demonstrated by Nutt et al. (2016) who found *Parashorea tomentella* seedlings with
115 greater heterozygosity had a greater survival rate, as did those with larger seeds,
116 although neither seedling growth nor germination rate were influenced by
117 heterozygosity. Ng et al. (2016) further fill a gap by providing new data on genome
118 sizes for over 100 species of dipterocarps. Genome sizes were found to be
119 consistently small (< 0.8 picograms in all cases). Because of the high nutrient
120 demand for nucleic acids, it has been suggested that infertile soils, as found in much
121 of South-east Asia (e.g. Banin et al. 2015), will lead to small genome sizes (Kang et
122 al. 2015) supported by the data of Ng et al. (2016). However, there is still work to
123 be done to determine the evolutionary importance and ecological correlates of
124 genome size variation in dipterocarps and Ng et al. (2016) provides the starting
125 point for this.

126

127 ***Dispersal and predation***

128 Mast fruiting is hypothesised to be competitively advantageous to trees by satiating
129 seed predators (Janzen 1974). Chong et al. (2016) studied the fates of seeds
130 following a masting event at a fragmented site in Singapore to examine how human
131 impacts on the forest might influence reproduction. Overall, they found that long-

132 tailed macaques were the dominant pre-dispersal seed predators whereas insects
133 dominated predation post-dispersal. Vertebrate post-dispersal predation was more
134 comparable to that of a logged forest than an intact forest in a previous study
135 (Curran and Webb 2000), indicating possible changes in seed predation patterns
136 associated with forest disturbance. Notably, Chong et al. (2016) identified a large
137 proportion of non-viable seeds, which could be attributed to lower rates of out-
138 crossing in a disturbed and fragmented landscape. Maintaining seed viability could
139 become increasingly important for future dipterocarp communities, since it has also
140 been established that successful reproduction may be lower in 'minor' masting
141 events (Maycock et al. 2005) that appear to be increasing in frequency.

142

143 ***Leaf and stem traits***

144 We are still learning how seedling ecophysiology drives species co-existence in
145 dipterocarp communities, for example through the growth and survival strategies
146 of light-demanding versus shade tolerant dipterocarps under resource-limited
147 environmental conditions. Saner et al. (2016) observed six dipterocarp species and
148 grouped the seedlings into light-demanding species that increased their growth
149 rates after a simulated gap opening in contrast to shade tolerant species that showed
150 a greater relative increase in non-structural carbohydrates. Although the role of
151 non-structural carbohydrates in light adaptation is not well understood, it was
152 found that enhanced non-structural carbohydrates were related to increased
153 dipterocarp seedling drought survival in an earlier study (O'Brien et al. 2014).
154 Kenzo et al. (2016b) looked at leaf traits of two common dipterocarps in dry
155 deciduous dipterocarp forest in Cambodia and found strong relationships with
156 height in the canopy. Canopy leaves had the fastest rate of photosynthesis -
157 comparable to those in evergreen forests - despite a dry, hot and bright
158 environment. These were maintained by thick leaves with a high nitrogen content
159 and minimal stomatal limitation even in the early dry season. There were also clear
160 seasonal differences with photosynthesis being faster in the wet season as stomata
161 could remain open due to less water stress and, in general, the two species showed
162 similar patterns in leaf ecophysiological traits, indicating their convergent
163 adaptation to a highly seasonal environment. In contrast, Dent and Burslem (2016)
164 showed differing leaf traits among saplings of nine dipterocarp species in a tropical

