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SEED DISPERSAL, SPATIAL AGGREGATION AND FINE-SCALE GENETIC STRUCTURE IN THE DIPTEROCARPACEAE

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Summary

Seed dispersal occupies a central role in plant ecology as it determines which plants germinate and establish in close proximity, and thus influences plant community structure, dynamics, and distributions. Consequently, this process is integral to species coexistence mechanisms including neutral theory, distance- or density-dependence, and the competition-colonization trade-off. At the landscape scale, long distance seed dispersal is important in maintaining habitat connectivity and gene flow between sub-populations, and determines migration rates. These dispersal dependent processes are pertinent to the long term persistence of tropical trees in the remaining lowland forests of Southeast Asia, which have become fragmented and degraded due to logging and land-use change.

In this thesis we quantify seed dispersal in the Dipterocarpaceae, and subsequently investigate how this trait contributes to patterns of spatial aggregation and fine-scale genetic structure. The Dipterocarpaceae is a family of primarily canopy and emergent late-successional tropical forest trees that is both species rich and abundant in the lowland tropical forests of Southeast Asia. Dipterocarps may contribute over 50% of forest biomass and therefore form the architectural skeleton of these forests. The production of their winged, gyration dispersed fruit is irregular and occurs after community wide 'general flowering' events. There is variation in fruit number of wings and mass of nut, suggesting that inter-specific differences in the fruit dispersal potential can be predicted based on fruit morphology. An improved understanding of fruit dispersal in the Dipterocarpaceae will thus improve our knowledge on the process of natural regeneration in primary forest and the vulnerability of SE Asian forests to fragmentation and logging.

Seed dispersal was quantified using experimental releases of fruit after measuring the fruit dimensions. In one experiment dispersal distance was recorded and a phenomenological model of dispersal generated. A second experiment measured fruit terminal velocity (rate of fruit descent through the air column), a necessary parameter of mechanistic models of seed dispersal. Patterns of spatial aggregation in this family were analysed using data on the coordinates of 28 species of dipterocarp located in a 160 ha forest plot in the highly topographically dissected Sepilok Forest Reserve. The fine-scale genetic structure (FSGS) of four species of dipterocarp was sampled from a 50 ha plot at Danum Valley. The FSGS results from three species at Danum were compared to the same species at different lowland dipterocarp forest plots to investigate the role of habitat heterogeneity in shaping patterns of FSGS.

Our results found significant differences in species dispersal potentials which are directly related to the fruit morphology. Species with large wing areas in relation to fruit mass dispersed greater distances, on account of lower terminal velocities, allowing wind to transport them farther distances laterally. Nevertheless, we observed that fruit dispersal was primarily local with 90% of fruit dispersing <10 m and no fruit dispersed >40 m. The models generated by the experimental releases allow dispersal distance and terminal velocity to be predicted for all Dipterocarpaceae fruit based on morphological dimensions. Over 90% of dipterocarps were more spatially aggregated than random in the Sepilok Forest Reserve. Spatial aggregation decreased in most species after controlling for topography, but did not disappear. Habitat associations are therefore prevalent in this family and contribute non-random distributions. Contrary to expectation there was no effect of seed dispersal or wood density on the residual patterns of spatial aggregation after controlling for habitat. Habitat was also observed to be an important factor shaping patterns of fine-scale genetic structure in the Dipterocarpaceae. Patterns of FSGS within species between sites were inconsistent in one of the three species. Habitat factors therefore play an important role in shaping patterns of FSGS, and the vulnerability of species to the loss of genetic diversity in fragmented and degraded forests cannot be predicted using reproductive traits alone.

Overall, the findings of this thesis show that significant differences in seed dispersal between dipterocarp species are observed, but the physical distribution of individuals and the genetic diversity within them is shaped by both dispersal and habitat factors.

Zusammenfassung

In der Pflanzenökologie spielt die Samenausbreitung eine zentrale Rolle. Sie bestimmt, welche Pflanzen nahe beieinander keimen und sich etablieren können, und beeinflusst damit die Struktur der Pflanzengesellschaft, deren Dynamik sowie die Verteilung. Daher ist dieser Prozess wesentlich für die Koexistenz-Mechanismen von Arten, wie beispielsweise die neutrale Theorie, Abstand- oder Dichte-Abhängigkeiten und der Trade-Off zwischen Konkurrenz und Besiedlung. Auf Landschaftsebene ist die Samenausbreitung wichtig für die Vernetzung von Lebensräumen über weite Distanzen sowie für den Genaustausch zwischen Subpopulationen und bestimmt zudem auch die Migrationsraten. Diese von der Samenausbreitung abhängigen Prozesse sind bedeutend für den längerfristigen Verbleib von tropischen Bäumen in den verbleibenden tieferliegenden Wäldern Südostasiens, welche infolge von Holzschlag und Änderungen der Landnutzung fragmentiert und damit degradiert sind.

In dieser Dissertation haben wir die Samenausbreitung der Dipterocarpaceae bestimmt und untersucht, wie diese Eigenschaften die räumliche Aggregation und die 'fine-scale genetic structure' (FSGS) beeinflussen. Die Bäume der Dipterocarpaceae schliessen typischerweise das Kronendach und kommen erst in den späten Sukzessionsphasen des tropischen Regenwaldes auf. In den tiefliegenden Regenwäldern Südostasiens sind deren Arten sowohl zahlreich als auch häufig vorkommend. Sie können einen Biomasse-Anteil dieser Wälder von über 50% ausmachen und bilden damit dessen strukturelles Rückgrat. Das Heranreifen ihrer geflügelten, durch Rotation verbreitenden Früchte erfolgt in unregelmässigen Zeitabständen und zu „gemeinschaftlichen Blüte-Zeitpunkten" einer gesamten Population. Bei den Früchten bestehen zwischen den Arten Unterschiede in der Anzahl der Flügel sowie der Masse der Nuss, was darauf hinweist, dass artspezifische Unterschiede im Ausbreitungspotential aufgrund der Eigenschaften der Frucht vorausgesagt werden können. Ein verbessertes Verständnis über die Samenausbreitung bei den Dipterocarpaceae wird daher unsere Kenntnisse über den Prozess der natürlichen Regeneration von Primärregenwäldern in Südostasien und deren Gefährdung durch Fragmentierung und Holzschlag verbessern.

Die Samenausbreitung wurde bestimmt, indem die Früchte ausgemessen und in kontrollierten Experimenten fallen gelassen wurden. Im ersten Experiment wurde die Ausbreitungsdistanz gemessen und darauf basierend ein phänomenologisches Modell der Ausbreitung erstellt. Im zweiten Experiment wurde die Grenzgeschwindigkeit der Früchte (Rate, mit der die Frucht durch die Luftsäule absinkt) ermittelt, ein notwendiger Parameter von mechanistischen Modellen zur Samenausbreitung.

Um die Muster der räumlichen Aggregation der Arten dieser Familie zu analysieren, wurden weitere Daten, basierend auf 28 Arten und deren Koordinaten in einem 160 ha grossen, topographisch stark unterteilten Waldareal des "Sepilok Forest Reserve", hinzugezogen. Die Daten zur FSGS von vier Dipterocarpaceae-Arten wurde in einem 50 ha grossen Areal im Danum Valley gesammelt. Die Resultate zur FSGS von drei dieser Arten wurden mit den gleichen Arten in verschiedenen anderen tiefliegenden Dipterocarpaceae-Waldarealen verglichen, um die Rolle der Habitats-Heterogenität bei der Gestaltung der Muster der FSGS zu ermitteln.

Unsere Resultate zeigen signifikante Unterschiede im Ausbreitungspotential der Arten. Diese sind direkt abhängig von der Morphologie der Früchte. Arten, welche grosse Flügelflächen im Verhältnis zur Fruchtmasse aufweisen, breiteten sich aufgrund der tieferen Grenzgeschwindigkeit über grössere Distanzen aus, da der Wind sie lateral über weitere Distanzen transportieren kann. Dennoch erfolgt die Samenausbreitung hauptsächlich lokal, wobei 90% der Früchte <10 m und keine Früchte >40 m weit flogen. Die Modelle, welche basierend auf den beiden Experimenten erstellt wurden, erlauben uns, die Ausbreitungsdistanz sowie die Grenzgeschwindigkeit für alle Früchte der Dipterocarpaceae aufgrund ihrer Morphologie vorauszusagen. Über 90% der Dipterocarpaceae waren im Sepilok Forest Reserve aggregierter als bei einer Zufallsverteilung anzutreffen. Die Aggregation nahm bei den meisten Arten unter Berücksichtigung der Topographie jedoch ab. Habitatsbindungen sind in dieser Familie somit verbreitet und tragen zu nicht-zufälligen Verbreitungen bei. Entgegen den Erwartungen konnten keine Auswirkungen der Samenausbreitung oder der Holzdichte auf die residuen Muster der räumlichen Aggregation festgestellt werden, nachdem das Habitat in die Auswertung einbezogen wurde. Ebenso wurde beobachtet, dass das Habitat ein wichtiger Faktor zur Bildung von FSGS-Mustern bei den Dipterocarpaceae ist. Die artspezifischen FSGS-Muster der verschiedenen Areale waren bei einer Art uneinheitlich. Demzufolge spielen Faktoren des Lebensraumes eine wichtige Rolle bei der Bildung von FSGS-Mustern und die Gefährdung der Arten durch den Verlust von genetischer Vielfalt in fragmentierten und degradierten Wäldern kann nicht alleine aufgrund der Reproduktions-Eigenschaften vorausgesagt werden.

Gesamthaft zeigen die Resultate dieser Dissertation, dass signifikante Unterschiede bei der Samenausbreitung zwischen den Arten der Dipterocarpaceae bestehen. Allerdings wird sowohl die physische Verteilung von Individuen als auch die genetische Diversität zwischen ihnen sowohl durch die Ausbreitung als auch durch Faktoren des Lebensraumes bestimmt.

General Introduction

ABSTRACT

Seed dispersal directly influences plant regeneration, distribution, competition and gene flow and consequently community structure (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000, Rees et al. 2001, Wang and Smith 2002, Levine and Murrell 2003, Howe and Miriti 2004). Despite the critical influence of this trait to the above processes, dispersal has not been accurately quantified in the vast majority of tropical tree species (Kettle 2012). Dispersal is difficult to measure in animal dispersed plants due to factors such as feeding visits per hour, home range size, gut passage times and maximum flight range (Howe 1977, Russo et al. 2006); whilst efforts to measure wind dispersed seed are hampered by the difficulties of tracking thousands of seeds across long-distances (Bullock et al. 2006). Quantitative data on seed dispersal over ecologically relevant scales is becoming of increasing importance. Tropical forests have been reduced in extent by deforestation driven by land-use change, and once contiguous forests have become fragmented within agricultural matrices. Quantifying seed dispersal is of value in these human-dominated systems to understand habitat connectivity, gene flow and meta-population dynamics (Hanski and Gilpin 1991, McConkey et al. 2012) — processes which increase the resilience of these fragmented systems and support their long term viability.

The tropical lowland forests of Southeast Asia are an excellent system for studying seed dispersal from theoretical and applied perspectives, as they are extremely species rich yet have been subjected to substantial forest degradation (Sodhi et al. 2009, Sodhi et al. 2010, Wilcove et al. 2013). These forests are dominated by the Dipterocarpaceae, a family of tropical trees with winged fruits which disperse via gyration (Ashton 1988). This thesis focuses on dipterocarp seed dispersal, with the objective of generating quantitative estimates of seed dispersal across a range of species. We further investigated how interspecific differences in seed dispersal shape patterns of spatial aggregation and fine-scale spatial genetic structure, to better understand the importance of seed dispersal to dipterocarp ecology and their vulnerability to forest degradation.

Seed dispersal — a unifying process in plant ecology

As sessile organisms, tree populations have distinct spatial distributions. Whilst the final distribution of adult individuals will be determined by the interplay between the processes of niche partitioning (Denslow 1987, Harms et al. 2001), environmental filtering (Engelbrecht et al. 2007), competition and density dependent processes (Janzen 1970, Connell 1971, Tilman 1994, Wright 2002), these processes can only act upon the initial distributions of recruiting individuals determined by seed deposition and thus seed dispersal is an important component of multiple theories of plant species coexistence. While neutral theories of species coexistence centre on not all species recruiting in suitable sites of establishment due to dispersal limitation (Hubbell 1979, Hubbell 2001), non-neutral theories focus on the relative position of con- and heterospecifics to control growth and mortality via competition and density dependent mechanisms (Janzen 1970, Connell 1971, Tilman 1994) — seed dispersal is thus an integral component in both schools of thought on plant coexistence.

Seed dispersal and spatial aggregation

Many tropical tree species are aggregated at multiple scales (Condit et al. 2000, Harms et al. 2001, Valencia et al. 2004). At a broad landscape scale most species are restricted to certain habitats due to niche partitioning (Grubb 1977, Denslow 1987, John et al. 2007). This is a consequence of plants faceing trade-offs in their limited resource budgets to survive and reproduce in complex, heterogeneous abiotic and biotic environments and consequently investment in one suite of adaptations necessarily prevents investment in a second. This leads to species being 'filtered' out of environments they are poorly adapted to whilst positively associating to those they possess a suitable suite of traits to tolerate the abiotic and biotic conditions (Comita et al. 2007, Engelbrecht et al. 2007, Kraft et al. 2015). Distributions at a fine-scale are also non-randomly distributed within a species' preferred habitat. Individuals may be to be more or less aggregated than expected at this local scale due to dispersal and density-dependent processes.

Tree seeds can be dispersed by animals (zoochory), wind (anemochory), water (hydrochory) or using ballistic mechanisms (Howe and Smallwood 1982). There is wide variation in the distances seed can be dispersed both within and between these dispersal 'syndromes' (Vittoz and Engler 2007, Muller-Landau et al. 2008, Corlett 2009, Tamme et al. 2014), and trees possessing different dispersal abilities are likely to have contrasting patterns of spatial aggregation (Condit et al. 2000, Plotkin et al. 2002, Seidler and Plotkin 2006). Limited seed dispersal is expected to promote fine-scale spatial aggregation (Bleher et al. 2002, Chave et al. 2002, Svenning and Skov 2002). Spatial aggregation

patterns are, however, also modified by post-dispersal processes, many of which are mediated in either a positive or negative manner by local conspecific densities (Murrell 2009, Bagchi et al. 2011).

Spatial aggregation and fine-scale spatial genetic structure

Seed dispersal can similarly impact the distribution of genes in a population. Many tropical tree species exhibit fine-scale spatial genetic structure (FSGS), the non-random distribution of alleles in a population (Vekemans and Hardy 2004, Hardy et al. 2006, Dick et al. 2008, Kettle et al. 2011a). FSGS is influenced by a variety of species properties, including population density and spatial aggregation patterns, but particularly the reproductive traits of seed and pollen dispersal (Vekemans and Hardy 2004). It develops primarily where seed dispersal is limited, leading to the establishment of related individuals in close proximity and mating between them unless counteracted by pollen dispersal at greater scales (Dick et al. 2008). Fine-scale genetic structure has been widely reported in the Dipterocarpaceae (Ng et al. 2004, Takeuchi et al. 2004, Kettle et al. 2011a, Harata et al. 2012, Tito de Morais et al. 2015), reflecting their limited seed and pollen dispersal. Intense FSGS can erode genetic diversity by elevating levels of inbreeding and facilitating genetic drift between distant sections of the population.

Widespread FSGS in tropical trees could have implications for forests degraded by logging or affected by fragmentation (Lowe et al. 2005, Aguilar et al. 2008, Kramer et al. 2008, Ng et al. 2009, Ismail et al. 2012, Ismail et al. 2014, Vinson et al. 2015). Logging reduces effective population sizes by removing reproductively mature individuals, which in turn alters the spatial distribution of remaining trees (Biscaia de lacerda et al. 2008, Sebbenn et al. 2008). This has the potential to exacerbate intensities of FSGS if pollen exchange is restricted to fewer trees within the aggregation (Stacy et al. 1996, Ghazoul et al. 1998, Ghazoul 2005). Similarly, fragmentation in the absence of gene flow between fragments will accelerate the loss of genetic diversity via genetic drift by reducing effective population sizes and increasing inbreeding (Aguilar et al. 2008, Jones and Comita 2008). In both scenarios, lower rates of outbreeding can either reduce the total population seed crop via the preferential abortion of selfed or inbred seed (Jones and Comita 2008), or increase the number of inbred seed. Inbred seed have lower fitness than out-crossed seed, documented by reduced growth rates and increased mortality (Naito et al. 2005, Naito et al. 2008, Ismail et al. 2014, Nutt et al. in revision), thereby reducing their competitiveness and resulting in reduced natural regeneration. Inbred populations are further impaired by their reduced potential to adapt to environmental change, diminishing the population's overall resilience. The genetic consequences of forest degradation have received limited attention by forest managers and conservationists, yet consideration of FSGS and

gene flow within degraded forests is important to the long-term management of timber tree species (Riina et al. 2014) and those inhabiting fragmented landscapes (although see Lowe et al. 2005, Kramer et al. 2008).

The role of seed dispersal in maintaining resilient plant populations

Most habitats are heterogeneously distributed in a landscape and regional species populations are divided into a number of sub-populations. The movement of individuals at these wider landscape scales, via 'long distance dispersal' events (LDD) (Nathan 2006), is fundamental to the long term persistence of tree populations. In degraded forest landscapes, valuable timber species are harvested, and sections of the once contiguous forest are converted to agriculture leaving remnant fragments. Seed dispersal is integral to maintaining connectivity between fragments. In the absence of pollen dispersal this process allows gene-flow between fragmented sub-populations preventing the loss of genetic diversity via drift and inbreeding (Kramer et al. 2008), and helps form resilient meta-populations (Hanski and Gilpin 1991). Without such dispersal numerous species are likely to be driven to local extirpation. If fragmentation occurs at scales above those of seed dispersal then fragmentation can reduce connectivity (Soons et al. 2005, Montoya et al. 2008), and hence limit recolonization of extirpated sites. Maximum dispersal distance per reproductive event or per generation determines the rates at which tree species can migrate across a landscape, critical to species response to environmental and climate change (Higgins and Richardson 1999, Cain et al. 2000, Corlett 2009).

Quantifying LDD is therefore important to adequately parameterise these processes and model how species will be impacted by forest fragmentation and climate change. LDD events necessarily deal with dispersal events at the extreme tail of a dispersal kernel (a probability distribution function describing the movement of diaspore (Nathan and Muller-Landau 2000)). They are notoriously difficult to measure and model phenomenologically, as such events occur at low probabilities. Instead, mechanistic models of seed dispersal are used to estimate LDD (Higgins et al. 2003, Soons et al. 2004, Nathan 2006, Nathan et al. 2008). The most advanced mechanistic models of seed dispersal include parameters of wind speed, turbulence and updrafts, boundary layer effects of surrounding vegetation on wind conditions (Tackenberg 2003, Kuparinen et al. 2007, Bohrer et al. 2008, Greene and Quesada 2011, Nathan et al. 2011, Damschen et al. 2014), and plant traits such as height of seed release (Thomson et al. 2011), abscission threshold (Soons and Bullock 2008, Maurer et al. 2013) and the terminal velocity of the seed — a trait currently unavailable for most anemochorous tree species

(Tamme et al. 2014). To adequately investigate these processes using mechanistic models for wind dispersed tropical trees we need quantitative estimates of their terminal velocity.

Forest degradation in Southeast Asia

Human civilisation has destroyed half of the world's trees (Crowther et al. 2015). The tropical lowland forests of Southeast Asia have been particularly affected by forest degradation, driven by sequential logging and land-use change particularly for oil palm and timber plantations (Koh and Wilcove 2008, Sodhi et al. 2009, Sodhi et al. 2010, Wilcove et al. 2013). Deforestation in this region has been rapid with the lowland forests of the Sundaland biogeographic region now reduced to under 30% of their original extent (Sodhi et al. 2009, Wilcove et al. 2013). With high levels of endemism in plant and vertebrate biodiversity the region is considered a biodiversity 'hotspot' (Myers et al. 2000). The opportunity costs of forest protection in this region are high (Edwards et al. 2011, Fisher et al. 2011a, Fisher et al. 2011b), encouraging continued forest loss at annual deforestation rates of 1% during the 21st Century, (Miettinen et al. 2011). Much of the remaining forest cover has been logged at least once (Reynolds et al. 2011, Bryan et al. 2013), and is retained as fragments within human-modified agricultural landscapes. In the Malaysian states of Sabah and Sarawak, Northern Borneo, less that 10% of forest remains in primary condition within protected areas (Bryan et al. 2013).

The Dipterocarpaceae — the dominant tree family of SE Asia's lowland tropical forests

The forests of Southeast Asian are dominated by the Dipterocarpaceae. This pan-tropical tree family reaches its maximum diversity on the island of Borneo, with over 270 species (Newman et al. 1996), up to 87 of which can be present in a single 50 ha area (Davies et al. 2005). They are not only species rich, but found in extremely high abundance, particularly as canopy and emergent trees, and consequently account for 28–53% of above-ground biomass (Ashton and CTFS Working Group 2004).

Dipterocarpaceae flower and fruit synchronously on an supra-annual periodicity in forest wide 'general flowering' (GF) events (Ashton 1988, Sakai 2002, Brearley et al. 2007). These events are thought to be triggered by prolonged droughts and reductions in minimum air temperatures (Ashton 1988, Ashton et al. 1988, Sakai 2002, Brearley et al. 2007, Kobayashi et al. 2013). Up to 90% of mature dipterocarps from over 40 species may participate in a single GF event (Curran 1999). Flowers are hermaphroditic and pollinated by a range of insects depending on size, including thrips, beetles, moths, and the giant Asian honey bee (*Apis dorsata*) (Ashton 1983, Momose et al. 1998, Sakai 2002, Kettle et al. 2011b). Flowering is sequential but fruiting is synchronous. Synchronous fruiting is

hypothesized to satiate large mobile vertebrate seed predators which can decimate seed crops and lead to complete reproductive failure during smaller fruiting events (Curran and Leighton 2000, Curran and Webb 2000). Sequential flowering is considered an adaptation to avoid competition for pollinators (REF). Fruit are recalcitrant and germinate rapidly (Tompsett 1985, Tompsett 1998, O'Brien et al. 2013), forming persistent seedling banks.

Dipterocarp fruit are composed of a nut and calyx, the sepals of which become elongated to form wings in most species (Ashton 2004). These wings cause the fruit to gyrate once released from the mother tree, but this action does not generate lateral movement and therefore their dispersal is dependent on the direction and velocity of the wind. Whilst there are observations of dipterocarp fruit dispersing many hundreds of meters during extreme weather events (Webber 1934), dispersal is considered primarily local, with fruit predominantly falling below the crown of the mother tree (Tamari and Jacalne 1984, Itoh et al. 1997, Osada et al. 2001). Whilst there have been some limited attempts to quantify dispersal for this family (Osada et al. 2001), most of our understanding is anecdotal or comes from more observational work recording distances to the nearest fruiting tree – which tells us nothing of the relative quantities dispersing each distance – and therefore quantitative predictions of dipterocarp fruit dispersal are absent. Nevertheless, mechanistically there is a strong expectation that dipterocarp fruit dispersal is determined by fruit morphology (Suzuki and Ashton 1996, Osada et al. 2001), as has been observed in other winged and gyration dispersed fruit (Green 1980, Augspurger 1986, Augspurger and Franson 1987).

Outline of the thesis

This thesis focuses on seed dispersal in the Dipterocarpaceae. First, experimental approaches are used to quantify dispersal and link this to easily measured fruit morphological traits. Second, we used tree coordinate data from a long term forest plot to investigate how seed dispersal and life-history traits influence spatial aggregation patterns in this family, independently of spatial distributions driven by environmental filtering or habitat associations. Lastly we investigate the consistency of patterns of fine-scale spatial genetic structure across forests sites. A brief introduction to each of the chapters is provided below.

Chapter 2: Predicting dipterocarp dispersal

There is wide variation in fruit size and morphology in the Dipterocarpaceae. We performed experimental releases of fruit from 13 dipterocarp species to investigate the effect of variation in fruit

morphology on dispersal distance. We hypothesize that fruit with greater 'inverse wing-loadings' (IWL) — the ratio of fruit wing area to fruit mass — would disperse farther distances.

Chapter 3: Predicting the terminal velocity of dipterocarp fruit

Terminal velocity, the rate at which seed fall through the air column, is a critical parameter in mechanistic models of seed dispersal as it determines the length of time seed are in the air column and can be moved laterally by the wind. Dipterocarpaceae fruit are winged and disperse via gyration. Using experimental releases of dipterocarp fruit, we investigate whether fruit terminal velocity can be predicted by fruit wing-loading, the fruit mass divided by wing area.

Chapter 4: Spatial aggregation in the Dipterocarpaceae

The Dipterocarpaceae are hypothesized to vary widely in their fruit dispersal potential and wood density, a surrogate proxy for regeneration strategy. At the same time, the majority of dipterocarp species show strong habitat associations to particular soil types or elevations. We explore spatial aggregation patterns of mature individuals from 28 dipterocarp species located in a 160 ha forest in Sepilok Forest Reserve, Malaysian Borneo. Using an emerging statistical method we remove the spatial aggregation signal from species' habitat associations to assess the relative importance of dispersal limitation and regeneration strategy on spatial aggregation patterns in this family.

Chapter 5: Consistency of dipterocarp FSGS between sites

The scale and intensity of fine–scale spatial genetic structure (FSGS) in the *Dipterocarpaceae* is influenced by a range of species traits including flower size, fruit dispersal potential, wood density, population density and clump size. In this chapter we explore the role that differences in site environmental conditions, specifically topographical heterogeneity, might play in shaping patterns of FSGS in the Dipterocarpaceae. Using nuclear microsatellites we analyse FSGS in mature individuals from three species of dipterocarp present in the Danum Valley 50 ha CTFS – ForestGEO FDP plot, and compare the scales and intensity of FSGS observed at Danum to the same species located in three different lowland mixed dipterocarp forest plots (Lambir Hills, Pasoh and Sepilok).

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Predicting dispersal of auto-gyrating fruit in tropical trees: a case study from the Dipterocarpaceae

with Robert Bagchi, Judith Ellens, Chris Kettle, David Burslem, Colin Maycock, Eyen Khoo & Jaboury Ghazoul

ABSTRACT

Seed dispersal governs the distribution of plant propagules in the landscape, and hence forms the template on which density-dependent processes act. Dispersal is therefore a vital component of many species coexistence and forest dynamics models, and is of applied value in understanding forest regeneration. Research on the processes that facilitate forest regeneration and restoration is given further weight in the context of widespread loss and degradation of tropical forests, and provides impetus to improve estimates of seed dispersal for tropical forest trees. Southeast Asian lowland rainforests, which have been subject to severe degradation, are dominated by trees of the Dipterocarpaceae family which constitute over 40% of forest biomass. Dipterocarp dispersal is generally considered to be poor given their large, gyration dispersed fruits. However there is wide variability in fruit size and morphology which we hypothesize mechanistically underpins dispersal potential through the lift provided to seeds mediated by the wings. We explored experimentally how the ratio of fruit wing area to mass ('inverse wing loading', IWL) explains variation in seed dispersal kernels among 13 dipterocarp species by releasing fruit from a canopy tower. Horizontal seed dispersal distances increased with IWL, especially at high wind speeds. Seed dispersal of all species was predominantly local, with 90% of seed dispersing <10 m, although maximum dispersal distances varied widely among species. We present a generic seed dispersal model for dipterocarps based on attributes of seed morphology, and provide modelled seed dispersal kernels for all dipterocarp species with IWLs of 1 to 50, representing 75% of species in Borneo.

INTRODUCTION

Seed dispersal represents the primary, and often sole, opportunity for seed-bearing plants to colonize new habitats and overcome the constraints to the survival of progeny close to conspecific adults. Differential seed dispersal among species contributes to plant community structure and dynamics by determining which species or combination of species reach suitable establishment sites. Trade-offs among traits governing dispersal, establishment, and survival mean that dispersal can have long-term implications for plant community structure (Rees et al. 2001). Furthermore, seed dispersal is an integral process involved in several mechanisms of species coexistence (Chesson 2000), including neutral theory (Hubbell 2001), distance- or density-dependence (Janzen 1970, Connell 1971) and the competition-colonization trade-off (Tilman 1994). Seed dispersal is similarly critical to species persistence, as the negative effects of small population size may be ameliorated by dispersal capability through the formation of more resilient metapopulations (Hanski et al. 2013) and by maintaining gene flow between populations. Long distance dispersal capability determines rate of population spread into favourable habitat, for example post-glacial range expansion or climate driven range shifts, and of founding events in new locations such as oceanic islands.

Understanding seed dispersal is therefore of fundamental importance to plant ecology, and seed dispersal capability is consequently included in a range of dynamic models of plant ecological processes. Despite this central role there remains a dearth of accurate dispersal kernels for the majority of plant species, and those available are often for species from temperate grasslands or temperate forests. Many models that include a seed dispersal component, including those that address climate-driven range shifts, species coexistence, spatial aggregation patterns, and habitat connectivity, are limited to generalizing dispersal capacity across many species using, for example, dispersal syndromes (Seidler and Plotkin 2006, Bagchi et al. 2011). Increasing the number of taxonomic groups or fruit morphologies for which we have accurate dispersal kernels can therefore improve ecological modelling of seed dispersal and derived processes.

An understanding of seed dispersal also has applied relevance for forest management, especially in the context of anthropogenic environmental change. Of particular interest are the tropical forests of Southeast Asia, which have the highest annual deforestation rates in the tropics (Sodhi et al. 2009). Much of the remaining forest cover is degraded and fragmented, with uncertain implications for the viability of remaining tree populations and associated biodiversity (Sodhi et al. 2009, Wilcove et al. 2013). Given current economic pressures, logging and forest conversion to agriculture are likely to continue (Fisher et al. 2011).

Southeast Asian lowland rainforests are dominated by trees of the Dipterocarpaceae family, which generally constitute over 40% of basal area (Newbery et al. 1992, Curran and Leighton 2000, Davies et al. 2005). The dispersal of the mostly winged fruits of dipterocarps is generally considered to be poor, but there is wide variability in fruit size and morphology which might reflect species-specific differences in seed dispersal. In view of the substantial fragmentation and degradation of Southeast Asian forests, a thorough understanding of dipterocarp seed dispersal could provide insights into changing patterns of regeneration, including changes to the template on which density-dependence might act, and hence shifts in future species composition.

Dipterocarp fruit are composed of a nut and calyx. In most species the sepals become elongated to form wings which cause fruits to gyrate when abscised (Suzuki and Ashton 1996). Substantial variation exists in both nut and wing size, and in wing number which varies from zero to five. Such variation suggests substantial differences in seed dispersal among dipterocarp species based on wing and nut morphology. Hereafter we refer to seed dispersal rather than fruit dispersal as dipterocarp fruit are single seeded, and lack of a fleshy, nutritious animal-dispersed pericarp limits potential for secondary dispersal. Thus fruit and seed dispersal is equivalent.

Green (1980) observed that the rate of descent of single winged fruits (samaras) is proportional to the square root of fruit 'wing-loading', defined as fruit mass divided by wing surface area. Dispersal distance of a falling fruit can therefore be modelled using a simple ballistic model composed of the terminal velocity of the fruit, height of release, and lateral wind speed (Nathan et al. 2011). A slower rate of descent increases the time available for fruit to be dispersed horizontally (Green 1980). An inverse relationship is therefore expected between wing loading and dispersal distance (Augspurger and Franson 1987, Osada et al. 2001). Wing loading values can similarly be calculated for dipterocarps, and seed dispersal potential ranked on this basis (Suzuki and Ashton 1996). We hypothesize that fruit morphology mechanistically underpins dispersal distance in dipterocarps through the lift provided to seeds mediated by wing loading. We therefore hypothesize that species-level seed dispersal is correlated to wing loading. We tested this hypothesis experimentally by releasing over 650 fruit from 13 species, representing a broad range of wing loading values, from a 30 m canopy tower at a site in Malaysian Borneo to determine seed dispersal distances. Using the data generated, we constructed generic models of seed dispersal distance as a function of inverse wing loading (IWL; ratio of wing area to fruit mass) to approximate seed dispersal kernels for all dipterocarp species with IWLs of 1 to 50, which spans a range that includes 75% of all dipterocarp species found in Borneo.

METHODS

Fruit collection

We collected mature fruit belonging to 13 dipterocarp species from three genera (10 *Shorea*, two *Dipterocarpus,* and one *Hopea*) (Table 1) growing in Sepilok Forest Reserve (SFR), Malaysian Borneo (5°51' N 117°56' E). SFR is a 4420 ha fragment of primarily tropical lowland dipterocarp forest, ranging in altitude 0 – 170 m.a.s.l. (Fox 1973). Fruit were collected from the ground during the 2010 community-wide mast fruiting event from the vicinity of identified mother trees in a 160 ha inventoried plot of mature dipterocarps (diameter at breast height (d.b.h.) > 30 cm). Any fruit exhibiting external signs of predation were excluded.

Wing loading calculations

The air-dried mass (g), and lengths and widths of the wings (cm) were measured for each fruit. From these data the 'inverse wing loading' (IWL) was calculated, defined as 'long' wing area divided by mass. Wing areas in the genera *Dipterocarpus* and *Hopea* were calculated by summing the product of wing length and wing width of their two wings. Species in the genus *Shorea* have three 'long wings' and two 'short wings'. We excluded short wings from the IWL calculation as their areas are much smaller than that of the long wings and we assume they contribute little to lift (Suzuki and Ashton 1996). The wing area of *Shorea* was therefore calculated as the total area of the longest and shortest long wings multiplied by 1.5 to account for the third long wing. We use the inverse of wing loading rather than the traditional wing loading as this value generates a more intuitive dispersal index where higher values equate to higher dispersal distances. Moreover, IWL also avoids mathematical inconsistencies arising from the inclusion of fruits that lack wings (e.g. *S. xanthophylla*). Each fruit was uniquely numbered and partially covered by a thin layer of spray paint to aid recovery.

Experimental release

Dispersal was assessed by releasing fruits individually from a 30 m canopy observation tower. The tower is located in a forest gap where no trees taller than 28 m are located within 10 m. A single fruit was released for each species in turn before repeating the cycle so as to avoid temporal autocorrelation, which might be relevant on account of changing wind speeds. Wind speed (m/s) was recorded for the duration of each individual fruit's flight using an electronic anemometer (Windmaster 2, Kaindl Electronic, Germany) located at the release point. The maximum and mean wind speed per

Table 1. Fruit morphology measures (± standard error) and dispersal parameters for the fruit of the 13 dipterocarp species released from the 30 m canopy tower.

Species	Number of fruit	Mean Fruit dry mass (g)	Mean IWL (cm^2/g)	Minimum distance dispersed (m)	Maximum distance dispersed (m)	Median distance dispersed (m)	90th percentile distance dispersed (m)
Dipterocarpus humeratus	59	19.85 (± 1.097)	9.29 (± 0.27)	0.86	10.86	3.84	7.94
Dipterocarpus kerrii	75	6.04 (± 0.267)	8.93 (± 0.47)	0.83	10.94	4.00	8.14
Hopea beccariana	38	0.16 (± 0.004)	26.39 (± 0.83)	1.30	19.90	3.96	11.26
Shorea acuminatissima	60	0.76 (± 0.023)	17.37 (± 0.75)	1.00	9.65	3.40	6.75
Shorea argentifolia	55	0.68 (± 0.022)	44.60 (± 1.86)	1.40	39.54	8.20	15.58
Shorea beccariana	51	3.97 (± 0.083)	21.55 (± 0.45)	0.42	17.82	6.57	12.2
Shorea falciferoides	61	1.64 (± 0.094)	24.85 (± 1.03)	1.11	16.33	5.20	10.61
Shorea gibbosa	60	1.04 (± 0.038)	11.53 (± 0.58)	0.94	7.45	2.62	3.95
Shorea macroptera	54	2.01 (± 0.121)	39.83 (± 1.98)	1.22	19.41	7.01	12.57
Shorea mexistopteryx	48	11.79 (± 0.536)	16.49 (± 0.73)	0.94	22.73	5.42	10.76
Shorea seminis	61	1.94 (± 0.116)	1.97 (± 0.14)	0.76	6.33	1.99	4.13
Shorea smithiana	61	2.64 (± 0.113)	20.95 (± 0.65)	0.86	20.71	4.84	12.00
Shorea xanthophylla	45	2.48 (± 0.235)	0.00 (± 0.00)	0.32	8.26	1.84	4.52

release were obtained from these measurements. Subsequently, the area surrounding the tower was exhaustively searched for marked fruit, and the horizontal distance travelled by each fruit was measured using a laser distance meter (Leica Disto A8, Leica Geosystems, Switzerland). The dispersal distance was measured for fruits reaching the forest floor only, as some fruits became entangled in understory vegetation. More than 90% of released fruits were however recovered. We assume that the dispersal from gyration encapsulates the full dispersal potential in the field, though there have been some observations of rare short-distance secondary dispersal by rodents (Maycock et al. 2005, Wells and Bagchi 2005).

Statistical analysis

A linear mixed-effects model (LMM) was fitted to the data using the lme4 package (version 1.0.5) in R-3.0.2 (R Core Team, 2013). The response was measured distance dispersed and the predictors were individual fruit IWL, wind speed during release and their interaction. Maximum wind speed was used instead of mean wind speed as this greatly improved model fit (model AIC reduced by 12 points). To control for the effect of intra- and inter-specific differences in fruit morphology on dispersal, we included random effects for mother tree nested within species, nested in turn within genus. The mother tree and genus terms were subsequently dropped from the model as both accounted for $< 0.1\%$ of the total variance in the response. Plus one was added to IWL and maximum wind speed to account for zeroes in these data and subsequently all variables were log-transformed to ensure that the residuals were normally distributed. Given difficulties in modeling the long tail of dispersal kernels (Nathan 2006), the variance was expected to increase with distance dispersed. The full model therefore initially explicitly modeled the variance as a power function of the expected mean (using the nlme package, version 3.1.113). However, this model did not perform better than a simpler homoscedastic model, so the variance function was dropped for subsequent analyses.

Dispersal kernels and their 95% confidence bounds were estimated using a parametric bootstrapping approach implemented with the "bootMer" function in lme4. Approximate *p*-values for the LMM parameter estimates were calculated from the bootstrap models following Gelman & Hill (2007). Details of this bootstrap approach and approximate *p*-value calculations are provided in the supplements (Table S1). Dispersal kernels for a sample of 50 hypothetical dipterocarp species with IWLs spanning 1 to 50 were simulated using this bootstrapping technique for a range of wind speeds spanning 1to10 m/s (Table S2). These IWL values represent 75% of the Dipterocarpaceae on Borneo (Data from Newman et al. (1996, 1998). IWLs calculated using long wing area / nut volume as mass data unavailable).

RESULTS

Substantial variation in fruit morphology and distances dispersed were observed (Table 1). Mean IWL values ranged from 0 in wingless *S. xanthophylla*, to 44.60 (± 1.86) cm^2/g in *S. argentifolia*. These species recorded the shortest and furthest dispersal distances of 0.32 m and 39.54 m respectively. Fifty percent of all released fruits dispersed less than 4 m, and 90% were recovered within a horizontal distance of 10.5 m of the release point (Table 1). The majority of fruits were released at relatively low wind speeds (mean maximum wind speed during releases was 1.72 m/s, and the highest recorded wind speed was 10.5 m/s). The mean maximum wind speed of 1.72 m/s observed corresponds closely to the mean annual wind speed of 2.05 m/s (2000-2013; data from Sandakan Airport 11 km distant, http://www.tutiempo.net/en/) and therefore conditions during the releases were close to the site's normal atmospheric conditions.

The best fitting LMM model included IWL, maximum wind speed and their interaction as independent variables and species as a random effect. Significant positive effects on dispersal distance were found for IWL ($\beta = 0.186$, 95% C.I. = 0.0759 to 0.237, *p*-value = 0.001) and the interaction between IWL and maximum wind speed ($\beta = 0.191$, 95% C.I. = 0.115 to 0.259, *p*-value = 0.001), indicating that fruit disperse greater distances with higher IWLs and that this is especially true at higher wind speeds (Table 2). Dispersal kernels and associated 95% confidence bands were generated for each of the 13 species released at the mean maximum wind speed of 1.72 m/s (Figure 1). The dispersal kernels of species with greater IWLs had longer tails with wider 95% confidence intervals (shown clearly in supplement S3), as expected given the important effects of IWL and its interaction with maximum wind speed.

Table 2. Parameter estimates from the bootstrapped LMM model fitting IWL, maximum wind speed and their interaction to log-transformed fruit dispersal distance of the 13 species released.

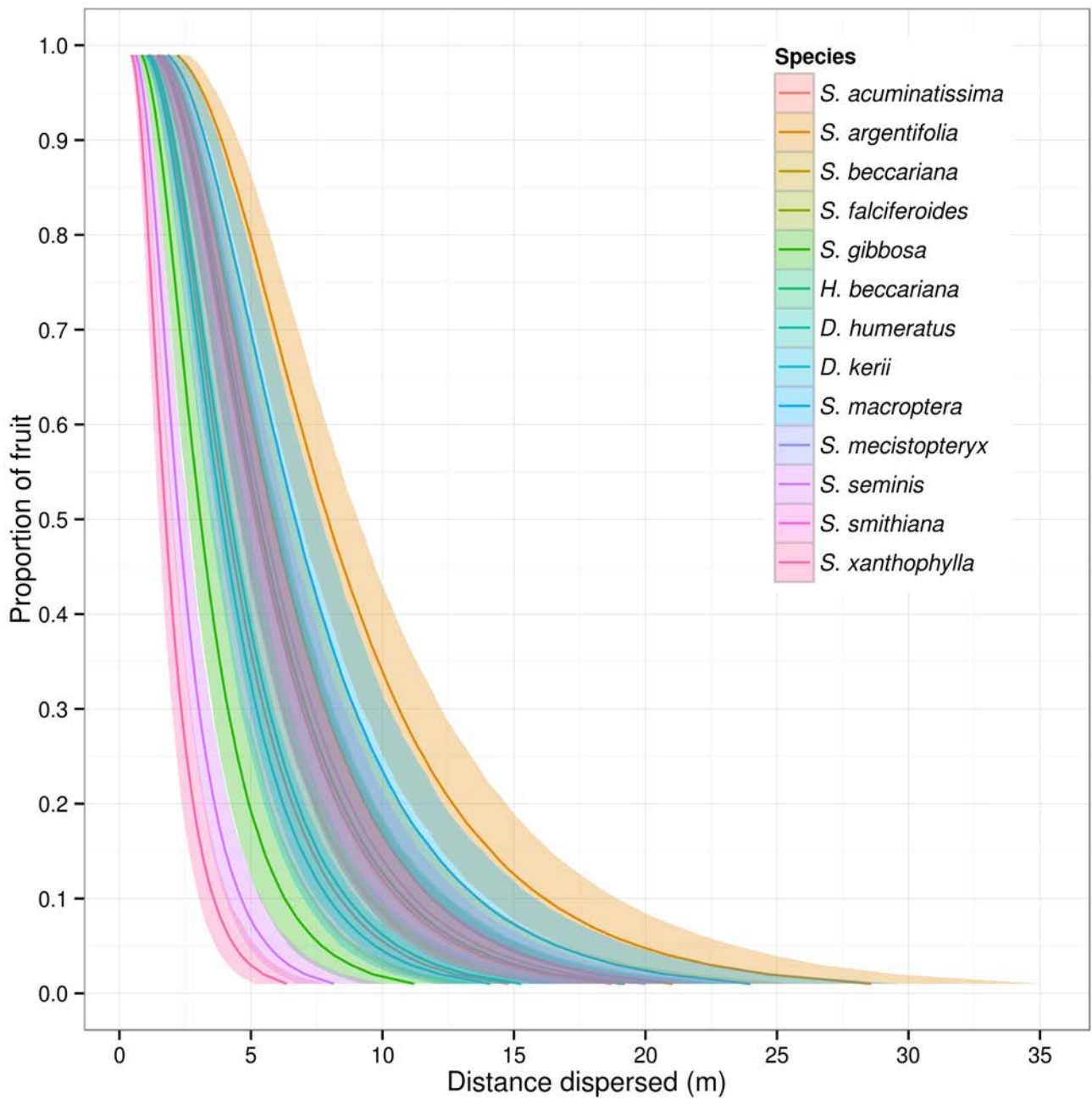| Parameter	Estimate	95% C.I.	Approximate *p*-value
Intercept	0.517	(0.377, 0.817)	0.001
Log(IWL + 1)	0.186	(0.0759, 0.237)	0.001
Log(Maximum wind speed + 1)	-0.036	(-0.231, 0.171)	0.816
Log(IWL +1 * Maximum wind speed + 1)	0.191	(0.115, 0.259)	0.001
Residual error (st. Dev.)	0.558	(0.530, 0.591)	
Species random effect (st. Dev)	0.154	(0.144, 0.235)	

Figure 1. Simulated dispersal kernels of the 13 observed species released at the mean maximum wind speed of 1.72 m/s and associated 95% confidence bands.

Table 3. Comparison of median predicted dispersal distances (m) from the bootstrapped LMM model presented in this study and distance predicted from the ballistic model when released from a height of 30 m and wind speed of 1.72 m/s.

Species	Mean IWL (cm^2/g)	(Wing-loading)$^{1/2}$ *	Predicted distance dispersed (m)	
			LMM model	Ballistic model**
Dipterocarpus humeratus	9.29 (± 0.27)	326.37	4.25	21.93
Dipterocarpus kerrii	8.93 (± 0.47)	346.34	3.90	20.54
Hopea beccariana	26.39 (± 0.83)	189.54	5.30	40.45
Shorea acuminatissima	17.37 (± 0.75)	231.89	4.13	32.07
Shorea argentifolia	44.60 (± 1.86)	147.71	7.90	54.53
Shorea beccariana	21.55 (± 0.45)	207.50	5.86	36.42
Shorea falciferoides	24.85 (± 1.03)	199.76	5.31	38.05
Shorea gibbosa	11.53 (± 0.58)	292.07	3.08	24.78
Shorea macroptera	39.83 (± 1.98)	162.65	6.70	48.50
Shorea mexistopteryx	16.49 (± 0.73)	242.07	5.48	30.55
Shorea seminis	1.97 (± 0.14)	724.03	2.27	9.41
Shorea smithiana	20.95 (± 0.65)	212.99	5.18	35.34
Shorea xanthophylla	0.00 (± 0.00)	0.00	1.76	NA

* Mean IWL (cm^2/g) was converted to (Wing-loading)$^{1/2}$ (in unit millidynes cm^2) by first converting fruit mass (g) to millidynes and dividing by wing area (cm^2), before square-rooting this value.