165 forest of Malaysian Borneo that had soil-specific edaphic preferences. Seedlings
166 specialised to more nutrient-poor sandy soil had strategies for nutrient and water
167 conservation such as lower foliar nitrogen and phosphorus concentrations, reduced
168 stomatal density and less negative $\delta^{13}\text{C}$, whereas those species specialised to more
169 nutrient-rich clay soils generally had traits with a broader range of values
170 (particularly for leaf mass per area and leaf lifespan). This has implications for the
171 high diversity of dipterocarps seen across Borneo as high alpha diversity on
172 nutrient-rich soils may be driven by a wider range of growth strategies (see also
173 Coomes et al. 2009) and the considerable edaphic variation leads to high beta
174 diversity across the island. Dong et al. (2016a) examined the ecophysiology of
175 *Hopea odorata* within artificial gaps in an *Acacia* plantation in a silvicultural
176 restoration experiment in Vietnam. They showed optimal physiological traits and
177 growth towards the centre of the gaps where irradiance was greatest; this species
178 demonstrated high phenotypic plasticity and rapid growth under high light
179 conditions indicating that it could be a good candidate for initial forest restoration.
180 In follow-up research, Dong et al. (2016b) showed that these seedlings achieved
181 such growth rates through a greater light-use efficiency, obtained by changes in
182 crown structure under the higher irradiance conditions. There was, however,
183 competition for water when growing near the gap edge and closer to the *Acacia*
184 nurse crop, suggesting consideration should be given to the choice of nurse crops to
185 minimise competitive interactions in restoration plantings (Dong et al. 2016a).
186 These studies indicate how information on species-level functioning can provide
187 insights for applied conservation and forest management, as well as fundamental
188 ecological understanding of factors influencing community assembly and diversity.

189

190 ***Mycorrhizas and soil processes***

191 Dipterocarps have long been known to be ectomycorrhizal (Singh 1966) with
192 ectomycorrhizas often credited as promoting faster growth rates and the high
193 species diversity and dominance of the family. Brearley et al. (2016) combined four
194 independent studies that manipulated connection to an ectomycorrhizal hyphal
195 network and found very little supporting evidence that this network influenced
196 seedling growth or survival over the short term. They hypothesised this was due to
197 low host specificity of ectomycorrhizal fungi meaning that there would be little

198 chance for adult trees to exclusively support kin through a hyphal network and it
199 would not, therefore, provide an adaptive benefit. However, they did not actually
200 examine the ectomycorrhizal fungi found in their study system, as did Disyatat et al.
201 (2016); the latter looked at fungal diversity and composition in a dry dipterocarp
202 forest fragment and a dipterocarp plantation in Thailand. They found lower
203 ectomycorrhizal richness in the plantation and differences in ectomycorrhizal
204 species composition between wet and dry seasons elucidating a previously
205 overlooked temporal dimension to dipterocarp-associated ectomycorrhizal
206 communities. Their traditional molecular research methods can be complemented
207 in the future by using next generation sequencing for improving our understanding
208 of tropical soil microbial processes (Peay et al. 2015; Thomas et al. 2015) and their
209 links with their respective above-ground communities.

210

211 ***Structure and composition***

212 Monitoring forest structure and composition has become increasingly important
213 with a need to accurately and efficiently quantify carbon stocks and fluxes in
214 association with REDD+ (Reducing Emissions from Deforestation and forest
215 Degradation) policies (Miles and Kapos 2008). Changes in community composition
216 may also alter the ability of a forest to sequester and store carbon. Thuy and Baker
217 (2016) present a study on the dry dipterocarp forests of Vietnam based on
218 numerous small sampling plots where four dipterocarp species made up about 80%
219 of the trees. In terms of regeneration, the seedling composition in each plot was not
220 always representative of the canopy composition and *Shorea siamensis* appeared to
221 have poor regeneration capacity that is likely to lead to a changing species
222 composition over time. Temporal forest dynamics were also explored by Antin et
223 al. (2016) who used direct observations of diameter growth over a 21-year period
224 in the Western Ghats of India, combined with allometric projections of height and
225 crown dimensions to predict dynamics of the two dominant dipterocarps
226 *Dipterocarpus indicus* and *Vateria indica*. They found that *Vateria indica* was a faster
227 growing species in all dimensions in the majority of situations suggesting that it was
228 increasing in dominance in the forest, possibly from some past disturbance. Yamada
229 et al. (2016) examined the impacts of logging on five common dipterocarp species
230 at Pasoh Forest Reserve in Peninsular Malaysia. An influence of past logging on tree