** The rate of descent V_t per species was calculated from the regression fitted values from 'helicopter' fruit class from table 3 in Augspurger (1986).

DISCUSSION

We found significant differences in dispersal distance among dipterocarp species based on their fruit morphologies: larger wing areas relative to fruit mass (IWL) facilitates lateral dispersal. Wind speed amplified these effects by increasing seed dispersal for all winged species, but particularly those with high IWL. Seed dispersal for all species was highly localized, with only 10% of fruit dispersing beyond 10 m. Although our experimental results were generated during a period of comparatively low wind speed, variation in wind speed during the course of the experimental releases allows us to build models from which dispersal distances at higher wind speed might be projected. We discuss our model results in relation to the theoretically predicted dispersal distances from mechanistic ballistic models and previous dipterocarp seed dispersal studies. Further, we highlight potential applications of the seed dispersal kernels generated using the LMM model.

The theoretical mechanisms linking wing-loading measurements to dispersal distance are well established (Nathan et al. 2011), and experimental tests confirm that dispersal distances increase with both increasing wing area to mass ratio and increasing wind speed (Green 1980, Augspurger 1986, Augspurger and Franson 1987, Greene and Johnson 1989). The mean dispersal distances predicted using the LMM developed in this study (Table 3) are lower than those predicted by the simple ballistic model of Nathan et al. (2011), as used in previous studies (Green 1980, Augspurger 1986, Matlack 1987). This in itself is not surprising, as the ballistic model applies a constant lateral wind speed throughout each fruits' fall. Whilst this might be applicable to seed dispersal in an open landscape (Nathan et al. 2008), it does not reflect wind speed variation within a tropical forest where a rapid decline in wind speed is encountered with increasing vertical displacement beneath the forest canopy (Aoki et al. 1975, Whitmore 1998). The ballistic model estimates are hence idealistic, inappropriate for forest conditions, and therefore likely to over-estimate dispersal distances in tropical rain forest settings. More recent mechanistic models of wind dispersal do incorporate complex wind dynamics and turbulence (Kuparinen et al. 2007, Nathan et al. 2011, Fontan et al. 2013, Damschen et al. 2014), but these require accurate and continuous measures of wind speed along multiple axes and heights within the canopy and are hence generally restricted to computer simulations or laboratory experiments. These data were not available in this study, and obtaining such information is neither practical nor relevant for the purpose of generating generic dispersal models. Nonetheless, we are able to differentiate seed dispersal kernels among species based on fruit morphologies.

Our results corroborate experimental and observational studies in concluding that seed dispersal in this family is predominantly local (Whitmore and Burnham 1984, Ashton 2004). Under

similar wind conditions to this study (mean and maximum wind speed of 0.65 and 1.93 m/s), the mean dispersal distances of *Dipterocarpus crinitus* and *Dipterocarpus cornutus* fruits (IWL 10.62 and 7.91 respectively) released from a 40 m canopy tower were 9 and 7 m respectively (Osada et al. 2001). Itoh et al. (1997) observed the greatest density of newly established seedlings within 10 m of the mother tree for *Dryobalanops lanceolata* and *Dryobalanops aromatica*, with none found beyond 40 m. Fox (1972) observed a rapid decrease in fruit dispersing from 10 to 40 m across 12 dipterocarp species from four genera (*Dipterocarpus*, *Dryobalanops*, *Parashorea* and *Shorea*), with on average only 9.1 % of fruit reaching 40 m. Similarly, data compiled by Tamari and Jacalne (1984) from 12 species from the same four genera (three species overlapping with Fox) recorded maximum dispersal distances ranging 20 to 80 m, with the majority of seed dispersing 20 – 40 m. Even more extreme, wingless fruits or those possessing rudimentary but ineffective wings precluding gyration (30% of dipterocarps) (Suzuki and Ashton 1996) do not disperse beyond the crown of the mother tree; for example, 98% of *Shorea fallax* fruit fell within 10 m (Whitmore and Burnham 1984). Ridley's premise (1930) that, barring extreme events, dipterocarp species attain maximum fruit dispersal distances of 100 yards (90 m) appears sound. Nonetheless, it is the extreme events that might have disproportionate ecological importance (Nathan 2006, Nathan et al. 2008).

The maximum observed dispersal distance of 39.54 m in this study, by a single *Shorea argentifolia* seed, is 50% of the maximum observed by Tamari and Jacalne (1984) and short of Ridley's 90 m (1930). This suggests that whilst our study models short distance dispersal, the experimental release of fruit did not reflect the full range of natural dispersal events. This is likely due to the normal atmospheric conditions and hence relatively low wind speeds under which the experiment was conducted. However, the release height of 30 m is also slightly lower than the maximum heights of the study species of 40 – 60 m (Ashton 2004). Our models also take no account of wind turbulence (Tackenberg 2003, Bohrer et al. 2008). Long distance dispersal of wind-dispersed seed is primarily expected to occur with unusual or extreme atmospheric conditions, particularly those which cause strong updrafts (Tackenberg 2003, Wright et al. 2008). Fruits might also be disproportionately released during periods of high wind speed or persistent updrafts, such as those preceding storm events (Soons and Bullock 2008, Greene and Quesada 2011, Maurer et al. 2013). As Ridley (1930) acknowledges, this is pertinent to dipterocarp dispersal, with anecdotal reports of fruit being dispersed many 100s of meters by strong updrafts (Webber 1934, Whitmore and Burnham 1984). The frequency of such events, the dispersal distances attained, and subsequent fate of these seeds remains unknown. Nevertheless, the positive interaction effect among wind speed and IWL observed in our model implies that species with high IWL might disproportionately extend their seed

dispersal range during high winds (Supplement S3). IWL might therefore serve as a simple, albeit crude, proxy for LDD in this system, allowing conservationists and forest managers to identify dipterocarp species that might be most reproductively vulnerable to habitat fragmentation.

Our results have allowed us to develop a generalised dispersal model for dipterocarp species based on only two variables, IWL and wind speed. Using this model, we provide projected seed dispersal kernels for all dipterocarp species with IWLs of 1 to 50, representing 75% of those found in the region (Table S2). We additionally provide the parameter estimates for our bootstrapped LMM model (Table S1) for simulating dispersal kernels of any dipterocarp species. We believe that this model provides a robust basis for estimating dispersal kernels across the family under a range of typical wind conditions. This model can be extended to higher wind speeds, but this requires further experimental validation. This model has utility for projecting species' dispersal patterns, information that is particularly relevant in the context of degraded, logged and fragmented forests where patterns of gap formation and distribution might be very different to that of undisturbed forests. Furthermore, variation in IWL provides a theoretical framework to guide trait-based analyses of dipterocarp ecology (McGill et al. 2006, Westoby and Wright 2006), including trade-offs in reproductive traits (Westoby et al. 1996), demographic rates (Poorter et al. 2008) and community assembly.

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SUPPLEMENTARY INFORMATION

Supplement S1

Generating dispersal kernels and calculation of approximate *p*-values

Dispersal kernels and their confidence intervals were estimated using a parametric bootstrapping approach implemented with the "bootMer" function in lme4. This function generates a new response by simulating a set of residuals drawn from a normal distribution of mean 0 and variance equal to the residual variance of the model, and adding this to the model fitted values. In addition, the random effects were dealt with in two ways: (1) the best linear unbiased predictor (BLUP) (Pinheiro and Bates 2000) of the difference of each species' mean dispersal distance to the expectation based on the fixed effects was added to the simulated responses for that species; or (2) new BLUPS were drawn for each species from a normal distribution of mean 0 and variance equal to the variance component for species from the model. The first approach (hereafter the "known species" approach) corresponds to the situation where we are simulating dispersal for the set of species used to fit the original model. In the second approach (hereafter "new species" approach), the simulated data represents a new set of species drawn from the same distribution as the original set. We ran 1000 simulations under both approaches and then refitted the model to these simulated data. This resulted in 1000 simulated models from both approaches.

Dispersal kernels for each species, and their confidence bands, were estimated from the prediction intervals of the simulated "known species" models given the mean IWL for the species and setting maximum wind speed to the mean observed during the experiment (1.72 m/s). We used each of the 1000 models to simulate 1000 dispersal distances for each species. These distances were simulated by summing the model's expectation for the species and a vector of 1000 random numbers drawn from a normal distribution with mean 0 and variance equal to the model's residual variance. We back-transformed the distances to the original scale (by taking the exponent) and then extracted the percentiles of these distances between 1 and 99 with increments of 1. We calculated the median distance for each percentile across the 1000 simulated "known species" models. This value represents the distance to which the corresponding percentage of seeds disperses. Confidence bands were similarly estimated as the 0.25 and 0.975 quantiles across the 1000 models for each percentile. Dispersal kernels for a sample of 50 hypothetical dipterocarp species with IWLs spanning 1 to 50

were simulated in a similar method to above; however the models from the "new species" approach were used as species identities were not known.

The calculation of *p*-values, and hence testing of hypotheses using LMM is much debated and no consensus methodology has emerged. The bootstrap approach allows us to circumvent these problems by calculating approximate, two-tailed *p*-values from the posterior distribution of the 1000 models as recommended by Gelman & Hill (2007) using the formula:

$$p = 1 - 2 \left| \frac{x}{1000} - 0.5 \right|,$$

where *x* equals the number of samples greater than zero.

Supplement S2

Table S1. Parameter estimates from the bootstrapped LMM model fitting IWL, maximum wind speed and their interaction to log-transformed fruit dispersal distance using the "new species" approach for unidentified dipterocarps.

Parameter	Estimate	95% C.I.	Approximate p-value
Intercept	0.559	(0.269, 0.838)	0.001
Log(IWL + 1)	0.170	(0.071, 0.274)	0.001
Log(Maximum wind speed + 1)	-0.0353	(-0.244, 0.173)	0.802
Log(IWL +1 * Maximum wind speed + 1)	0.189	(0.116, 0.264)	0.001
Residual error (st. Dev.)	0.558	(0.531, 0.588)	
Species random effect (st. Dev)	0.152	(0.106, 0.274)	

Supplement S3
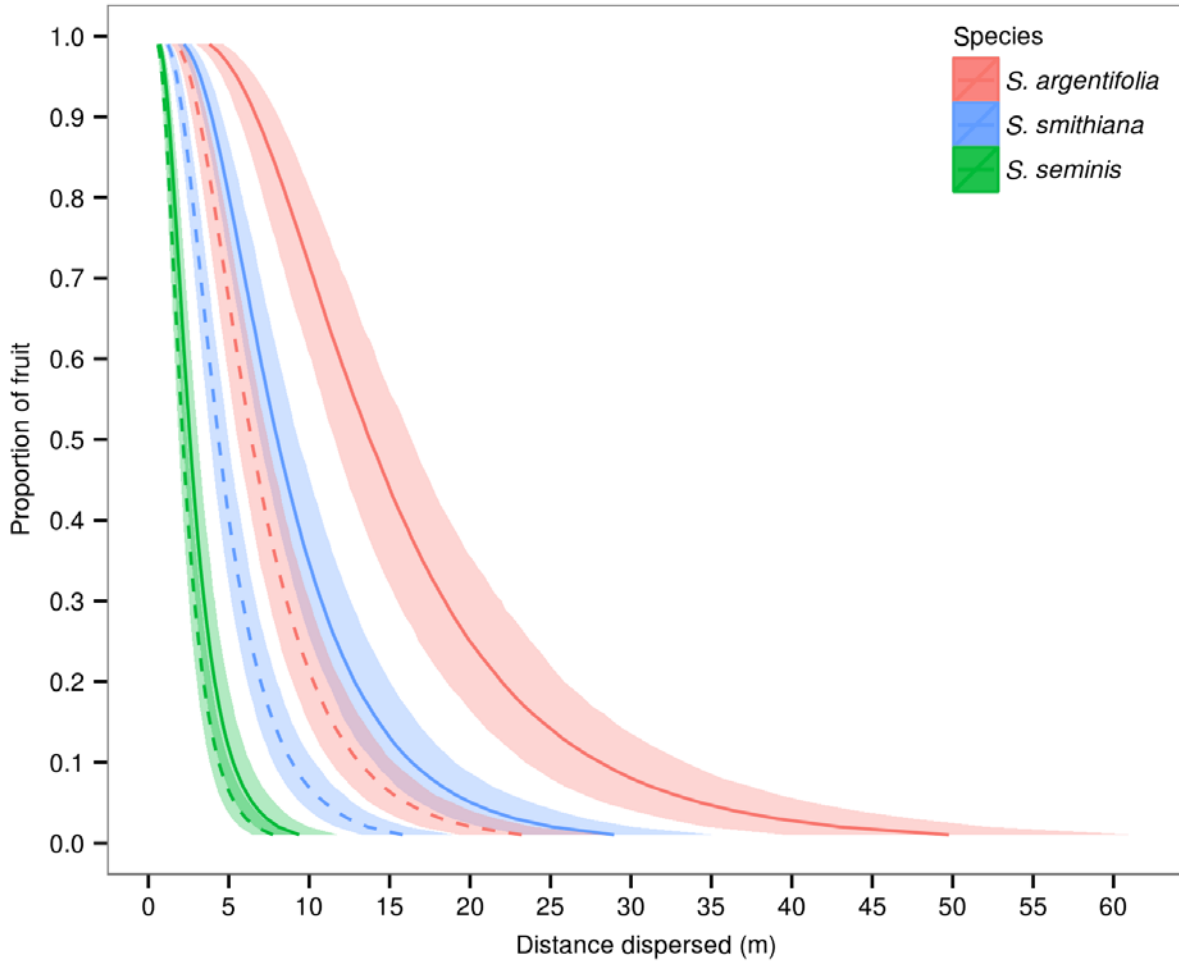
Figure S1. Simulated dispersal kernels of *S. seminis*, *S. smithiana* and *S. argentifolia* at maximum wind speed 1 and 5 m/s (dashed and full lines respectively) with associated 95% confidence bands.

Predicting the Terminal Velocity of Dipterocarp Fruit

with Robert Bagchi, Chris Kettle, Colin Maycock, Eyen Khoo & Jaboury Ghazoul

ABSTRACT

We measured the terminal velocity of helicopter-like fruit from the Dipterocarpaceae family and present a model predicting the terminal velocities for all dipterocarp species in the Malesiana region. A ballistic model of seed dispersal using the observed terminal velocities predicted dispersal distances of 17–77 m under normal atmospheric conditions. These data are of applied use in parameterizing models of species coexistence, forest regeneration and habitat connectivity in SE Asian tropical forests.

INTRODUCTION

Seed dispersal occupies a critical position in plant ecology. Differential seed dispersal among species influences community structure and dynamics (Rees et al. 2001), is a key parameter in neutral (Hubbell 2001) and density-dependent (Janzen 1970, Connell 1971) mechanisms of species coexistence, maintains gene-flow between populations, and determines migration rates (Higgins and Richardson 1999, Cain et al. 2000). However, quantitative descriptions of seed dispersal are rare; one recent review found only 34 quantitative estimates of seed dispersal from tropical tree species (Kettle 2012). This scarcity of quantitative data is due to the difficulty of measuring dispersal (Bullock et al. 2006), which in case of animal dispersed (zoochorous) species includes disperser feeding visits per hour, disperser home range size, gut passage times and maximum flight range (Howe 1977, Russo et al. 2006). Elucidating the full extent of wind-dispersed (anemochorous) species' dispersal potentials is hampered by the difficulty of tracking often many hundreds or thousands of tiny windborne seeds capable of dispersing long-distances, particularly during extreme events such as tropical storms (Nathan et al. 2008). Such long-distance dispersal (LDD) events create long, fat-tailed dispersal kernels, for which traditional methods of measuring dispersal (including experimental release, seed traps and transects) are inadequate (Higgins et al. 2003, Nathan 2006, Nathan et al. 2008).

Research on anemochorous diaspores has turned to mechanistic modeling to overcome these constraints (Nathan et al. 2011). Simple ballistic models have evolved to complex multi-level models incorporating a range of plant traits, fruit morphologies, release heights, wind speeds, turbulence, and habitat variables (Kuparinen et al. 2007, Bohrer et al. 2008, Greene and Quesada 2011, Nathan et al. 2011, Fontan et al. 2013, Damschen et al. 2014). Field experiments confirm these mechanistic models are better at estimating long distance dispersal events than phenomenological models (Soons et al. 2004). Despite their complexity, analysis of these models repeatedly confirms that, together with height of release (Thomson et al. 2011), the terminal velocity of the seed is the most important variable in predicting dispersal distance by wind (Tamme et al. 2014). Seeds with low terminal velocities increase their timespan in the air column and hence opportunity to be dispersed horizontally and vertically by turbulence (Green 1980).

The terminal velocity of a falling fruit is proportional to the square root of its 'wing-loading', defined as fruit mass divided by wing surface area (Green 1980, Augspurger 1986). In an analysis of the terminal velocity of diaspores from 34 Neotropical tree species, Augsperger (1986) additionally observed that the slope of the relationship between rate of descent and wing-loading differed significantly between a range of aerodynamic groups, including auto-gyrating, rolling auto-gyrating,

undulating, tumbling and helicopter-like. Despite the importance of terminal velocity, a recent analysis predicting maximum dispersal distances from plant traits included only 53 entries for the terminal velocities of trees with adaptations to wind dispersal (Tamme et al 2014), and Augsperger's (1986) paper remains the only published study providing terminal velocities of tropical tree diaspores.

In this paper, we present the first estimates of seed terminal velocities for Paleotropical trees, and expand the dataset for the number of helicopter-like auto-gyrating fruit from 3 to 19, by measuring the terminal velocity of 16 species of Dipterocarpaceae on Borneo. Estimates of the terminal velocity as a basis for the subsequent generation of dispersal kernels is of both applied and theoretical importance for Southeast Asian tropical rainforests. Differences in terminal velocity and hence seed dispersal potential between species might play a role in maintaining species coexistence (Hubbell 2001). Critically, lowland tropical forests in the Malesiana region are dominated by dipterocarps which typically account for over 30% of basal area in these forests (Newbery et al. 1992, Curran and Leighton 2000, Lee et al. 2004), and are economically important due to their valuable timber. The extraction of timber coupled with rapid land-use change has left the forests of Southeast Asia largely fragmented and degraded (Sodhi et al. 2009, Wilcove et al. 2013), and hence an improved understanding of dipterocarp seed dispersal has direct relevance to the regeneration of logged forests and habitat connectivity and associated gene-flow in these Southeast Asian tropical forests (Kettle 2012, McConkey et al. 2012).

METHODS

Dipterocarp fruit have between zero and five elongated sepals which act as wings to disperse the fruit via gravity or gyration (Suzuki and Ashton 1996, Smith et al. 2015). We collected mature fruit belonging to 16 dipterocarp species from five genera (one *Dipterocarpus,* one *Dryobalanops,* three *Hopea*, two *Parashorea* and nine *Shorea*) (Table 1) found in the Sepilok Forest Reserve (SFR)(5°51' N 117°56' E) or the Danum Valley Conservation Area (DVCA), Sabah, Malaysian Borneo. SFR is a 4420 ha fragment of primarily tropical lowland dipterocarp forest, ranging in altitude 0 – 170 m.a.s.l. (Fox 1973). DVCA is a 438 km^2 area of uninhabited primary lowland dipterocarp forest (Marsh and Greer 1992). Fruit were collected from the ground during the 2014 community-wide mast fruiting event occurring between July and September.

The fruit fresh mass (g), and lengths and widths of the wings and nut (cm) were measured for each fruit. From these data the wing-loading was calculated, defined as fruit mass divided by 'long' wing area. We convert mass to force in millidynes (mg·cm/s^2) to be consistent with Augspurger (1986); however, millidynes can be converted to an equivalent SI unit nanonewtons (nN) by multiplying by ten. Wing areas were calculated by summing the products of individual wing lengths and widths in the genera *Dipterocarpus, Dryobalanops* and *Hopea*, which possess equal sized wings. Species in the genus *Parashorea* and *Shorea* have two 'short wings' and three 'long wings'. Short wings were excluded from the wing-loading calculation as their effect on lift is expected to be limited (Suzuki and Ashton 1996, Smith et al. 2015).

Fruits were released from a height of 12.5 m from the balcony of the Sabah Forest Department Research Centre in Sepilok, and at DVCA from an 18 m tree tower. Terminal velocity (m/s) was calculated by dividing the distance fallen by the time taken to hit the ground. Each fruit was released once. Fruits were released individually and, to ensure accuracy of terminal velocity measurements, in the early morning when wind speeds were < 1 m/s to limit the effect of turbulence. An electronic anemometer (Windmaster 2, Kaindl Electronic, Germany) mounted at the release height (i.e. 12.5 m in Sepilok and 18 m in Danum) was used to record wind speed (m/s) during fruit release. Following release the fruit were recovered and the wings were removed from a subsample using a scalpel. The wings were subsequently scanned using a flat-bed portable scanner (CanoScan LiDE 110, Canon Inc., Tokyo, Japan) and the mass of the nut without wings was measured. The total wing area of each fruit was calculated from the scans using ImageJ software (Rasband 1997-2014).

TABLE 1. Summary statistics (Means ± SE) relating to fruit morphology, experimentally derived terminal velocity, and predicted dispersal distance using the ballistic model of the 16 dipterocarp study species.

Species	No.	Fruit mass (g)	$\sqrt{\text{wing-loading}}$ $((\text{mg·cm/s}^2)/\text{cm}^2)$	Terminal velocity (m/s)	Scanned wing area (cm^2)	Fruit mass excluding sepals (g)	Predicted dispersal distance (m)
Dipterocarpus grandiflorus	17	43.38 (±2.95)	486.6 (±13.96)	4.09 (±0.16)	176.14 (±4.32)	42.80 (±3.23)	23.13
Dryobalanops lanceolata	83	8.91 (±0.21)	371.2 (±5.10)	2.94 (±0.04)	49.78 (±0.82)	6.81 (±0.17)	32.13
Hopea ferruginea	52	0.22 (±0.01)	166.1 (±2.85)	1.36 (±0.05)	5.56 (±0.11)	NA	69.70
Hopea nervosa	57	1.14 (±0.03)	210.5 (±3.67)	1.49 (±0.05)	21.81 (±0.64)	0.77 (±0.04)	63.29
Hopea sp.	45	3.82 (±0.10)	451.5 (±11.71)	3.46 (±0.12)	15.31 (±1.11)	2.95 (±0.15)	27.28
Parashorea malaanonan	40	5.51 (±0.19)	297.5 (±5.58)	2.08 (±0.08)	59.60 (±2.35)	4.11 (±0.14)	45.40
Parashorea tomentella	140	8.32 (±0.16)	317.0 (±7.63)	2.12 (±0.05)	67.93 (±2.67)	6.48 (±0.18)	44.52
Shorea argentifolia	31	0.80 (±0.03)	168.8 (±3.86)	1.22 (±0.07)	23.59 (±0.62)	NA	77.38
Shorea beccariana	41	9.43 (±0.25)	327.0 (±3.52)	2.20 (±0.07)	80.90 (±2.10)	5.34 (±0.29)	42.91
Shorea johorensis	36	2.65 (±0.08)	225.0 (±2.26)	1.66 (±0.06)	50.74 (±1.13)	1.80 (±0.08)	56.83
Shorea leprosula	138	1.06 (±0.02)	208.7 (±2.21)	1.62 (±0.03)	19.25 (±0.43)	0.65 (±0.02)	58.42
Shorea macrophylla	42	34.50 (±1.26)	516.0 (±13.62)	4.04 (±0.15)	129.65 (±7.31)	NA	23.41
Shorea mexistopteryx	37	15.30 (±0.39)	342.3 (±5.57)	2.38 (±0.08)	127.61 (±2.56)	8.69 (±0.35)	39.75
Shorea parvifolia	70	0.95 (±0.03)	175.0 (±2.58)	1.36 (±0.05)	27.46 (±0.92)	NA	69.61
Shorea seminis	48	2.63 (±0.14)	621.9 (±18.99)	5.39 (±0.16)	9.38 (±0.35)	2.83 (±0.17)	17.54
Shorea smithiana	75	6.33 (±0.13)	298.8 (±4.41)	1.90 (±0.06)	77.82 (±1.93)	2.98 (±0.14)	49.77

RESULTS

Mean $\sqrt{\text{wing-loading}}$ ((mg·cm/s^2)/cm^2) ranged from 166.1 in *H. ferruginea* to 621.9 in *S. seminis*

(Table 1). A linear regression between terminal velocity and $\sqrt{\text{wing-loading}}$ showed a highly-

significant positive relationship ($R^2 = 0.97$; $F_{(1,14)} = 429.3$; $P < 0.001$) (Fig. 1), confirming that

dipterocarp species with lower ratios of fruit mass to wing area descend over a longer period of time.

The high R-squared value ($R^2 = 0.97$) confirms this relationship is consistent across the family and

fruit morphologies given that the 16 data points represent species in five genera. To assess if the

model was sensitive to data from individual species, we reran the regression 100 times, using a

random selection of 14 of the 16 species in each model. The coefficients were highly consistent

between the full species model and models excluding two species at a time (Full model: slope = -

0.362, intercept = 0.0087; 14 species models: mean slope = -0.374 (95% percentiles: -0.466 – -0.226),

intercept = 0.0087 (95% percentiles: 0.0082 – 0.0089)). Despite overlaps in the species composition

between Danum and Sepilok, local differences in the species participating in the mast fruiting and

timing of fruit abscission meant only *S. leprosula* fruit were released at both locations and release

heights. An analysis of variance confirmed that there was no significant difference in the terminal

velocity of *S. leprosula* fruit released from the two heights ($F_{(1,136)} = 0.706$; $P = 0.402$) (Fig. S1).

Using the terminal velocities observed, we predicted dispersal distances for each species using

the ballistic model presented in (Augspurger 1986), where distance dispersed is calculated as height of

release divided by terminal velocity multiplied by wind speed. A release height of 45 m was used,

corresponding to the mean canopy height at Sepilok, together with a wind speed of 2.1 m/s (the mean

annual wind speed 2000-2014 at Sandakan Airport 11 km from Sepilok) (Tutiempo.net 2015). The

mean predicted dispersal distance was 46.32 m, and predictions ranged from 17.5 m in *S. seminis* to

77.4 m in *S. argentifolia* (Table 1). Predictions from the ballistic model must however be interpreted

with caution as multiple factors might decrease (e.g. low wind speeds under the canopy (Whitmore

2006), entanglement of fruit in vegetation) or increase these estimates (e.g. timing of fruit abscission

(Maurer et al. 2013), extreme weather events (Nathan et al. 2008), and updrafts (Tackenberg 2003)).
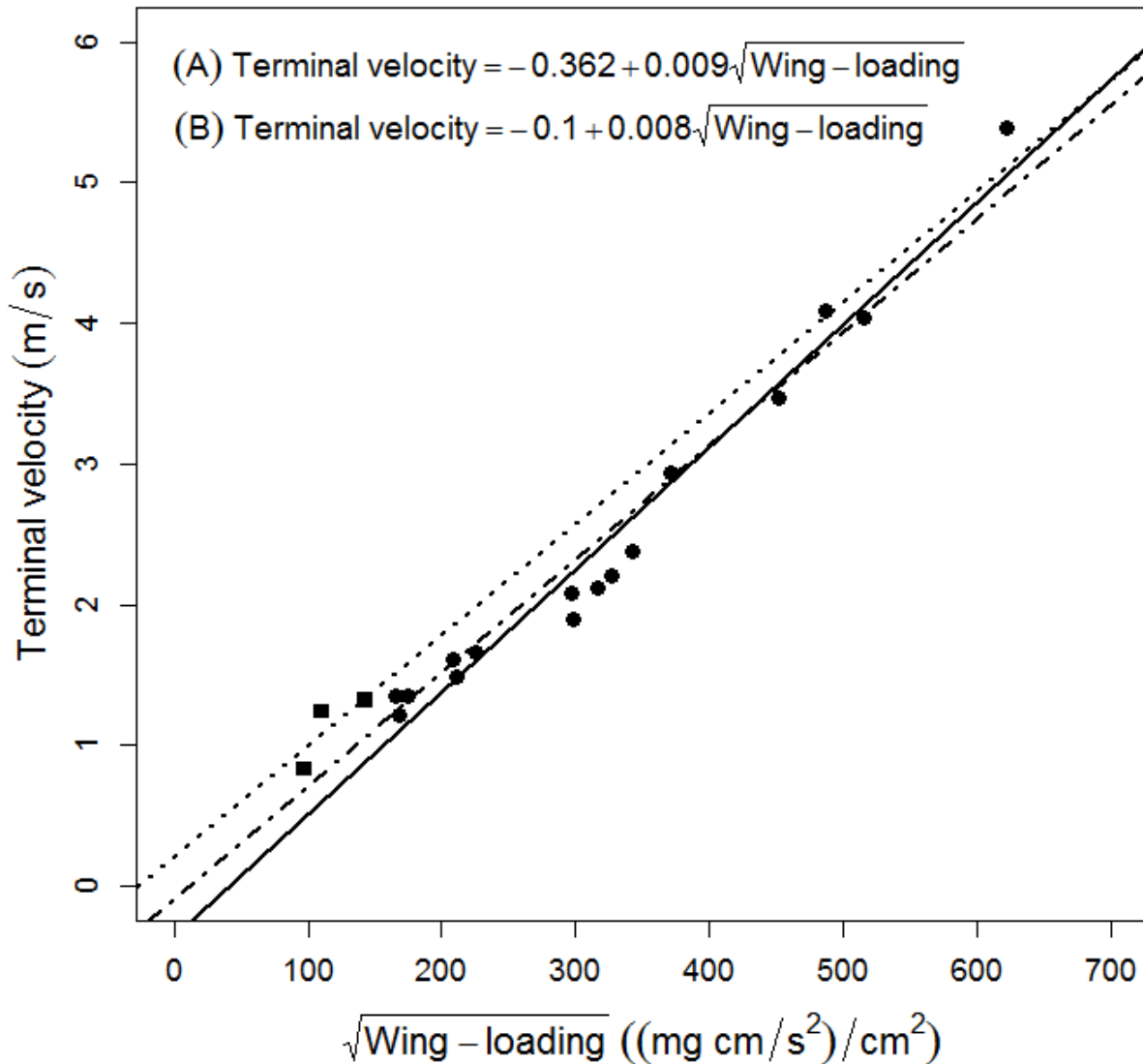
FIGURE 1. Figure one plots mean fruit $\sqrt{\text{wing-loading}}$ ((mg·cm/s²)/cm²) against terminal velocity (m/s) for the 16 dipterocarp species used in this study (circles) and the three 'helicopter-like' species (squares) from Augspurger (1986). The solid line represents the line of best fit from regression of mean fruit $\sqrt{\text{wing-loading}}$ against terminal velocity for the 16 dipterocarp species, and the regression fitted equation is given by equation A. The dotted line represents the line of best fit for the regression of mean fruit $\sqrt{\text{wing-loading}}$ against terminal velocity for 'helicopter-like' diaspores from Augspurger (1986). The 'dot-dash' line represents the line of best fit for the regression of mean fruit $\sqrt{\text{wing-loading}}$ against terminal velocity using the combined dataset of the dipterocarp fruit presented and the three 'helicopter-like' fruit from Augspurger (1986); the regression fitted equation is given by equation B.

Measurements of total wing area and nut mass are only available for a small subset of dipterocarps whereas wing dimensions and nut dimensions, from which area and volume can be

calculated respectively, are available for almost the complete dipterocarp flora in the Malesiana region (Ashton 1983). We regressed total scanned fruit wing areas against calliper measured wing areas. We also regressed fruit mass against nut volume calculated from nut dimensions. In both cases the relationships between fruit morphology and easily measured proxies was extremely strong (Wing area regression: $R^2 = 0.99$, $F_{(1,15)} = 3749$, $P < 0.001$; Fruit mass regression: $R^2 = 0.93$, $F_{(1,11)} = 131.1$, $P < 0.001$) (Fig. S2, Fig. S3). Using this approach we calculated the wing loading for 367 dipterocarp species with fruit dimension data contained in the Flora Malesiana (Ashton 1983) (data is presented as minimum and maximum for each dimension and therefore we used mean values to calculate species wing loadings). Terminal velocities for all 367 species were subsequently calculated using the fitted values from the regression model of terminal velocity and wing loading from our 16 species (Fig. 1). These data are presented in the supplementary data (Table S1).

DISCUSSION

The estimated dipterocarp terminal velocities open up a range of research avenues. Inter-specific differences in seed dispersal is a component of multiple species coexistence mechanisms (Janzen 1970, Connell 1971, Tilman 1994, Hubbell 2001). The data can be used to parameterize coexistence models, thereby improving our understanding of this trait in maintaining species richness in hyper-diverse tropical forests. The data also possess applied value. Particularly pertinent, given the rapid pace of deforestation and forest fragmentation, is that of processes of forest regeneration. Logged forests, often surrounded by oil-palm agriculture, are now widespread across Southeast Asia (Koh and Wilcove 2008). Their trajectories of recovery will be shaped by patterns of seed dispersal, establishment and growth. Opportunities for regeneration are constrained by the low densities of remaining mature trees (Cannon et al. 1994, Berry et al. 2010, Bagchi et al. 2011), which is exacerbated by the limited seed dispersal capacities of many dipterocarps (Smith et al. 2015). Differential dispersal among species might favor species with longer range dispersal capacities (coupled with regeneration strategy), as such species might be better placed to occupy sites in degraded forests far from competitors. This implies possible shifts in dipterocarp species composition as forest recovery proceeds (Bagchi et al. 2011). Should fruit morphologies be linked to other plant traits, such as growth rates and wood density (King et al. 2005, King et al. 2006, Wright et al. 2010), such compositional shifts might have far reaching implications for ecosystem function.

Recent studies suggest that dipterocarp seedlings struggle to recruit naturally in forest fragments under 100 ha in size, though the causes remain unclear (Yeong 2015). This observation casts the long-term persistence of dipterocarps in small fragments into uncertainty as they lack a seed bank, due to the recalcitrant nature of their fruit (Li and Pritchard 2009), and the means to rapidly proliferate as they mast fruit on a supra-annual periodicity (Ashton 1988, Sakai 2002, Brearley et al. 2007). Their long-term population persistence might therefore depend on seed influx from larger fragments or contiguous forests and the formation of more resistant meta-populations. Terminal velocities are a necessary pre-requisite for accurate models of LDD in wind-dispersed seed and consequently spatial models predicting seed movement between fragments (Soons et al. 2005). Our estimates of dipterocarp terminal velocities should catalyze such modeling efforts and generate data necessary for policy-makers to deliver evidence-based management and conservation plans addressing the issue of forest fragment persistence in Southeast Asian agricultural landscape matrices (McConkey et al. 2012). We emphasize that such research is timely given the high level of threat faced by the

Dipterocarpaceae (Maycock et al. 2012) and the additional burden of determining rates of population spread driven by climate change (Higgins and Richardson 1999, Colwell et al. 2008, Corlett 2009).

Beyond the Dipterocarpaceae, this study substantially increases the wing loading and terminal velocity data available on helicopter-like fruit from three species to 19. There is no significant difference between the fitted equation of Augsperger's (Augspurger 1986) Neotropical data for helicopter-like fruit and our Paleotropical data (Fig. 1), although the $\sqrt{\text{wing-loading}}$ values of Dipterocarpaceae fruit (Table 1) are substantially higher than the measured Neotropical species, which range only between 97.7 and 143.7 ((mg·cm/s^2)/cm^2). We therefore combined the datasets and re-analyzed the wing loading to terminal velocity relationship (Fig. 1), providing an updated regression equation with which to calculate the terminal velocity of helicopter-like diaspores ($R^2 = 0.95$; $F_{(1,17)} = 373.4$; $P < 0.001$). Recognizing that this equation is derived primarily from data from a single family, the Dipterocarpaceae, we believe it can nevertheless be generalized for helicopter-like diaspores globally with $\sqrt{\text{wing-loading}}$ values between 97.7 and 621.9 ((mg·cm/s^2)/cm^2).

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SUPPORTING INFORMATION

TABLE S1. Predicted wing areas (cm^2), fruit masses (expressed in millidynes), $\sqrt{\text{wing-loadings}}$ (($mg \cdot cm/s^2$)/cm^2), and terminal velocities (cm/s) with upper (UCI) and lower (LCI) confidence intervals for 367 species of Dipterocarpaceae from the Flora Malesiana (Ashton 1983).

(Continued overleaf)

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
1 Dipterocarpus verrucosus	35.99	34.74	37.25	1651360	1460787	1866795	214.20	205.06	223.88	150.16	134.69	165.63
2 Dipterocarpus crinitus	21.81	21.05	22.57	780052	648782	937882	189.10	175.54	203.83	128.33	111.32	145.33
3 Dipterocarpus caudiferus	92.71	89.48	95.94	23673555	20067086	27928180	505.32	473.56	539.54	403.40	383.20	423.60
4 Dipterocarpus validus	159.06	153.52	164.60	26850290	22517707	32016496	410.86	382.98	441.04	321.23	306.99	335.47
5 Dipterocarpus gracilis	63.62	61.41	65.84	4868535	4533791	5227994	276.62	271.71	281.79	204.46	191.82	217.10
6 Dipterocarpus baudii	98.16	94.75	101.58	4868535	4533791	5227994	222.70	218.75	226.86	157.56	142.56	172.55
7 Dipterocarpus obtusifolius	81.80	78.96	84.65	9144166	8329942	10037977	334.34	324.81	344.36	254.67	242.73	266.60
8 Dipterocarpus rotundifolius	40.90	39.48	42.33	2253605	2038353	2491588	234.73	227.23	242.63	168.02	153.66	182.38
9 Dipterocarpus chartaceus	75.62	72.99	78.26	3609572	3345193	3894846	218.48	214.08	223.09	153.88	138.65	169.11
10 Dipterocarpus caudatus	76.35	73.69	79.01	4868535	4533791	5227994	252.52	248.04	257.24	183.50	169.97	197.02
11 Dipterocarpus kerrii	76.35	73.69	79.01	23673555	20067086	27928180	556.84	521.83	594.55	448.21	424.11	472.32
12 Dipterocarpus hasseltii	119.98	115.80	124.15	15314439	13451289	17435656	357.27	340.82	374.75	274.62	262.35	286.89
13 Dipterocarpus retusus	204.51	197.39	211.63	23673555	20067086	27928180	340.23	318.85	363.28	259.80	247.81	271.79
14 Dipterocarpus littoralis	174.51	168.44	180.59	17701615	15370018	20386910	318.49	302.08	335.99	240.88	228.97	252.79
15 Dipterocarpus kunstleri	29.99	28.95	31.04	17570099	15265007	20223272	765.36	726.14	807.19	629.60	588.12	671.09
16 Dipterocarpus applanatus	155.43	150.02	160.84	53190849	42015621	67338441	585.00	529.22	647.05	472.71	446.37	499.06
17 Dipterocarpus rigidus	163.61	157.91	169.30	53190849	42015621	67338441	570.19	515.82	630.67	459.83	434.67	484.99
18 Dipterocarpus costulatus	145.43	140.37	150.49	3709843	3441081	3999596	159.72	156.57	163.02	102.77	83.79	121.75
19 Dipterocarpus globosus	95.44	92.11	98.76	17246110	15005981	19820651	425.10	403.62	447.99	333.62	318.63	348.60
20 Dipterocarpus humeratus	163.61	157.91	169.30	26850290	22517707	32016496	405.11	377.62	434.87	316.23	302.27	330.19
21 Dipterocarpus cornutus	190.87	184.23	197.52	19144438	16517202	22189563	316.70	299.43	335.17	239.32	227.41	251.24
22 Dipterocarpus lamellatus	63.62	61.41	65.84	3609572	3345193	3894846	238.19	233.40	243.22	171.03	156.84	185.22
23 Dipterocarpus lowii	89.07	85.97	92.18	34527615	28333769	42075453	622.60	574.08	675.63	505.42	476.01	534.82
24 Dipterocarpus pachyphyllus	70.90	68.43	73.36	6010382	5580298	6473614	291.17	285.57	297.05	217.11	204.85	229.37
25 Dipterocarpus confertus	76.35	73.69	79.01	5250809	4887459	5641172	262.25	257.53	267.21	191.96	178.82	205.09
26 Dipterocarpus dyeri	199.96	193.00	206.92	20079176	17255901	23364372	316.88	299.01	336.02	239.48	227.57	251.40
27 Dipterocarpus fagineus	21.81	21.05	22.57	456782	362486	575608	144.71	131.21	159.68	89.71	69.65	109.77

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
28 Dipterocarpus cinereus	10.91	10.53	11.29	938365	792884	1110540	293.31	274.44	313.68	218.98	206.76	231.20
29 Dipterocarpus semivestitus	17.72	17.11	18.34	1010865	859524	1188854	238.82	224.15	254.60	171.58	157.42	185.73
30 Dipterocarpus oblongifolius	32.72	31.58	33.86	1333497	1160006	1532937	201.87	191.65	212.77	139.44	123.24	155.64
31 Dipterocarpus grandiflorus	119.98	115.80	124.15	45487659	36433789	56791434	615.74	560.91	676.33	499.45	470.61	528.29
32 Dipterocarpus palembanicus spp. Palembanicus	63.62	61.41	65.84	4791864	4462440	5145605	274.43	269.57	279.56	202.56	189.85	215.27
33 Dipterocarpus fusiformis	47.26	45.62	48.91	5479349	5097270	5890067	340.49	334.27	347.03	260.01	248.02	272.01
34 Dipterocarpus borneensis	24.54	23.69	25.40	1010865	859524	1188854	202.96	190.49	216.37	140.38	124.24	156.52
35 Dipterocarpus nudus	51.81	50.01	53.61	1627953	1438514	1842340	177.26	169.61	185.38	118.03	100.25	135.81
36 Dipterocarpus geniculatus spp. geniculatus	54.54	52.64	56.43	2161669	1949767	2396600	199.09	192.46	206.08	137.02	120.65	153.39
37 Dipterocarpus costatus	52.26	50.44	54.08	4868535	4533791	5227994	305.21	299.80	310.91	229.33	217.31	241.35
38 Dipterocarpus conformis spp. conformis	36.36	35.09	37.62	6010382	5580298	6473614	406.59	398.78	414.81	317.52	303.48	331.55
39 Dipterocarpus conformis spp. borneensis	36.36	35.09	37.62	6010382	5580298	6473614	406.59	398.78	414.81	317.52	303.48	331.55
40 Dipterocarpus acutangulus	45.45	43.86	47.03	9144166	8329942	10037977	448.56	435.78	462.00	354.03	337.68	370.38
41 Dipterocarpus sublamellatus	65.44	63.16	67.72	15314439	13451289	17435656	483.75	461.47	507.41	384.64	365.97	403.31
42 Dipterocarpus concavus	116.34	112.29	120.39	29994284	24916187	36107335	507.75	471.05	547.64	405.51	385.13	425.90
43 Dipterocarpus stellatus spp. stellatus	65.44	63.16	67.72	11538293	10351151	12861586	419.90	404.82	435.80	329.09	314.39	343.79
44 Dipterocarpus stellatus spp. parvus	65.44	63.16	67.72	11538293	10351151	12861586	419.90	404.82	435.80	329.09	314.39	343.79
45 Dipterocarpus sarawakensis	32.72	31.58	33.86	2664618	2435183	2915670	285.37	277.68	293.44	212.07	199.67	224.47
46 Dipterocarpus coriaceus	63.62	61.41	65.84	8531994	7803783	9328158	366.20	356.48	376.40	282.38	269.89	294.87
47 Dipterocarpus cuspidatus	26.18	25.27	27.09	3987517	3705626	4290851	390.29	382.97	398.00	303.34	290.03	316.65
48 Dipterocarpus eurhynchus	29.09	28.07	30.10	4175654	3883963	4489252	378.90	371.96	386.20	293.43	280.54	306.32
49 Dipterocarpus ochraceus	26.18	25.27	27.09	2562255	2336286	2810079	312.86	304.09	322.08	235.98	224.04	247.93
50 Dipterocarpus perakensis	65.44	63.16	67.72	6377154	5910471	6880685	312.16	305.90	318.75	235.38	223.43	247.33
51 Dipterocarpus philippinensis	71.26	68.78	73.74	7224507	6663675	7832541	318.41	311.26	325.91	240.81	228.90	252.72
52 Anisoptera marginata	43.63	42.11	45.15	1439920	1260273	1645176	181.67	173.00	190.89	121.87	104.38	139.35
53 Anisoptera curtisii	34.36	33.16	35.55	1779746	1583242	2000639	227.60	218.50	237.22	161.82	147.09	176.55
54 Anisoptera costata	58.17	56.15	60.20	962569	815090	1136733	128.64	120.49	137.42	75.73	54.49	96.97