231 growth or mortality was not detected, but there was still a signature on patterns of
232 recruitment that was an order of magnitude lower in logged forest, with the caveats
233 that the study was based on only a single plot of each forest type and the logged plot
234 may also have been impacted by edge effects. These studies indicate the need for
235 monitoring a variety of structural parameters (horizontal and vertical), dynamic
236 processes (growth, mortality and recruitment) and community members (adults,
237 saplings and seedlings) to understand changes and predict the future of dipterocarp
238 assemblages.

239

240 ***Disturbance and fragmentation***

241 Forest disturbance and fragmentation are prevalent in the forests of South-east Asia
242 (Sodhi et al. 2004; Wilcove et al. 2013) and understanding the impacts of these
243 human-driven processes on dipterocarp-dominated forests is thus pressing.
244 Numerous studies noted above addressed some aspects of forest disturbance or
245 fragmentation. Ang et al. (2016) showed how logging had minimal impacts on
246 seedling genetic diversity and Yamada et al. (2016) also found that logging did not
247 impact tree growth rates or mortality but did influence recruitment. A number of
248 studies used the small Bukit Timah Nature Reserve and surrounding secondary
249 forest as examples of fragmented forest within an urbanised matrix (Corlett 1992)
250 that may represent an extreme fate of dipterocarp forests in the future. Chong et al.
251 (2016) indicated that fragmentation and disturbance might affect patterns of
252 dipterocarp reproduction and successful seed dispersal and germination and Kenzo
253 et al. (2016a) suggested that fragmentation may increase rates of hybridisation. In
254 a dry dipterocarp forest, Disyatat et al. (2016) further demonstrated that
255 fragmentation can influence patterns of ectomycorrhizal fungal diversity. Varying
256 results indicate both that different stages of the dipterocarp life cycle may be
257 differentially affected by disturbance and fragmentation, and that the degree of
258 disturbance and the environmental setting also play a role in determining tangible
259 effects on dipterocarp communities.

260

261 ***Moving forward: applying autecological knowledge of dipterocarps to forest*** 262 ***change, regeneration and restoration***

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

278

279 Forest restoration is on the agenda in many Asian countries, with initiatives
280 proposed or underway, for example, in Sabah, Malaysia (The Star 2015) and in India
281 (Business Standard 2015). This is a welcome development and represents a distinct
282 opportunity. Contributions to this special issue have demonstrated that successful
283 regeneration and restoration programmes may require an understanding of the
284 entire life cycle of target species and communities (see also Kettle 2010). Seed
285 viability and seedling survival are affected by genetics of parent trees and their
286 landscape context, in both natural regeneration and enrichment planting situations
287 (Ang et al. 2016; Chong et al. 2016; Nutt et al. 2016; Kenzo 2016a). Seedling
288 physiology, performance and competition in given environmental settings (Dent
289 and Burslem 2016; Dong et al. 2016 a, b, Saner et al. 2016) and changes in
290 communities over time through mortality and recruitment processes ultimately
291 shape the future communities (Ang et al. 2016; Antin et al. 2016; Nguyen and Baker
292 2016). Perturbations to other biotic components (e.g. fungi, fauna) in these forest
293 systems will also interact to affect rehabilitation of dipterocarp communities (Chong
294 et al. 2016; Disyatat et al. 2016).

295

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

302

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309 working with us to produce Figure 3.

310

311 **Notes on Contributors**

312 Francis Q. Brearley is an ecologist interested in the functional importance of plant-
313 soil interactions for ecological processes in tropical forests with a focus on the
314 dipterocarp-dominated forests of South-east Asia.

315 Lindsay F. Banin is a plant and ecosystem ecologist with a particular interest in
316 tropical forest systems and the impact of environmental changes on their function.

317 Philippe Saner is an environmental scientist with a main interest in tropical plant
318 community ecology and the restoration of tropical forests.

319

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

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

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