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
55 Anisoptera grossivenia	90.89	87.73	94.06	1439920	1260273	1645176	125.87	119.86	132.25	73.32	51.88	94.77
56 Anisoptera megistocarpa	151.97	146.68	157.26	4868535	4533791	5227994	178.99	175.81	182.33	119.53	101.86	137.20
57 Anisoptera reticula	70.90	68.43	73.36	4868535	4533791	5227994	262.05	257.40	266.95	191.79	178.65	204.93
58 Anisoptera thurifera spp. thurifera	40.90	39.48	42.33	3071762	2828293	3336189	274.05	267.66	280.75	202.22	189.50	214.94
59 Anisoptera aurea	27.27	26.32	28.22	250881	188657	333627	95.92	84.67	108.74	47.27	23.54	71.01
60 Anisoptera scaphula	81.80	78.96	84.65	2161669	1949767	2396600	162.56	157.14	168.26	105.24	86.45	124.03
61 Anisoptera laevis	40.90	39.48	42.33	2161669	1949767	2396600	229.89	222.24	237.96	163.81	149.20	178.42
62 Upuna borneensis	63.81	61.59	66.03	4407346	4102505	4734839	262.82	258.10	267.79	192.45	179.34	205.57
63 Cotylelobium melanoxylon	9.82	9.47	10.16	157743	113719	218810	126.77	109.56	146.77	74.10	52.73	95.48
64 Cotylelobium burckii	12.27	11.84	12.70	157743	113719	218810	113.38	97.99	131.27	62.46	40.07	84.85
65 Cotylelobium lanceolatum	12.27	11.84	12.70	157743	113719	218810	113.38	97.99	131.27	62.46	40.07	84.85
66 Vatica umbonata spp. umbonata	21.27	20.53	22.01	15314439	13451289	17435656	848.55	809.48	890.05	701.97	653.26	750.68
67 Vatica stapfiana	24.04	23.20	24.88	14240598	12578647	16122135	769.64	736.27	805.02	633.32	591.47	675.18
68 Vatica venulosa spp. venulosa	17.72	17.11	18.34	681660	560360	829217	196.11	180.99	212.63	134.43	117.87	150.99
69 Vatica venulosa spp. simalurensis	17.04	16.45	17.64	1142974	981851	1330538	258.97	244.32	274.67	189.11	175.85	202.37
70 Vatica chartacea	40.90	39.48	42.33	1046995	892869	1227726	159.99	150.39	170.31	103.01	84.04	121.97
71 Vatica pauciflora	1.14	1.10	1.18	15314439	13451289	17435656	3671.40	3502.33	3850.97	3157.49	2855.85	3459.13
72 Vatica ridleyana	0.41	0.39	0.42	8563723	7831164	9364808	4575.74	4453.87	4703.80	3944.15	3561.13	4327.17
73 Vatica bella	17.72	17.11	18.34	9144166	8329942	10037977	718.28	697.80	739.80	588.64	551.20	626.09
74 Vatica rassak	3.82	3.68	3.95	33127884	27283300	40224484	2945.84	2721.16	3191.00	2526.34	2289.96	2762.72
75 Vatica granulata spp. granulata	1.27	1.23	1.32	30444524	25257671	36696536	4891.33	4534.85	5279.03	4218.67	3807.25	4630.10
76 Vatica granulata spp. sabaensis	10.91	10.53	11.29	30444524	25257671	36696536	1670.71	1548.95	1803.13	1417.14	1295.30	1538.98
77 Vatica sarawakensis	5.09	4.91	5.27	9144166	8329942	10037977	1340.34	1302.14	1380.49	1129.76	1037.48	1222.04
78 Vatica albiramis	2.18	2.11	2.26	1142974	981851	1330538	723.85	682.88	767.74	593.49	555.57	631.41
79 Vatica oblongifolia spp. oblongifolia	27.27	26.32	28.22	4868535	4533791	5227994	422.55	415.05	430.44	331.40	316.55	346.24
80 Vatica oblongifolia spp. elliptifolia	1.45	1.40	1.50	4868535	4533791	5227994	1829.68	1797.22	1863.86	1555.43	1419.33	1691.52
81 Vatica oblongifolia spp. crassilobata	8.18	7.90	8.47	4868535	4533791	5227994	771.46	757.77	785.87	634.91	592.90	676.92

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
82 Vatica oblongifolia spp. multinervosa	4.73	4.56	4.89	4868535	4533791	5227994	1014.92	996.92	1033.88	846.69	783.35	910.03
83 Vatica oblongifolia spp. selakoensis	0.55	0.53	0.56	4868535	4533791	5227994	2987.86	2934.85	3043.67	2562.89	2322.74	2803.05
84 Vatica dulitensis	3.18	3.07	3.29	367604	286113	472306	339.93	305.26	378.78	259.53	247.55	271.52
85 Vatica pedicellata	1.09	1.05	1.13	5272601	4907517	5664845	2198.66	2159.09	2240.31	1876.39	1707.17	2045.61
86 Vatica rotata	1.27	1.23	1.32	46376	29878	71984	190.91	155.97	233.81	129.90	113.01	146.79
87 Vatica vinosa	3.27	3.16	3.39	367604	286113	472306	335.18	300.99	373.48	255.40	243.45	267.34
88 Vatica scortechinii	1.27	1.23	1.32	2161669	1949767	2396600	1303.37	1259.96	1349.09	1097.60	1008.62	1186.58
89 Vatica globosa	0.55	0.53	0.56	4868535	4533791	5227994	2987.86	2934.85	3043.67	2562.89	2322.74	2803.05
90 Vatica lobata	3.64	3.51	3.76	2425376	2204087	2668882	816.76	792.53	842.25	674.32	628.38	720.25
91 Vatica hullettii	12.72	12.28	13.17	4868535	4533791	5227994	618.55	607.57	630.10	501.89	472.82	530.96
92 Vatica pallida	1.09	1.05	1.13	681660	560360	829217	790.55	729.58	857.13	651.51	607.85	695.18
93 Vatica flavida	2.18	2.11	2.26	681660	560360	829217	559.00	515.89	606.09	450.10	425.82	474.38
94 Vatica heteroptera	11.36	10.97	11.76	1416314	1237990	1620324	353.07	336.00	371.24	270.96	258.78	283.15
95 Vatica maritima	9.09	8.77	9.41	250881	188657	333627	166.14	146.64	188.34	108.35	89.82	126.89
96 Vatica teysmanniana	35.99	34.74	37.25	157743	113719	218810	66.20	57.21	76.65	21.42	-4.66	47.51
97 Vatica cinerea	22.90	22.11	23.70	250881	188657	333627	104.66	92.38	118.64	54.87	31.82	77.93
98 Vatica odorata spp. odorata	15.00	14.48	15.52	250881	188657	333627	129.34	114.16	146.62	76.34	55.16	97.53
99 Vatica odorata spp. mindanensis	15.00	14.48	15.52	250881	188657	333627	129.34	114.16	146.62	76.34	55.16	97.53
100 Vatica compressa	11.82	11.40	12.23	103039	71444	148607	93.38	79.15	110.24	45.07	21.13	69.00
101 Vatica congesta	47.99	46.32	49.66	532366	428241	661809	105.32	96.15	115.44	55.45	32.45	78.46
102 Vatica coriacea	29.27	28.25	30.29	367604	286113	472306	112.07	100.64	124.88	61.32	38.84	83.81
103 Vatica brunigii	17.72	17.11	18.34	316060	242679	411630	133.54	119.10	149.81	80.00	59.12	100.87
104 Vatica pachyphylla	16.54	15.97	17.12	367604	286113	472306	149.07	133.86	166.10	93.51	73.77	113.25
105 Vatica obovata	17.72	17.11	18.34	157743	113719	218810	94.34	81.53	109.22	45.90	22.04	69.76
106 Vatica borneensis	15.00	14.48	15.52	681660	560360	829217	213.20	196.75	231.15	149.29	133.76	164.82
107 Vatica bantamensis	40.90	39.48	42.33	681660	560360	829217	129.10	119.14	139.97	76.13	54.93	97.34
108 Vatica mangachapoi spp. mangachapoi	15.00	14.48	15.52	116853	81962	166599	88.27	75.25	103.61	40.62	16.29	64.95

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
109 Vatica parvifolia	7.63	7.37	7.90	46376	29878	71984	77.94	63.67	95.45	31.63	6.48	56.78
110 Vatica rynchocarpa	15.78	15.23	16.33	780052	648782	937882	222.34	206.40	239.67	157.25	142.23	172.26
111 Vatica endertii	29.09	28.07	30.10	116853	81962	166599	63.38	54.03	74.40	18.97	-7.34	45.28
112 Vatica brevipes	12.72	12.28	13.17	367604	286113	472306	169.97	152.63	189.39	111.68	93.41	129.96
113 Vatica micrantha	15.82	15.26	16.37	619726	505225	760177	197.95	181.93	215.52	136.03	119.58	152.47
114 Vatica flavovirens	13.91	13.42	14.39	250881	188657	333627	134.31	118.56	152.26	80.67	59.86	101.49
115 Vatica badiifolia	36.36	35.09	37.62	367604	286113	472306	100.55	90.30	112.04	51.30	27.93	74.68
116 Vatica perakensis	19.63	18.95	20.32	681660	560360	829217	186.33	171.96	202.03	125.92	108.74	143.11
117 Vatica nitens	47.26	45.62	48.91	15314439	13451289	17435656	569.23	543.01	597.07	458.99	433.91	484.07
118 Vatica cuspidata	19.09	18.42	19.75	367604	286113	472306	138.78	124.62	154.63	84.55	64.07	105.04
119 Vatica maingayi	36.36	35.09	37.62	250881	188657	333627	83.07	73.32	94.17	36.09	11.35	60.84
120 Vatica lowii	15.27	14.74	15.80	103039	71444	148607	82.15	69.62	96.98	35.29	10.47	60.11
121 Dryobalanops oblongifolia	1.59	1.54	1.65	14517189	12804031	16459565	3021.05	2887.92	3162.25	2591.77	2348.63	2834.91
122 Dryobalanops keithii	36.36	35.09	37.62	2288022	2071540	2527127	250.86	242.97	259.17	182.05	168.45	195.65
123 Dryobalanops lanceolata	81.80	78.96	84.65	4868535	4533791	5227994	243.96	239.63	248.51	176.05	162.13	189.96
124 Dryobalanops aromatica	54.54	52.64	56.43	4142492	3852584	4454215	275.61	270.54	280.94	203.58	190.91	216.25
125 Dryobalanops beccarii	23.63	22.81	24.45	1779746	1583242	2000639	274.43	263.46	286.02	202.55	189.84	215.26
126 Dryobalanops fusca	35.45	34.21	36.68	2161669	1949767	2396600	246.94	238.72	255.61	178.65	164.87	192.42
127 Dryobalanops rappa	13.63	13.16	14.11	263992	199434	349449	139.15	123.11	157.38	84.88	64.42	105.34
128 Parashorea aptera	1.91	1.84	1.98	9144166	8329942	10037977	2188.76	2126.38	2254.34	1867.78	1699.45	2036.11
129 Parashorea densiflora	1.64	1.58	1.69	15314439	13451289	17435656	3059.50	2918.61	3209.14	2625.21	2378.62	2871.81
130 Parashorea globosa	0.82	0.79	0.85	34527615	28333769	42075453	6496.78	5990.47	7050.16	5615.22	5059.28	6171.15
131 Parashorea macrophylla	107.98	104.22	111.74	2288022	2071540	2527127	145.57	140.98	150.39	90.46	70.47	110.45
132 Parashorea parvifolia	39.40	38.03	40.77	1651360	1460787	1866795	204.72	195.99	213.97	141.92	125.89	157.95
133 Parashorea stellata	89.98	86.85	93.12	2834694	2599486	3091186	177.49	173.00	182.20	118.23	100.46	135.99
134 Parashorea malaanonan	74.17	71.59	76.75	2127131	1916516	2360891	169.35	163.62	175.39	111.15	92.83	129.47
135 Parashorea tomentella	125.43	121.06	129.80	4868535	4533791	5227994	197.01	193.52	200.69	135.21	118.71	151.71

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
136 Parashorea lucida	37.08	35.79	38.38	9144166	8329942	10037977	496.57	482.42	511.44	395.79	376.21	415.36
137 Parashorea smythiesii	39.40	38.03	40.77	1651360	1460787	1866795	204.72	195.99	213.97	141.92	125.89	157.95
138 Neobalanocarpus heimii	16.36	15.79	16.93	19224953	16580966	22290548	1084.01	1024.71	1147.44	906.79	837.33	976.25
139 Hopea pubescens	3.27	3.16	3.39	60815	40172	92066	136.33	112.78	164.89	82.42	61.76	103.09
140 Hopea foxworthyi	6.36	6.14	6.58	277064	210225	365154	208.68	185.02	235.50	145.36	129.57	161.15
141 Hopea cernua	14.18	13.69	14.67	130568	92516	184271	95.96	82.22	112.07	47.31	23.58	71.04
142 Hopea coriacea	19.09	18.42	19.75	974657	826195	1149795	225.97	211.77	241.27	160.40	145.58	175.22
143 Hopea longirostrata	2.62	2.53	2.71	75045	50540	111430	169.32	141.43	202.82	111.12	92.80	129.44
144 Hopea sulcata	12.00	11.58	12.42	354762	275239	457262	171.96	154.17	191.91	113.42	95.28	131.55
145 Hopea mengarawan	15.27	14.74	15.80	184632	135028	252460	109.96	95.72	126.40	59.49	36.84	82.14
146 Hopea micrantha	10.91	10.53	11.29	263992	199434	349449	155.58	137.64	175.96	99.17	79.89	118.44
147 Hopea kerangasensis	1.36	1.32	1.41	144195	103103	201663	325.21	279.91	378.07	246.73	234.83	258.63
148 Hopea vesquei	4.94	4.77	5.12	103039	71444	148607	144.36	122.35	170.42	89.41	69.33	109.49
149 Hopea dryobalanoides	17.72	17.11	18.34	456782	362486	575608	160.54	145.57	177.15	103.48	84.55	122.41
150 Hopea malibato	5.73	5.53	5.93	89110	60967	130242	124.75	105.03	148.26	72.35	50.82	93.88
151 Hopea johorensis	5.82	5.61	6.02	103039	71444	148607	133.09	112.80	157.12	79.61	58.70	100.51
152 Hopea latifolia	15.27	14.74	15.80	290098	221030	380748	137.83	122.46	155.23	83.73	63.18	104.29
153 Hopea ferruginea	2.73	2.63	2.82	89110	60967	130242	180.77	152.20	214.84	121.09	103.54	138.63
154 Hopea pierrei	3.44	3.32	3.56	116853	81962	166599	184.42	157.21	216.47	124.26	106.95	141.57
155 Hopea inexpectata	19.09	18.42	19.75	103039	71444	148607	73.47	62.27	86.74	27.75	2.24	53.25
156 Hopea griffithii	2.73	2.63	2.82	130568	92516	184271	218.82	187.49	255.55	154.18	138.98	169.39
157 Hopea treubii	4.45	4.30	4.61	197985	145716	269003	210.84	184.11	241.59	147.24	131.57	162.91
158 Hopea beccariana	6.36	6.14	6.58	171220	124361	235735	164.05	142.31	189.22	106.53	87.85	125.22
159 Hopea dyeri	4.54	4.39	4.70	116853	81962	166599	160.35	136.69	188.22	103.32	84.38	122.26
160 Hopea myrtifolia	12.00	11.58	12.42	316060	242679	411630	162.31	144.76	182.08	105.02	86.22	123.82
161 Hopea pedocellata	2.73	2.63	2.82	75045	50540	111430	165.90	138.58	198.72	108.14	89.59	126.70
162 Hopea altocollina	6.54	6.32	6.77	89110	60967	130242	116.69	98.25	138.68	65.34	43.20	87.48

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
163 Hopea aequlis	13.09	12.63	13.54	3229179	2977971	3499228	496.71	485.69	508.29	395.91	376.33	415.49
164 Hopea rudiformis	32.72	31.58	33.86	367604	286113	472306	105.99	95.18	118.10	56.04	33.08	78.99
165 Hopea nervosa	39.27	37.90	40.63	681660	560360	829217	131.76	121.60	142.86	78.45	57.44	99.45
166 Hopea sublanceolata	41.81	40.35	43.27	2161669	1949767	2396600	227.38	219.81	235.36	161.63	146.89	176.37
167 Hopea nigra	10.00	9.65	10.35	211282	156424	285380	145.37	127.32	166.08	90.29	70.28	110.30
168 Hopea sphaerocarpa	2.54	2.46	2.63	456782	362486	575608	423.65	384.15	467.51	332.36	317.46	347.27
169 Hopea mesuoides	7.63	7.37	7.90	1779746	1583242	2000639	482.81	463.52	503.21	383.82	365.21	402.42
170 Hopea subalata	3.64	3.51	3.76	456782	362486	575608	354.45	321.40	391.15	272.17	259.95	284.38
171 Hopea auriculata	19.09	18.42	19.75	354762	275239	457262	136.33	122.23	152.15	82.43	61.76	103.09
172 Hopea montana	10.91	10.53	11.29	130568	92516	184271	109.41	93.75	127.77	59.01	36.32	81.70
173 Hopea vaccinifolia	0.64	0.61	0.66	211282	156424	285380	576.26	504.70	658.37	465.11	439.47	490.75
174 Hopea bracteolata	1.14	1.10	1.18	237727	177896	317681	457.43	402.77	519.81	361.74	344.83	378.65
175 Hopea celtidifolia	9.09	8.77	9.41	380419	296997	487272	204.58	184.00	227.61	141.80	125.76	157.83
176 Hopea dasyrrhachis	25.45	24.56	26.34	2161669	1949767	2396600	291.44	281.74	301.66	217.35	205.10	229.61
177 Hopea similis	20.45	19.74	21.16	507249	406297	633286	157.49	143.47	172.99	100.83	81.69	119.97
178 Hopea forbesii	11.82	11.40	12.23	780052	648782	937882	256.94	238.51	276.95	187.34	173.99	200.68
179 Hopea helferi	21.27	20.53	22.01	354762	275239	457262	129.15	115.79	144.14	76.18	54.98	97.38
180 Hopea aptera	2.18	2.11	2.26	263992	199434	349449	347.88	307.77	393.45	266.44	254.35	278.54
181 Hopea novoguineensis	29.09	28.07	30.10	743249	615597	897372	159.86	148.08	172.67	102.89	83.91	121.86
182 Hopea scabra	26.18	25.27	27.09	211282	156424	285380	89.84	78.68	102.64	41.98	17.77	66.20
183 Hopea papuana	18.00	17.37	18.62	877686	737408	1044648	220.84	206.04	236.84	155.94	140.84	171.03
184 Hopea acuminata	10.00	9.65	10.35	157743	113719	218810	125.61	108.56	145.43	73.10	51.63	94.56
185 Hopea sangal	19.09	18.42	19.75	89110	60967	130242	68.33	57.53	81.20	23.27	-2.64	49.19
186 Hopea ferrea	7.27	7.02	7.52	157743	113719	218810	147.29	127.29	170.53	91.96	72.09	111.83
187 Hopea odorata	20.00	19.30	20.69	116853	81962	166599	76.44	65.17	89.73	30.33	5.06	55.60
188 Hopea centipeda	3.05	2.95	3.16	31651	19684	50891	101.80	81.72	126.90	52.39	29.11	75.67
189 Hopea plagata	16.36	15.79	16.93	354762	275239	457262	147.25	132.02	164.34	91.93	72.06	111.80

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190	Hopea nutans	21.81	21.05	22.57	656930	538293	801713	173.54	159.89	188.46	114.79	96.76	132.82
191	Hopea bancana	40.90	39.48	42.33	237727	177896	317681	76.24	67.13	86.64	30.15	4.87	55.44
192	Hopea pentanerva	10.91	10.53	11.29	46376	29878	71984	65.21	53.27	79.86	20.56	-5.61	46.72
193	Hopea basilanica	12.27	11.84	12.70	116853	81962	166599	97.59	83.19	114.54	48.72	25.12	72.33
194	Hopea andersonii spp. andersonii	21.81	21.05	22.57	144195	103103	201663	81.30	69.98	94.52	34.56	9.68	59.44
195	Hopea semicuneata	0.43	0.42	0.45	116853	81962	166599	520.25	443.50	610.65	416.39	395.08	437.69
196	Hopea megacarpa	23.63	22.81	24.45	816748	681995	978125	185.91	172.92	199.99	125.55	108.34	142.76
197	Hopea nodosa	2.54	2.46	2.63	263992	199434	349449	322.07	284.94	364.27	244.00	232.10	255.90
198	Hopea iriana	22.90	22.11	23.70	444113	351551	561046	139.25	126.10	153.85	84.96	64.51	105.42
199	Hopea glabrifolia	16.54	15.97	17.12	619726	505225	760177	193.55	177.88	210.73	132.20	115.48	148.92
200	Hopea glaucescens	19.09	18.42	19.75	316060	242679	411630	128.68	114.77	144.36	75.77	54.54	97.01
201	Hopea wyatt-smithii	3.64	3.51	3.76	1142974	981851	1330538	560.69	528.96	594.69	451.57	427.16	475.98
202	Hopea cagayanensis	1.15	1.11	1.19	1010865	859524	1188854	939.50	881.81	1001.58	781.08	724.40	837.77
203	Hopea apiculata	5.68	5.48	5.88	1861148	1661110	2085275	572.38	550.41	595.59	461.74	436.40	487.07
204	Hopea pachycarpa	13.63	13.16	14.11	2161669	1949767	2396600	398.19	384.92	412.15	310.21	296.56	323.85
205	Hopea bilitonensis	10.91	10.53	11.29	263992	199434	349449	155.58	137.64	175.96	99.17	79.89	118.44
206	Hopea bullatifolia	21.81	21.05	22.57	354762	275239	457262	127.53	114.34	142.33	74.77	53.45	96.09
207	Hopea pterygota	27.27	26.32	28.22	130568	92516	184271	69.20	59.29	80.81	24.03	-1.82	49.87
208	Hopea philippinensis	65.44	63.16	67.72	494663	395334	618948	86.94	79.11	95.60	39.46	15.02	63.90
209	Hopea mindanensis	29.99	28.95	31.04	532366	428241	661809	133.22	121.62	146.02	79.72	58.83	100.62
210	Hopea tenuinervula	30.90	29.83	31.98	532366	428241	661809	131.25	119.82	143.86	78.01	56.96	99.05
211	Hopea enicosanthoides	70.90	68.43	73.36	263992	199434	349449	61.02	53.99	69.02	16.92	-9.58	43.42
212	Shorea collina	17.72	17.11	18.34	12553196	11193527	14078022	841.58	808.90	876.11	695.90	647.80	744.00
213	Shorea ochrophloia	28.63	27.63	29.63	1321641	1148866	1520399	214.85	203.90	226.53	150.73	135.29	166.16
214	Shorea guiso	15.00	14.48	15.52	144195	103103	201663	98.05	84.40	113.99	49.13	25.56	72.70
215	Shorea havilandii	3.64	3.51	3.76	1010865	859524	1188854	527.29	494.91	562.13	422.51	400.68	444.35
216	Shorea scrobiculata	16.36	15.79	16.93	354762	275239	457262	147.25	132.02	164.34	91.93	72.06	111.80

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217	Shorea leptoderma	32.72	31.58	33.86	316060	242679	411630	98.28	87.66	110.26	49.33	25.78	72.88
218	Shorea ciliata	24.54	23.69	25.40	532366	428241	661809	147.29	134.46	161.43	91.95	72.09	111.82
219	Shorea submontana	44.17	42.64	45.71	2253605	2038353	2491588	225.87	218.65	233.47	160.31	145.49	175.13
220	Shorea geniculata	10.23	9.87	10.58	64877927	50344879	83606228	2518.89	2258.56	2810.92	2154.95	1956.96	2352.94
221	Shorea seminis	16.36	15.79	16.93	681660	560360	829217	204.12	188.38	221.31	141.39	125.33	157.46
222	Shorea sumatrana	68.17	65.80	70.54	1627953	1438514	1842340	154.53	147.86	161.61	98.26	78.91	117.61
223	Shorea lumutensis	28.63	27.63	29.63	1861148	1661110	2085275	254.96	245.17	265.30	185.62	172.19	199.04
224	Shorea exelliptica	52.35	50.53	54.18	1010865	859524	1188854	138.95	130.42	148.14	84.71	64.23	105.18
225	Shorea inappendiculata	106.34	102.64	110.05	5119943	4766773	5499279	219.42	215.50	223.55	154.70	139.53	169.88
226	Shorea falcifera	46.63	45.00	48.25	3497959	3238255	3778491	273.90	268.24	279.84	202.09	189.36	214.82
227	Shorea materialis	73.62	71.06	76.19	1142974	981851	1330538	124.60	117.55	132.15	72.22	50.68	93.76
228	Shorea atrinervosa	74.99	72.38	77.60	2161669	1949767	2396600	169.79	164.13	175.74	111.53	93.24	129.82
229	Shorea crassa	61.35	59.22	63.49	6010382	5580298	6473614	312.99	306.98	319.32	236.10	224.16	248.04
230	Shorea obscura	54.54	52.64	56.43	669302	549325	815483	110.78	102.16	120.21	60.20	37.61	82.79
231	Shorea falciferoides spp. falciferoides	56.99	55.01	58.97	2161669	1949767	2396600	194.76	188.27	201.59	133.25	116.61	149.89
232	Shorea superba	19.63	18.95	20.32	418707	329704	531737	146.04	131.91	161.78	90.87	70.91	110.83
233	Shorea hypoleuca	39.40	38.03	40.77	1010865	859524	1188854	160.17	150.34	170.76	103.17	84.21	122.12
234	Shorea astylosa	24.54	23.69	25.40	656930	538293	801713	163.61	150.75	177.68	106.16	87.44	124.87
235	Shorea domatiosa	106.34	102.64	110.05	28974811	24141172	34776259	521.98	484.97	562.15	417.89	396.46	439.33
236	Shorea glauca	34.36	33.16	35.55	2161669	1949767	2396600	250.83	242.48	259.63	182.03	168.43	195.63
237	Shorea laevis	17.72	17.11	18.34	828957	693072	991483	216.26	201.28	232.50	151.96	136.60	167.31
238	Shorea asahii	0.73	0.70	0.75	290098	221030	380748	631.63	561.19	711.34	513.27	483.13	543.42
239	Shorea micans	20.45	19.74	21.16	644543	527266	787906	177.53	163.44	192.95	118.26	100.50	136.03
240	Shorea ladiana	2.91	2.81	3.01	2127131	1916516	2360891	855.18	826.25	885.66	707.74	658.45	757.02
241	Shorea biawak	2.86	2.76	2.96	877686	737408	1044648	553.67	516.57	593.79	445.46	421.60	469.32
242	Shorea maxwelliana	40.90	39.48	42.33	2834694	2599486	3091186	263.26	256.61	270.25	192.84	179.74	205.93
243	Shorea siamensis	42.54	41.06	44.02	1861148	1661110	2085275	209.17	201.14	217.65	145.79	130.02	161.55

	SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
244	Shorea contorta	98.16	94.75	101.58	4791864	4462440	5145605	220.94	217.02	225.07	156.03	140.94	171.12
245	Shorea isoptera	37.49	36.19	38.80	619726	505225	760177	128.57	118.16	139.98	75.67	54.43	96.91
246	Shorea polyandra	30.54	29.48	31.60	3161774	2915054	3429374	321.76	314.47	329.42	243.73	231.82	255.63
247	Shorea kuantanensis	4.00	3.86	4.14	1942332	1738923	2169535	696.90	671.19	724.04	570.05	534.43	605.68
248	Shorea longiflora	2.23	2.15	2.30	7693771	7075674	8365861	1858.76	1814.39	1905.36	1580.72	1442.02	1719.42
249	Shorea macrobalanos	2.91	2.81	3.01	17570099	15265007	20223272	2457.81	2331.87	2592.13	2101.82	1909.32	2294.32
250	Shorea peltata	1.82	1.75	1.88	1581076	1393961	1793308	932.60	891.33	976.38	775.08	719.01	831.16
251	Shorea richetia	7.73	7.46	7.99	3497959	3238255	3778491	672.87	658.99	687.47	549.15	515.56	582.74
252	Shorea laxa	4.54	4.39	4.70	12553196	11193527	14078022	1661.99	1597.46	1730.18	1409.56	1288.49	1530.62
253	Shorea balanocarpoides	1.14	1.10	1.18	3161774	2915054	3429374	1668.19	1630.42	1707.88	1414.95	1293.34	1536.57
254	Shorea multiflora	0.91	0.88	0.94	1861148	1661110	2085275	1430.96	1376.04	1488.97	1208.59	1108.21	1308.97
255	Shorea patoiensis	0.73	0.70	0.75	656930	538293	801713	950.50	875.78	1032.21	790.65	732.99	848.30
256	Shorea induplicata	2.18	2.11	2.26	6010382	5580298	6473614	1659.90	1628.00	1693.45	1407.74	1286.86	1528.61
257	Shorea subcylindrica	4.91	4.74	5.08	3643015	3377193	3929759	861.53	844.33	879.61	713.26	663.41	763.10
258	Shorea obovoidea	1.27	1.23	1.32	4418360	4112863	4746549	1863.39	1829.95	1898.59	1584.75	1445.63	1723.87
259	Shorea collaris	4.09	3.95	4.23	7128295	6578776	7723715	1320.15	1290.91	1350.87	1112.20	1021.72	1202.68
260	Shorea angustifolia	1.14	1.10	1.18	456782	362486	575608	634.07	574.94	699.70	515.39	485.04	545.74
261	Shorea maxima	6.82	6.58	7.05	14773004	13012099	16772209	1472.11	1406.28	1541.95	1244.38	1140.32	1348.45
262	Shorea tenuiramulosa	1.36	1.32	1.41	1071038	915106	1253541	886.33	833.91	942.60	734.83	682.81	786.84
263	Shorea conica	3.64	3.51	3.76	2057952	1849966	2289320	752.36	726.08	780.06	618.29	577.93	658.66
264	Shorea bakoensis	0.55	0.53	0.56	3071762	2828293	3336189	2373.31	2318.02	2431.39	2028.32	1843.41	2213.22
265	Shorea xanthophylla	2.23	2.15	2.30	2161669	1949767	2396600	985.25	952.44	1019.81	820.88	760.16	881.60
266	Shorea blumutensis	44.17	42.64	45.71	3161774	2915054	3429374	267.54	261.48	273.90	196.56	183.62	209.50
267	Shorea iliasii	47.99	46.32	49.66	456782	362486	575608	97.56	88.46	107.66	48.70	25.09	72.31
268	Shorea faguetioides	28.63	27.63	29.63	507249	406297	633286	133.10	121.25	146.20	79.62	58.71	100.52
269	Shorea alutacea	39.27	37.90	40.63	1439920	1260273	1645176	191.50	182.36	201.22	130.41	113.56	147.26
270	Shorea longisperma	36.81	35.53	38.09	2115611	1905429	2348977	239.73	231.58	248.32	172.37	158.26	186.49

	SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
271	Shorea acuminatissima	21.27	20.53	22.01	669302	549325	815483	177.39	163.58	192.49	118.15	100.37	135.92
272	Shorea gibbosa	49.08	47.37	50.79	1686433	1494193	1903407	185.36	177.60	193.59	125.08	107.83	142.32
273	Shorea hopeifolia	28.63	27.63	29.63	2471054	2248194	2716005	293.78	285.23	302.77	219.39	207.18	231.59
274	Shorea kudatensis	16.36	15.79	16.93	865520	726321	1031396	230.01	214.47	246.82	163.91	149.31	178.51
275	Shorea cuspidata	20.45	19.74	21.16	3497959	3238255	3778491	413.57	405.04	422.55	323.59	309.22	337.97
276	Shorea mujongensis	28.63	27.63	29.63	730957	604542	883807	159.78	147.91	172.71	102.83	83.84	121.81
277	Shorea faguetiana	19.63	18.95	20.32	277064	210225	365154	118.80	105.33	134.07	67.17	45.19	89.15
278	Shorea dealbata	31.90	30.79	33.01	780052	648782	937882	156.37	145.15	168.55	99.85	80.63	119.08
279	Shorea farinosa	76.35	73.69	79.01	4142492	3852584	4454215	232.93	228.65	237.44	166.46	152.00	180.91
280	Shorea polita	70.90	68.43	73.36	1895967	1694466	2121430	163.53	157.36	170.05	106.09	87.37	124.81
281	Shorea gratissima	24.81	23.95	25.68	656930	538293	801713	162.71	149.92	176.70	105.37	86.60	124.15
282	Shorea henryana	41.45	40.00	42.89	1439920	1260273	1645176	186.39	177.49	195.85	125.97	108.79	143.15
283	Shorea montigena	44.99	43.43	46.56	2834694	2599486	3091186	251.01	244.66	257.67	182.18	168.59	195.77
284	Shorea assamica spp. globifera	59.99	57.90	62.08	2161669	1949767	2396600	189.83	183.51	196.49	128.96	112.00	145.92
285	Shorea ochracea	54.54	52.64	56.43	1010865	859524	1188854	136.15	127.79	145.14	82.27	61.58	102.95
286	Shorea virescens	28.36	27.37	29.35	877686	737408	1044648	175.93	164.14	188.67	116.87	99.00	134.74
287	Shorea javanica	73.62	71.06	76.19	938365	792884	1110540	112.90	105.63	120.73	62.04	39.61	84.47
288	Shorea roxburghii	29.45	28.42	30.47	1010865	859524	1188854	185.27	173.89	197.51	125.00	107.75	142.25
289	Shorea bentongensis	16.36	15.79	16.93	7406029	6823448	8038351	672.81	657.35	689.05	549.10	515.51	582.68
290	Shorea hypochra	120.52	116.33	124.72	15915793	13937264	18175192	363.39	346.14	381.74	279.94	267.52	292.36
291	Shorea symingtonii	122.70	118.43	126.98	1627953	1438514	1842340	115.18	110.21	120.45	64.03	41.78	86.28
292	Shorea retinodes	20.45	19.74	21.16	144195	103103	201663	83.97	72.27	97.62	36.88	12.21	61.55
293	Shorea cordata	88.62	85.54	91.71	938365	792884	1110540	102.90	96.28	110.05	53.35	30.15	76.54
294	Shorea bracteolata	46.36	44.74	47.97	1321641	1148866	1520399	168.85	160.24	178.03	110.72	92.36	129.07
295	Shorea resinosa	64.76	62.51	67.02	2161669	1949767	2396600	182.70	176.62	189.11	122.76	105.34	140.18
296	Shorea agamii	71.99	69.48	74.49	2834694	2599486	3091186	198.44	193.42	203.71	136.45	120.04	152.87
297	Shorea albida	30.54	29.48	31.60	669302	549325	815483	148.04	136.51	160.64	92.61	72.80	112.43

	SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
298	Shorea rubella	32.72	31.58	33.86	1686433	1494193	1903407	227.02	217.51	237.09	161.32	146.56	176.08
299	Shorea elliptica	32.72	31.58	33.86	1416314	1237990	1620324	208.05	197.99	218.75	144.81	128.98	160.64
300	Shorea smithiana	152.70	147.38	158.01	5294387	4927558	5688524	186.20	182.85	189.74	125.81	108.62	143.00
301	Shorea inaequilateralis	76.35	73.69	79.01	2253605	2038353	2491588	171.80	166.31	177.58	113.28	95.13	131.43
302	Shorea selanica	40.90	39.48	42.33	656930	538293	801713	126.73	116.77	137.63	74.08	52.70	95.46
303	Shorea flemmichii	26.59	25.66	27.51	1010865	859524	1188854	194.99	183.02	207.88	133.45	116.83	150.08
304	Shorea almon	95.44	92.11	98.76	2834694	2599486	3091186	172.34	167.99	176.92	113.75	95.64	131.87
305	Shorea parvistipulata spp. parvistipulata	136.34	131.59	141.08	6010382	5580298	6473614	209.96	205.93	214.21	146.48	130.76	162.19
306	Shorea balangeran	9.54	9.21	9.88	75045	50540	111430	88.68	74.07	106.22	40.97	16.67	65.27
307	Shorea coriacea	36.81	35.53	38.09	974657	826195	1149795	162.72	152.49	173.74	105.38	86.60	124.15
308	Shorea venulosa	21.27	20.53	22.01	865520	726321	1031396	201.73	188.10	216.48	139.31	123.10	155.53
309	Shorea waltoni	87.80	84.75	90.86	4923256	4584629	5286894	236.80	232.59	241.22	169.82	155.56	184.07
310	Shorea pachyphylla	152.70	147.38	158.01	6398687	5929773	6904682	204.70	200.58	209.04	141.90	125.87	157.93
311	Shorea pauciflora	36.81	35.53	38.09	1333497	1160006	1532937	190.33	180.69	200.60	129.40	112.47	146.32
312	Shorea johorensis	75.26	72.64	77.88	2482465	2259215	2727776	181.62	176.36	187.15	121.82	104.33	139.31
313	Shorea palembanica	9.54	9.21	9.88	12553196	11193527	14078022	1146.88	1102.35	1193.94	961.48	886.43	1036.52
314	Shorea andulensis	16.36	15.79	16.93	482056	384377	604557	171.65	156.02	188.97	113.15	94.99	131.31
315	Shorea polysperma	44.17	42.64	45.71	2253605	2038353	2491588	225.87	218.65	233.47	160.31	145.49	175.13
316	Shorea platyclados	27.27	26.32	28.22	1010865	859524	1188854	192.54	180.72	205.26	131.32	114.54	148.11
317	Shorea scaberrima	12.27	11.84	12.70	17570099	15265007	20223272	1196.62	1135.30	1262.01	1004.74	925.27	1084.21
318	Shorea fallax	10.91	10.53	11.29	1744790	1549855	1964243	399.96	383.69	417.17	311.75	298.02	325.48
319	Shorea pubistyla	95.44	92.11	98.76	5848139	5433367	6294574	247.54	242.87	252.46	179.17	165.42	192.91
320	Shorea palosapis	49.08	47.37	50.79	2834694	2599486	3091186	240.32	234.25	246.70	172.88	158.80	186.97
321	Shorea bullata	31.90	30.79	33.01	354762	275239	457262	105.45	94.54	117.69	55.56	32.57	78.56
322	Shorea flaviflora	106.34	102.64	110.05	2664618	2435183	2915670	158.29	154.03	162.77	101.53	82.44	120.61
323	Shorea monticola	28.63	27.63	29.63	1071038	915106	1253541	193.41	181.97	205.69	132.08	115.35	148.81
324	Shorea kunstleri	41.72	40.27	43.17	2834694	2599486	3091186	260.67	254.08	267.59	190.58	177.38	203.78

	SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
325	Shorea pilosa	115.89	111.85	119.92	3987517	3705626	4290851	185.50	182.01	189.16	125.19	107.95	142.43
326	Shorea splendida	47.04	45.40	48.67	27106550	22714154	32348335	759.13	707.33	815.22	624.19	583.24	665.13
327	Shorea stenoptera	40.90	39.48	42.33	24774846	20919985	29340030	778.28	727.96	832.59	640.84	598.24	683.44
328	Shorea macrophylla	89.98	86.85	93.12	50596474	40144672	63769439	749.86	679.87	827.55	616.12	575.97	656.27
329	Shorea praestans	122.70	118.43	126.98	4868535	4533791	5227994	199.19	195.66	202.91	137.11	120.74	153.47
330	Shorea rotundifolia	88.62	85.54	91.71	4923256	4584629	5286894	235.70	231.52	240.11	168.86	154.55	183.18
331	Shorea amplexicaulis	147.25	142.12	152.37	13233848	11754428	14899470	299.79	287.59	312.70	224.62	212.52	236.72
332	Shorea mecistopteryx	206.96	199.76	214.17	14905920	13120062	16934862	268.37	256.28	281.20	197.28	184.37	210.19
333	Shorea beccariana	139.88	135.01	144.75	17630806	15313489	20298792	355.02	336.78	374.47	272.66	260.43	284.88
334	Shorea pinanga	267.22	257.92	276.53	7224507	6663675	7832541	164.42	160.74	168.30	106.86	88.21	125.52
335	Shorea slootenii	83.44	80.53	86.34	3665299	3398506	3953036	209.59	205.42	213.97	146.15	130.41	161.89
336	Shorea myrionerva	115.89	111.85	119.92	2664618	2435183	2915670	151.63	147.55	155.93	95.74	76.18	115.30
337	Shorea sagittata	74.99	72.38	77.60	656930	538293	801713	93.60	86.24	101.65	45.25	21.34	69.17
338	Shorea macroptera spp. macroptera	75.26	72.64	77.88	1686433	1494193	1903407	149.69	143.42	156.34	94.05	74.35	113.75
339	Shorea macroptera spp. baillonii	81.53	78.69	84.37	1686433	1494193	1903407	143.82	137.80	150.20	88.94	68.82	109.06
340	Shorea macroptera spp. sandakanensis	87.80	84.75	90.86	1686433	1494193	1903407	138.59	132.78	144.74	84.39	63.89	104.89
341	Shorea macroptera spp. macropterifolia	87.80	84.75	90.86	1686433	1494193	1903407	138.59	132.78	144.74	84.39	63.89	104.89
342	Shorea ferruginea	10.91	10.53	11.29	1744790	1549855	1964243	399.96	383.69	417.17	311.75	298.02	325.48
343	Shorea acuta	114.52	110.54	118.51	7128295	6578776	7723715	249.48	243.96	255.29	180.86	167.19	194.52
344	Shorea quadrinervis	28.36	27.37	29.35	507249	406297	633286	133.74	121.84	146.90	80.17	59.32	101.03
345	Shorea acuminata	29.45	28.42	30.47	380419	296997	487272	113.66	102.22	126.45	62.70	40.33	85.07
346	Shorea macrantha	22.72	21.93	23.51	19224953	16580966	22290548	919.81	869.49	973.63	763.96	709.00	818.91
347	Shorea hemsleyana spp. hemsleyana	12.27	11.84	12.70	34022565	27955208	41406772	1665.15	1536.37	1805.82	1412.30	1290.96	1533.65
348	Shorea hemsleyana spp. singkawang	17.45	16.84	18.06	20861090	17871278	24351090	1093.34	1030.05	1161.22	914.90	844.61	985.19
349	Shorea lepidota	74.99	72.38	77.60	1274150	1104313	1470107	130.35	123.52	137.64	77.23	56.12	98.34
350	Shorea foraminifera	22.90	22.11	23.70	1010865	859524	1188854	210.08	197.18	223.96	146.58	130.87	162.29
351	Shorea teysmanniana	21.81	21.05	22.57	532366	428241	661809	156.22	142.62	171.22	99.73	80.50	118.96

SPECIES	Wing area	Wing area 95% LCI	Wing area 95% UCI	Fruit mass (milli-dynes)	Fruit mass (milli-dynes) 95% LCI	Fruit mass (milli-dynes) 95% UCI	Sqrt wing-loading	Sqrt wing-loading 95% LCI	Sqrt wing-loading 95% UCI	Terminal velocity (cm/s)	Terminal velocity 95% LCI (cm/s)	Terminal velocity 95% UCI (cm/s)
352 Shorea argentifolia	24.54	23.69	25.40	767796	637717	924409	176.88	164.08	190.79	117.70	99.89	135.51
353 Shorea uliginosa	19.63	18.95	20.32	211282	156424	285380	103.74	90.86	118.52	54.07	30.95	77.20
354 Shorea rugosa	71.58	69.09	74.07	3229179	2979971	3499228	212.40	207.69	217.35	148.60	133.02	164.17
355 Shorea leprosula	54.54	52.64	56.43	1861148	1661110	2085275	184.74	177.65	192.23	124.53	107.24	141.82
356 Shorea platycarpa	21.27	20.53	22.01	211282	156424	285380	99.67	87.29	113.87	50.53	27.09	73.98
357 Shorea curtsii spp. curtsii	19.09	18.42	19.75	669302	549325	815483	187.26	172.68	203.19	126.72	109.60	143.85
358 Shorea scabrida	28.63	27.63	29.63	456782	362486	575608	126.31	114.53	139.38	73.71	52.30	95.12
359 Shorea revoluta	26.59	25.66	27.51	656930	538293	801713	157.19	144.84	170.71	100.57	81.41	119.74
360 Shorea ovata	15.00	14.48	15.52	494663	395334	618948	181.61	165.26	199.71	121.82	104.32	139.31
361 Shorea rubra	47.99	46.32	49.66	557410	450210	690137	107.77	98.59	117.88	57.58	34.77	80.40
362 Shorea dasyphylla	31.90	30.79	33.01	974657	826195	1149795	174.79	163.80	186.62	115.88	97.93	133.83
363 Shorea parvifolia spp. parvifolia	36.81	35.53	38.09	482056	384377	604557	114.43	104.01	125.98	63.38	41.07	85.69
364 Shorea ovalis spp. ovalis	41.99	40.53	43.45	2368205	2148899	2609892	237.48	230.26	245.07	170.41	156.19	184.64
365 Shorea carapae	28.63	27.63	29.63	354762	275239	457262	111.31	99.80	124.23	60.66	38.12	83.21
366 Shorea pallidifolia	28.63	27.63	29.63	669302	549325	815483	152.89	140.99	165.90	96.83	77.37	116.30
367 Shorea foxworthyii	68.17	65.80	70.54	3066845	2823552	3331101	212.11	207.16	217.30	148.34	132.75	163.93

FIGURE S1.
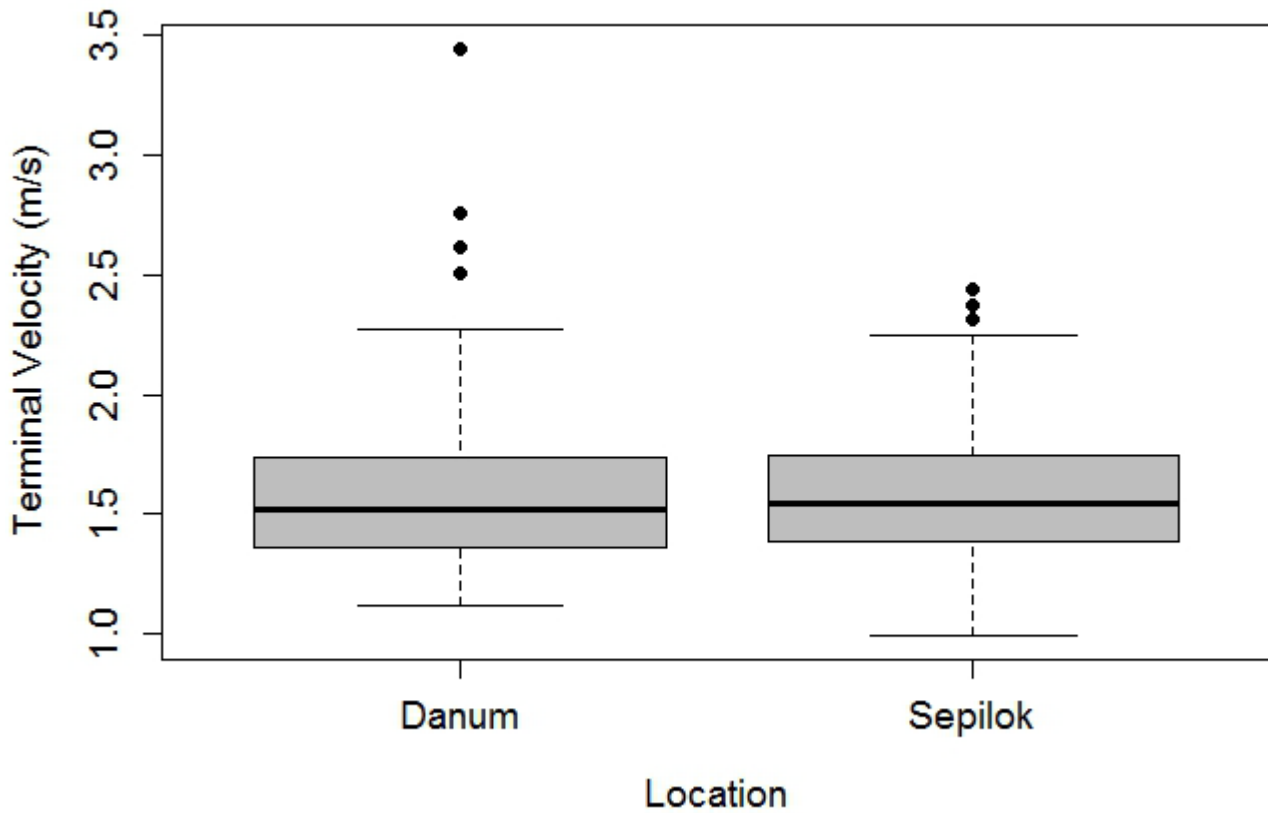
Figure S1. Boxplot of the terminal velocity (m/s) of *S. leprosula* fruit released at Sepilok (12.5 m height; 88 fruit) and Danum (18 m height; 50 fruit). An analysis of variance confirmed there was no significant difference in the terminal velocity of *S. leprosula* fruit released from the two heights ($F_{(1,136)}$ = 0.706; P = 0.402).

FIGURE S2.
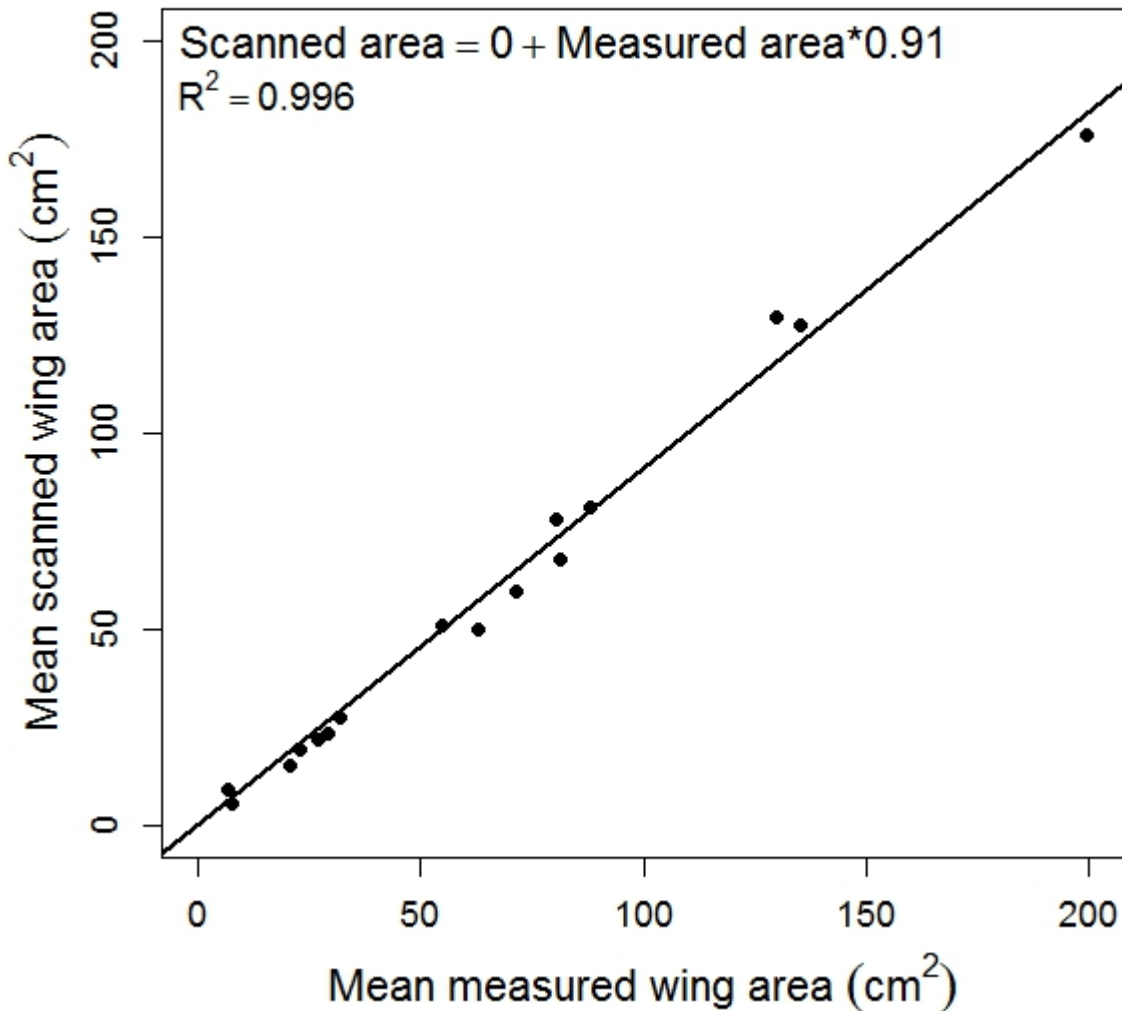
FIGURE S2. Regression of mean caliper measured long-wing area (cm^2) against scanned total wing area (cm^2) for the 16 dipterocarp study species experimentally released (R^2 = 0.99, $F_{(1,15)}$ = 3749, $P <$ 0.001). Measured long-wing area was calculated as the product of each long-wing length multiplied by maximum width summed from each fruit.

FIGURE S3.
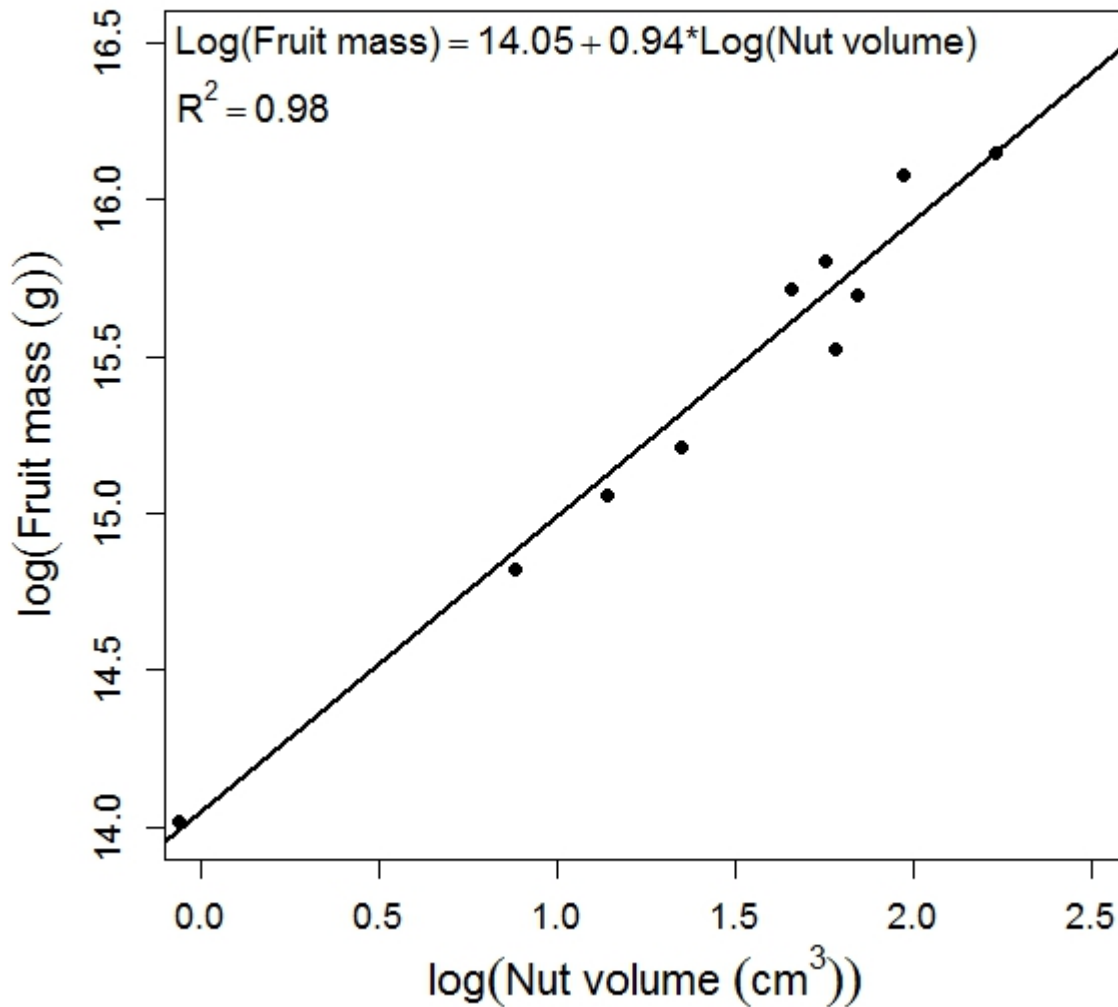
FIGURE S3. Regression of mean log(fruit volume(cm^3)) against log(fruit mass(g)) for 12 of the dipterocarp study species experimentally released ($R^2 = 0.93$, $F_{(1,11)} = 131.1$, $P < 0.001$). Time constraints prevented collection of nut only mass measurements in four species (Table 1). Fruit volume was calculated using the equation for the volume of an ellipsoid, $V = {}^4\!/_3\,\pi abc$, where a is the nut radius in the vertical plane (length), and b and c are measurements of the nut radii in the horizontal plane opposed at 90 degrees (width).

No evidence for dispersal limitation driving fine-scale spatial aggregation in populations of gyration dispersed late-successional tropical trees

with Robert Bagchi, David Burslem, Colin Maycock, Eyen Khoo and Jaboury Ghazoul

ABSTRACT

The majority of tropical trees are spatially aggregated. At a landscape scale this is driven by niche based mechanisms generating distinct habitat associations, yet within such broad scale non-random distributions trees are often aggregated at a finer-scale. Dispersal limitation is one mechanism predicted to generate spatially aggregated distributions, due to the successive recruitment of offspring near to parent trees over multiple reproductive events. Evidence from Southeast Asian forests suggests that trees categorized in dispersal syndromes with greater dispersal potential are less aggregated. Similarly, trees with juveniles adapted to shade tolerance, a trait correlated to wood density, might also exhibit spatial aggregation as they are less dependent on dispersal to, and recruitment in, gaps. In this paper we test the hypothesis that among species from a single dispersal syndrome, gyration, variation in dispersal potential and wood density drives variation in fine-scale spatial aggregation. We test these hypotheses using the adult distributions of 28 species of Dipterocarpaceae from an inventoried forest plot in Malaysian Borneo. We apply an emerging statistical technique, replicated point pattern analysis (RPP), that correlates second-order spatial statistics to continuous explanatory variables in a single statistical framework. The majority of dipterocarps (>90%) in Sepilok were non-randomly distributed and exhibited clear habitat associations. After controlling for habitat associations 79% of dipterocarp species continued to exhibit fine-scale spatial aggregation suggesting that intrinsic factors influenced patterns of aggregation. However, there was no significant correlation between seed dispersal or wood density and spatial aggregations at finer-scales. Our results on patterns of spatial aggregation of adult individuals suggest that negative density-dependent mechanisms acting at the seedling stage are not sufficiently strong to overcome the highly aggregated seedling distributions driven by limited seed dispersal and positive density-dependent survival of fruit during reproductive events.

INTRODUCTION

Spatial aggregation of individuals within populations can be generated by a range of processes including spatially heterogeneous environments (niche differentiation / habitat filtering) (Ashton 1969, Harms et al. 2001, Valencia et al. 2004, John et al. 2007, Kraft et al. 2015), temporally heterogeneous environments (gap-phase regeneration), and dispersal limitation (Hubbell 1979, Hubbell 2001, Wang et al. 2011, Detto and Muller-Landau 2016). Dispersal limitation is hypothesized to generate aggregated, or clustered, spatial patterns as related individuals germinate and establish in close proximity to the mother tree (Bleher et al. 2002, Chave et al. 2002, Plotkin et al. 2002, Svenning and Skov 2002). Evidence in support of dispersal limitation driving spatial aggregation in tropical forests was provided by Seidler and Plotkin (2006) who observed that the mean cluster size of tropical trees was significantly related to seed dispersal syndromes: animal dispersed fruit possessed wider cluster diameters to wind dispersed fruit, which in turn possessed wider cluster diameters to gyration and ballistically dispersed fruit. Yet dispersal within syndromes is highly variable and can operate on scales varying over many orders of magnitude (Augspurger 1986, Vittoz and Engler 2007, Muller-Landau et al. 2008, Thomson et al. 2011, Tamme et al. 2014). Zoochory, the dispersal of seeds or fruits by animals, can occur over meters to tens of kilometers depending on whether ants, rodents, primates, birds or bats are the primary dispersal vectors (Corlett 2009). The situation for wind dispersed fruit is similarly complex. A comprehensive investigation into the role of dispersal in driving spatial aggregation requires that realized dispersal can be measured accurately and compared on a common scale – analysis within dispersal syndrome is therefore required. In this paper we analyse the effect of dispersal limitation on patterns of spatial aggregation in the Dipterocarpaceae, a family of late-successional tropical trees possessing auto-gyrating winged fruit, the dispersal potential of which can be accurately predicted based on the fruit morphology alone (Smith et al. 2015).

Seidler and Plotkin's (2006) study was conducted in a lowland dipterocarp forest in Pasoh, Peninsula Malaysia (Manokaran et al. 2004). The Dipterocarpaceae dominate the forests that bear their name, regularly constituting over 40% of basal area (Newbery et al. 1992, Curran and Leighton 2000, Davies et al. 2005) and 60% of canopy trees (Newbery et al. 1992). The Dipterocarpaceae flower and fruit synchronously on an supra-annual periodicity in forest wide 'general flowering' events (Ashton 1988, Sakai 2002, Brearley et al. 2007). Dipterocarp fruit are composed of a nut and persistent calyx with lobes that become elongated to form wings in most species causing the fruits to gyrate and disperse laterally by wind when abscised (Suzuki and Ashton 1996, Ashton 2004). There is variability in the number and surface area of wings and fruit mass (Suzuki and Ashton 1996).

Nevertheless, there is a direct relationship between fruit morphology and terminal velocities (rate at which a fruit descends in the air column) (Smith et al. 2016) and therefore interspecific variation in dispersal potentials can be accurately assessed based on the fruit morphology alone (Smith et al. 2015). Fruit with low terminal velocities not only disperse further in lateral wind currents but are more likely to buoyed up and dispersed long distances by updrafts (Greene and Quesada 2011). Dispersal distances under normal atmospheric conditions are largely restricted to maximum distances <100 m (Ridley 1930, Tamari and Jacalne 1984), and are frequently constrained to distances no further than the edge of the mother tree's crown (Itoh et al. 1997, Osada et al. 2001, Smith et al. 2015). Dispersal potentials therefore vary considerably between species (Smith et al. 2016), as do patterns of spatial aggregation (Suzuki et al. 2009, Bagchi et al. 2011). Given the diversity of fruit morphologies in this family we hypothesize that species with low seed dispersal potential will be more spatially aggregated than species with high dispersal potentials.

Like most late-successional tropical tree species, dipterocarp seedlings are able to tolerate light limited conditions characteristic of the forest understory (Swaine and Whitmore 1988, Brown and Whitmore 1992, Philipson et al. 2012, Philipson et al. 2014). Yet there are interspecific differences in dipterocarp species' ability to persist in low light conditions and grow rapidly in high light conditions (Dent and Burslem 2009, Philipson et al. 2012). The well-known shade tolerance – growth rate trade-off is revealed across a range of dipterocarp species that are variously adapted to shade or light conditions (Barker et al. 1997, Philipson et al. 2012). This trade-off is also associated with other functional plant traits, including wood density which is correlated with lower growth and mortality rates (Philipson et al. 2014). This differential persistence in the forest understory between dipterocarp species has been hypothesized to act as a form of dispersal limitation underpinning the co-existence of the species-rich Dipterocarpaceae (Brown et al. 1999). Gap formation soon after a mast fruiting event favours species capable of rapid grow responses, whereas a long delay in gap formation results in the disproportionate mortality of these same species, favouring the slower growing, but shade tolerant, species (Brown et al. 1999). In view of this, we expect that more light demanding species gain a relative benefit from locating their seeds in gap environments, which favours broader dispersal to increase the probability that they encounter these relatively infrequent high-light sites. Shade-tolerant species, on the other hand, are more likely to benefit from abundant seed resources which favours seedling establishment in the shaded understory (Westoby et al. 1992, Westoby et al. 1996, Coomes and Grubb 2003). This invokes selection for larger seed mass and hence reduced dispersal potential (Westoby et al. 1996, Muller-Landau et al. 2008, Thomson et al. 2011). On this basis, we predict that shade tolerant (and therefore high wood density) species are more spatially aggregated than low wood

density species, on account of their more limited seed dispersal. Molecular evidence supports this hypothesis, with high wood density dipterocarps exhibiting more intense fine-scale spatial genetic structure than low wood density species; *i.e.* high wood density species are more genetically related at near distances among conspecific individuals than species with low wood density (Tito de Morais et al. 2015)

In addition to seed dispersal patterns and species regeneration niches, many tropical forest tree species, including the Dipterocarpaceae, show strong positive or negative associations with soil type (Palmiotto et al. 2004, Paoli et al. 2006, John et al. 2007, Itoh et al. 2010, Itoh et al. 2012) or topography (Webb and Peart 2000, Itoh et al. 2003, Sukri et al. 2012, Brown et al. 2013, Punchi-Manage et al. 2013, Punchi-Manage et al. 2014), driven by niche-partitioning and habitat filtering mechanisms (Palmiotto et al. 2004, Paoli et al. 2006, Dent and Burslem 2009, Suzuki et al. 2009, Margrove et al. 2015). Thus the distribution of mature individuals is expected to be non-random with respect to soil type, irrespective of species' dispersal traits that might determine spatial aggregation. Any analysis of spatial aggregation patterns in the context of species traits must, therefore, first control for this non-random, 'inhomogeneous' distribution of individuals generated by soil substrates and other habitat variables (Bagchi et al. 2011).

In this paper we use the co-ordinates of 5135 mature dipterocarp trees in a 160 ha forest plot in Sepilok, Malaysian Borneo, to investigate spatial aggregation patterns in the Dipterocarpaceae. We present an analysis of spatial aggregation patterns that first controls for habitat associations, and then investigates how the association of species traits, namely seed dispersal and wood density, with differential spatial distributions of among species. We achieve this using a novel statistical method, 'Replicated Point Process' (RPP) models (discussed in the methods section, Bagchi and Illian 2015), and ask the following questions:

1. To what extent are adult dipterocarp trees aggregated?
2. To what extent is aggregation driven by soil and topography?
3. After accounting for topography, do species traits correlate the degree of spatial aggregation? Specifically:
   a. Are species with high wood density more spatially aggregated than species with low wood density?
   b. Are species with lower seed dispersal potential more aggregated than species with high seed dispersal potential?

METHODS

Study Site

We analyzed data from a 160 ha forest plot of mature dipterocarp trees situated in Sepilok Forest Reserve (SFR), Malaysian Borneo (5°51' N 117°56' E). SFR is a 4420 ha fragment of tropical lowland dipterocarp forest, heath (kerangas forest) and mangroves ranging in elevation between 0–170 m.a.s.l. (Fox 1973). The plot is located in the lowland dipterocarp forest, which can be subdivided into periodically flooded low-lying alluvial areas with low mudstone hills between 15–30 m elevation, and sandstone hills reaching 100 m elevation (Fig. 1). In the plot, all mature dipterocarp individuals with diameter at breast height (DBH) ≥50 cm (although for some species down to 30 cm, Table 1) have been identified, coordinates repeatedly taken with a handheld GPS, and given a unique identification code (Margrove et al. 2015). The resulting dataset comprises over 5000 individuals from 42 species in seven genera.
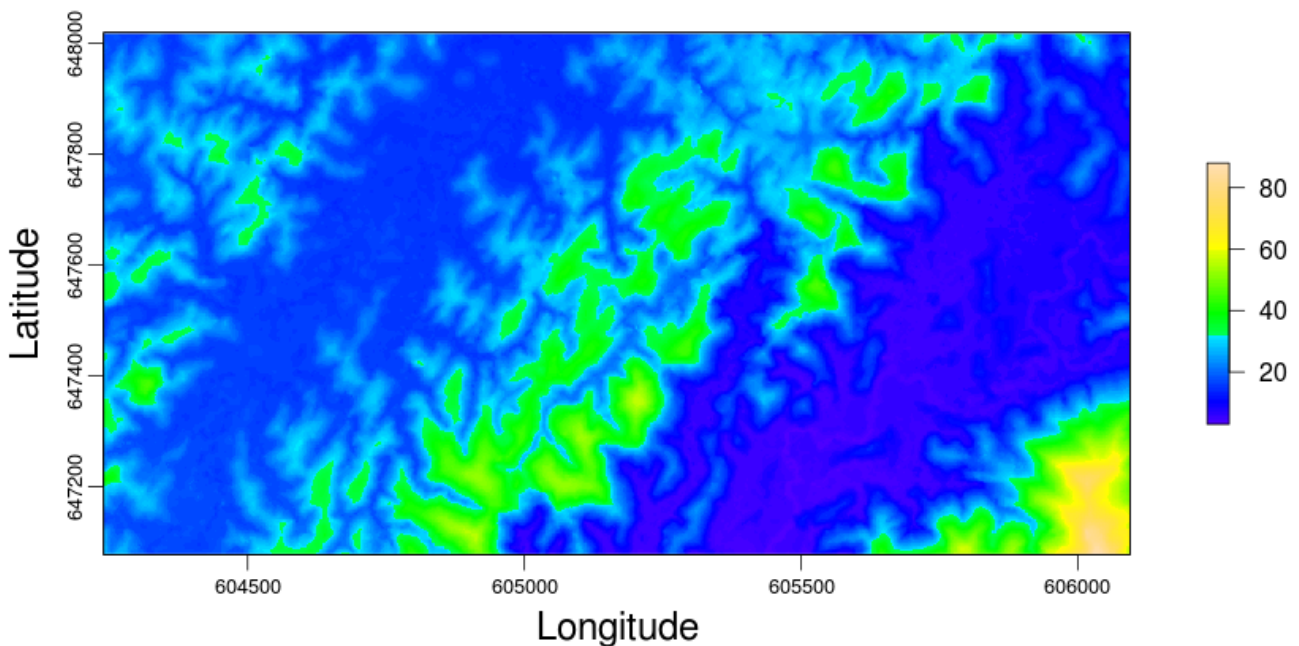
Figure 1. A digital elevation model (in meters) of the 160 ha plot of mature dipterocarp trees in the Sepilok Forest Reserve. Latitude and longitude are given in Universal Transverse Mercator (UTM) coordinates.

Species trait data

Wood density in units g/cm^3 at 0% moisture content was calculated for each species individually from published sources (Reyes 1938, Burgess 1966, Lee et al. 1979, Oey 1990, Basuki et al. 2009, Saner et al. 2012). Where wood density moisture contents were presented at 12–18% they were converted to 0% by applying a conversion factor of 0.861 following Chave et al. (2009). The inverse wing-loadings (IWL), a direct proxy for fruit dispersal potential in the Dipterocarpaceae (Smith et al. 2015), were calculated from the mean fruit dimensions given in the Flora Malesiana (Ashton 1983) according to Smith *et al.* (Chapter 2).

Statistical Analysis

Our analysis follows the 'Replicated Point Process' (RPP) approach detailed by Bagchi and Illian (2015). This method of analyzing spatial patterns goes beyond previous methods of analyzing second-order spatial statistics in relation to explanatory variables, by including them in a statistical framework to rigorously test their contribution to shaping the observed spatial patterns. In contrast, previous methods have first calculated spatial statistics of interest before correlating these to the ecological variables or traits of interest (Seidler and Plotkin 2006, Bagchi et al. 2011, Bagchi and Illian 2015). RPP treats each point process pattern (*i.e.* the location of points in the study area – individual trees in the research plot in the case of this study) as replicate outcomes of the same ecological process. In this way the effects of independent variables on point patterns can be assessed in a standard linear model framework by analyzing deviations in the spatial statistics of interest from the mean in relation to deviations of the covariate values to the covariate mean. Full details of the RPP procedure are outlined in Bagchi and Illian (2015), and (Ramón et al. 2016).

In this analysis we use the univariate K-function as the spatial statistic of interest (Ripley 1979). The K-function is a cumulative statistic that characterizes the neighbourhood around a typical point (a focal tree) as the proportion of points of the same type (e.g. same species) that lie within circles of increasing radii, *r*, centred on the focal tree. If points are randomly and homogeneously located through the plot, known as Complete Spatial Randomness (CSR), the expected K-function is πr^2 (Illian et al. 2008, Diggle 2014). If more points are observed than predicted by CSR a species is considered spatially aggregated, or 'clumped', and if fewer points are observed than predicted by CSR the pattern is considered 'inhibited'; a scenario equivalent to repulsion between points. This simple K-function assumes that there is no variation in the background substrate of the study area (*i.e.* points are located on a homogeneous 2D plane) and hence is termed the homogeneous K-function. To test

Table 1. The 28 Dipterocarpaceae species with ≥25 individuals in the 160 ha Sepilok Forest Reserve plot used in spatial aggregation analysis together with their minimum DBH thresholds within the plot (DBH plot), canopy position, height, maximum DBH, wood density, and IWL.

Species	DBH plot	N	Canopy position	Max. DBH (m)	Wood density (g/cm^3)	IWL
Dipterocarpus acutangulus	40	96	Emergent	1.2	0.69	6.12
Dipterocarpus caudiferus	40	191	Emergent	1.5	0.63	4.55
Dipterocarpus confertus	50	65	Emergent	1.5	0.69	18.53
Dipterocarpus grandiflorus	50	81	Emergent	1.5	0.68	2.94
Dipterocarpus humeratus	50	56	Emergent	1.0	0.64	7.02
Dipterocarpus kerri	40	131	Emergent	1.2	0.61	3.75
Dipterocarpus kunstleri	50	82	Canopy	1.0	0.62	2.02
Dryobalanops lanceolata	50	110	Emergent	2.5	0.71	21.51
Hopea beccariana	30	112	Canopy / Emergent	1.6	0.69	59.49
Parashorea malanoonan	50	207	Emergent	2.0	0.47	31.76
Parashorea tomentella	50	602	Emergent	2.0	0.42	32.98
Shorea acuminatissima	50	97	Emergent	2.0	0.46	15.54
Shorea agami	50	40	Emergent	2.0	0.58	33.65
Shorea almon	50	28	Emergent	1.2	0.45	44.61
Shorea argentifolia	50	74	Emergent	1.5	0.63	48.56
Shorea beccariana	50	258	Emergent	1.1	0.46	9.38
Shorea falciferoides	50	60	Emergent	1.1	0.81	40.37
Shorea gibbosa	50	82	Emergent	2.0	0.46	39.83
Shorea johorensis	50	402	Emergent	1.6	0.45	40.39
Shorea leprosula	50	129	Emergent	1.5	0.46	67.88
Shorea macroptera	50	309	Canopy / Emergent	1.4	0.46	92.95
Shorea mecistopteryx	50	209	Emergent	1.6	0.46	16.59
Shorea multiflora	30	524	Canopy / Emergent	1.0	0.55	0.00
Shorea parvifolia	50	210	Emergent	2.0	0.40	112.88
Shorea smithiana	50	346	Emergent	1.6	0.43	36.72
Shorea waltoni	50	54	Emergent	-	0.38	26.58
Shorea xanthophylla	30	541	Canopy	0.7	0.57	0.00
Vatica oblongifolia	30	39	Canopy	0.5	0.74	7.17

whether species were significantly more aggregated than the CSR null hypothesis we performed a goodness-of-fit test as proposed by (Loosmore and Ford 2006). This test simulates random poisson point processes with the same intensity of the species to be tested and calculates a K-function. Deviations from the observed K-function to the mean K-function of the simulated poisson processes are then summed across distance, r, and compared to the summed deviations from the simulated K-functions to the mean simulated K-function. A P value can be assigned according to the proportion summed deviations of simulated poisson processes K-functions which deviate more that the observed K-function.

We subsequently analyzed species' K-functions using the RPP linear model framework to predict the pooled K-function across species, *i.e.* the mean aggregation across species. We restricted the distance over which we analyzed spatial aggregation to only 50 m, which is the maximum potential scale of seed dispersal in dipterocarps under normal atmospheric conditions (Smith et al. 2015), and corresponds to the asymptotic limit of the K-functions obtained for the species we examined.

A large proportion of dipterocarp species show strong habitat affinities (Palmiotto et al. 2004, Paoli et al. 2006, Sukri et al. 2012). The 160 ha plot contains three distinct soil substrates and previous work (Nilus 2004, Born et al. 2014, Born et al. 2015, Margrove et al. 2015) has demonstrated that these soil types influence the distributions of individual dipterocarp species. Habitat associations cause trees to cluster in areas of suitable habitat (John et al. 2007), leading to the rejection of the null hypothesis. The effects of habitat heterogeneity on K-functions can be controlled for by accounting for variation in the intensity (density) of trees by modelling intensity as a function of environmental covariates. This allows us to evaluate an alternative null hypothesis that trees are randomly distributed after accounting for heterogeneity imposed by the environmental covariates using the inhomogeneous K-function (Baddeley et al. 2000). Elevation was used as a proxy for habitat type rather than soil substrate as the plot shows transitions between the habitat types listed above on the basis of elevation (0–15 m = alluvial flood plain; 16–30 m = mudstone hills; >61 m = sandstone ridges), and thus soil substrate and elevation are almost perfectly correlated. Elevation was considered preferable over soil type as a categorical variable in this system as deviations in the cut-off point between the soil categories can alter the results of habitat associations (Itoh et al. 2010), and elevation as a continuous variable will more readily account for species which might associate with intermediate habitat zones and slopes. We controlled for deviations from CSR driven by habitat associations by fitting point process models (PPM) (Renner et al. 2015) to each species individually, which modeled the intensity of individuals as a function of topography. Tree intensity was allowed to vary as a smooth function of

elevation, latitude and longitude, estimated using cubic splines with the number of turning points (k) restricted to a maximum of five. We selected the best PPM model for each species based on minimum values of the Akaike Information Criterion (AIC) score (intensity surfaces predicted by the PPMs for each species are provided in the supplementary information, SI2). The intensity surfaces predicted by these models were then used to control for variation in underlying species intensity driven by habitat when estimating the K-function (individual plots by species, showing homogeneous and inhomogeneous K-functions, are provided in the supplementary information SI3). We performed a non-parametric bootstrap emulating the goodness-of-fit test proposed by (Loosmore and Ford 2006) to test whether the inhomogeneous K-functions differed significantly from CSR. Further, a non-parametric bootstrap based on a subsample of 80% of points for each species was used to test for significant reductions in the inhomogeneous K-functions compared to the homogeneous K-functions following the method outlined by (Henrys and Brown 2009). Both bootstrapping procedures are described in the supplementary information (SI1).

A weighted mean inhomogeneous K-function was calculated across species (using the PPM predicted intensity surfaces), with weightings relative to species population size to minimize the influence of rare species. Even so, species with <25 individuals were excluded from the analysis as the point process models used to model species densities in relation to elevation are not robust to low abundances and consequently outliers from the modeled intensity surfaces have an excessively influential effect on the calculation of the inhomogeneous K-functions. The final dataset comprised 28 species in six genera (Table 1). Nevertheless, the inhomogeneous K-functions of five species were substantially influenced by large residual values for the intensity of outlier trees positioned at the edges of the species intensity surfaces predicted by the PPM models (i.e. areas with a low probability of occurrence). These extreme values were manually reduced to the 0.1 percentile intensity for each species (number of points down-weighted per species: *Dipterocarpus kerrii*: four points; *Hopea beccariana*: 10 points; *Shorea argentifolia*: seven points; *Shorea leprosula*: two points; *Shorea multiflora*: 25 points).

A linear model was fitted within the RPP framework using the inhomogeneous K-functions as response variable, with wood density, inverse wing-loading (IWL) and their interaction as predictor variables. A semi-parametric bootstrap of 1000 iterations was applied to the linear model generating 95% confidence intervals for the model predictors to provide inference on the strength of the model predictors on the inhomogeneous K-functions. The significance of the model predictors was tested using an ANOVA function. Example code is provided as supplementary information to Bagchi and Illian (2015).

To facilitate interpretation of the RPP linear model results, the inhomogeneous K-functions predicted by the bootstrapped LM were converted to L-functions, $\hat{L}(t) = \sqrt{\widehat{K(t)}/\pi}$, which stabilize the variance (Besag 1977). Under complete spatial randomness (CSR) $\hat{L}_{(r)-r} = 0$. Plotting L-functions against distance allows visual inspection of predictors inference on the spatial scale of aggregation (Law et al. 2009, Bagchi and Illian 2015). Plots of the L-function 95% confidence envelopes above 0 correspond to greater aggregation of points than expected at random, while L-functions below 0 indicate less points than expected at random (*i.e.* inhibition).

RESULTS

There was substantial variation in species traits, with wood density ranging 0.38–0.81 g/cm^3, and IWL ranging 0.00–112.88 (cm^2/cm^3) (Table 1). Homogeneous K-functions were calculated for these species and are presented in Figure 2. The goodness-of-fit tests confirmed that all but one species (*Shorea almon*), possessed initial distributions more spatially aggregated than predicted by CSR (Fig. 2, Table 2). *Dipterocarpus acutangulus* exhibited the strongest spatial aggregation, followed by *D. kerrii*, *S. beccariana* and *S. multiflora*. *Dipterocarpus confertus*, *D. humeratus* and *S. agamii* exhibited only weak aggregation. No species were inhibited (*i.e.* less spatially aggregated than predicted at CSR).

Once habitat associations had been controlled for, the distributions of six species (21%) were not significantly different from the null expectation (Fig. 3, Table 2). The remaining 79% of species were therefore more spatially aggregated than predicted after controlling for habitat associations. Six species were significantly more clustered than predicted by either CSR or the inhomogeneous null model, but homogeneous and inhomogeneous K-functions were not significantly difference from each other (Table 2), indicating that habitat associations are weak or absent. In 13 species, the inhomogeneous K-functions were significantly lower than the homogeneous K-functions (Fig. 3, Table 2), indicating that habitat associations contributed to some of the departure from CSR. However the inhomogeneous K-values of *H. beccariana* and *D. caudiferous*, and to a lesser extent *S. multiflora*, were higher than the homogeneous K-functions at the spatial scales observed, indicating a continued strong influence of outliers with large residuals in the predicted intensity surfaces from the PPMs.

The pooled inhomogeneous L-functions were lower than the pooled inhomogeneous L-functions, suggesting that habitat heterogeneity contributed to the clustering of species distributions (Fig. 2, Table 2). However, there remained substantial variation around the pooled L-functions (Fig. 4), and the reduction from accounting for habitat heterogeneity was not significant, as indicated by the overlapping confidence bands. None of the independent variables were correlated with either a significant decrease or increase in inhomogeneous K-values, and therefore did not explain variation in aggregation among species (Wood density: $D = 92.77$, $P = 0.22$; IWL: $D = 0.94$, $P = 0.88$; interaction: $D = 13.09$, $P = 0.89$) (Figure 5).
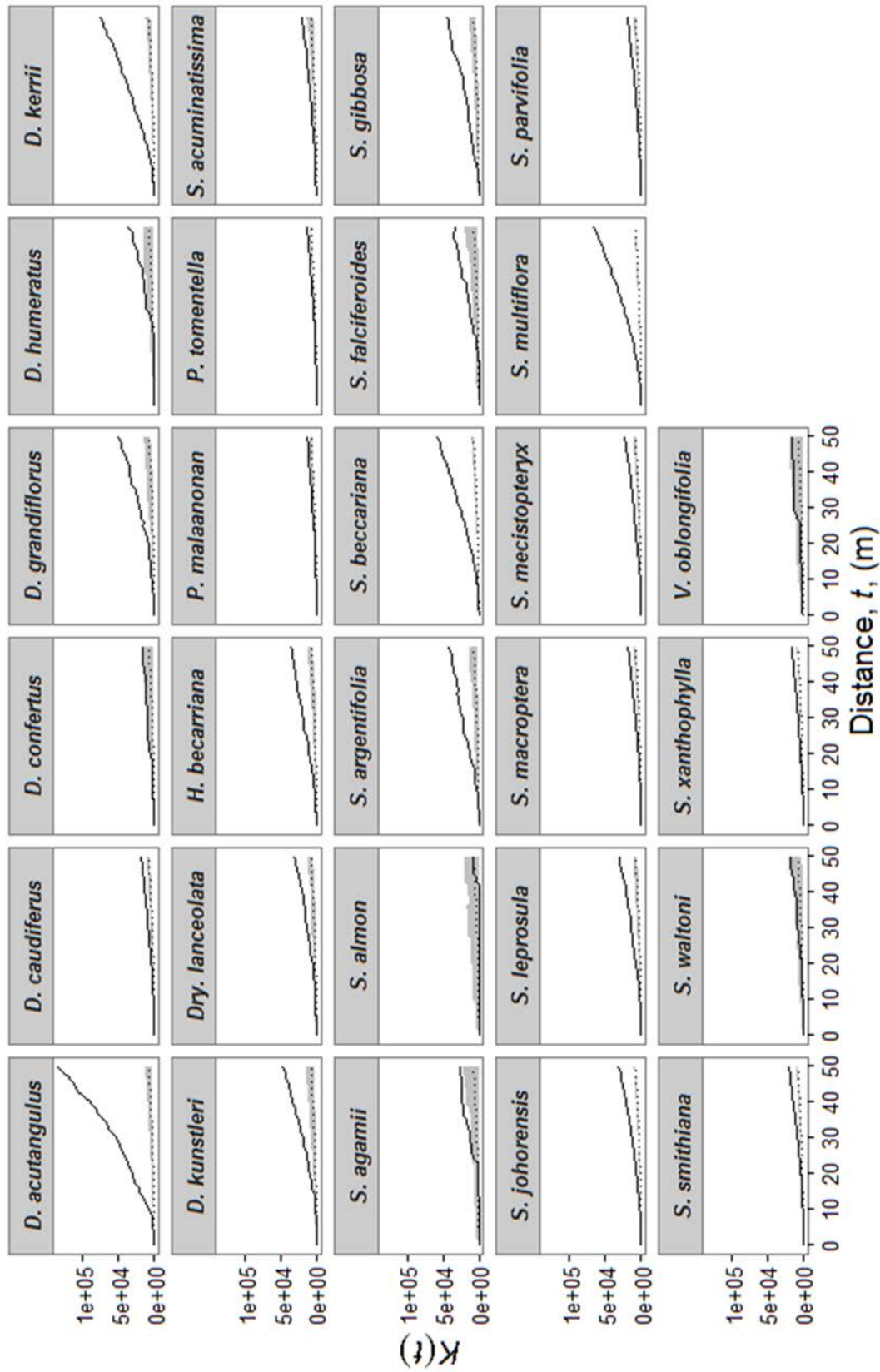
Figure 2. Panel plot showing the homogeneous K-functions (solid black line) for each of the 28 species of Dipterocarpaceae with abundance ≥25 in the 160 ha plot in the Sepilok Forest Reserve. The hypothetical K function generated by a poisson process (CSR) is given by the dotted line and its associated 95% confidence bands by the grey shading.

Table 2. Results of the bootstrap tests between observed homogeneous (K_{hom}) and inhomogeneous (K_{inhom}) K-functions and complete spatial randomness (CSR). The hypotheses are presented in the column titles with corresponding *P* values presented.

Species	$K_{hom} > CSR$	$K_{inhom} > CSR$	$K_{inhom} < K_{hom}$
Dipterocarpus acutangulus	0.01	0.01	0.01
Dipterocarpus caudiferus	0.01	0.01	0.99
Dipterocarpus confertus	0.01	0.05	0.02
Dipterocarpus grandiflorus	0.01	0.09	0.01
Dipterocarpus humeratus	0.01	0.09	0.04
Dipterocarpus kerri	0.01	0.01	0.01
Dipterocarpus kunstleri	0.01	0.01	0.06
Dryobalanops lanceolata	0.01	0.01	0.01
Hopea beccariana	0.01	0.01	0.99
Parashorea malanoonan	0.01	0.01	0.01
Parashorea tomentella	0.01	0.01	0.99
Shorea acuminatissima	0.01	0.03	0.01
Shorea agami	0.02	0.84	0.01
Shorea almon	0.65	0.55	0.59
Shorea argentifolia	0.01	0.01	0.02
Shorea beccariana	0.01	0.01	0.01
Shorea falciferoides	0.01	0.01	0.01
Shorea gibbosa	0.01	0.01	0.01
Shorea johorensis	0.01	0.01	0.88
Shorea leprosula	0.01	0.01	0.01
Shorea macroptera	0.01	0.01	0.18
Shorea mecistopteryx	0.01	0.01	0.01
Shorea multiflora	0.01	0.01	NA
Shorea parvifolia	0.01	0.01	0.01
Shorea smithiana	0.01	0.01	0.02
Shorea waltoni	0.02	0.03	0.44
Shorea xanthophylla	0.01	0.01	0.21
Vatica oblongifolia	0.01	0.60	0.03
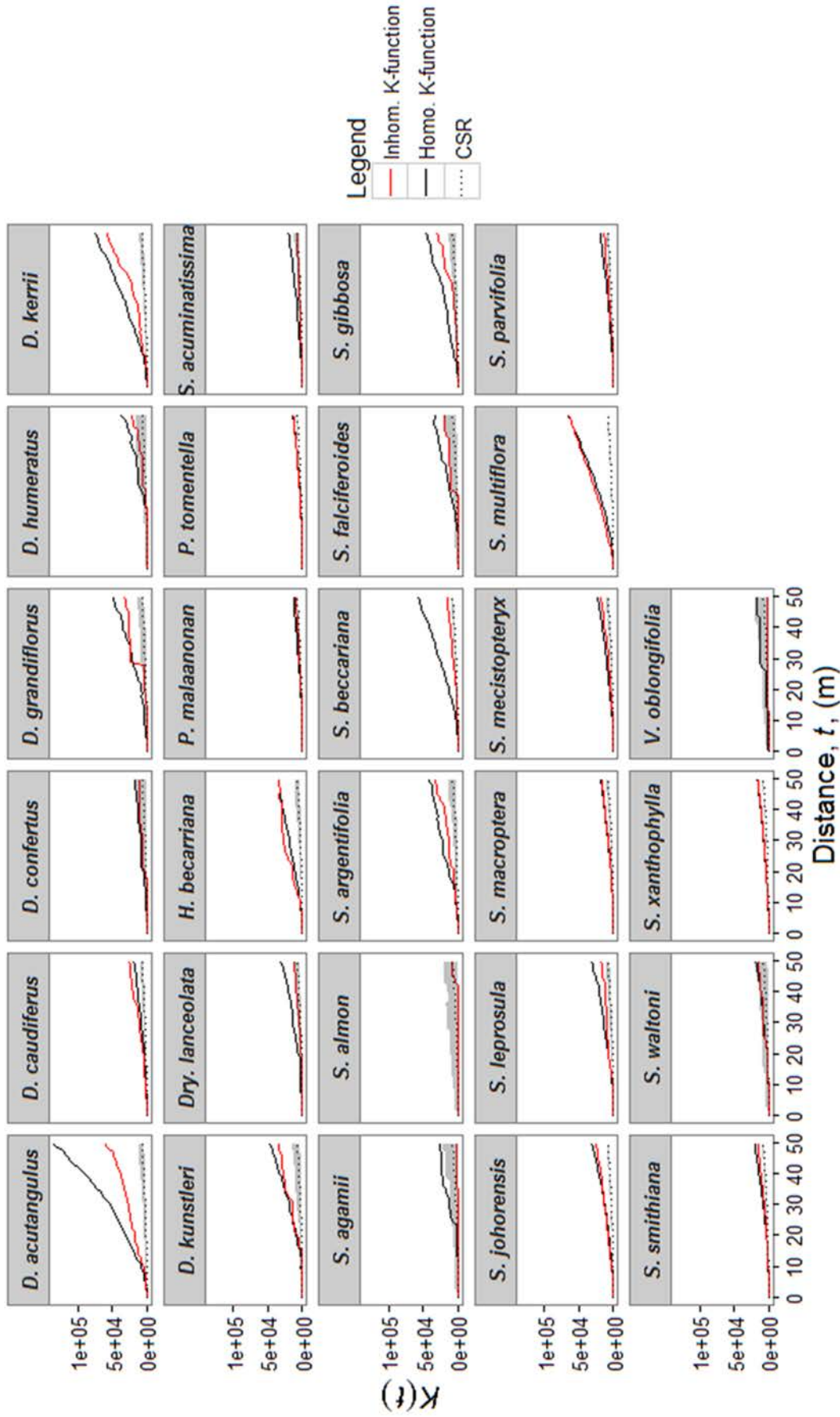
Figure 3. Panel plot showing the inhomogeneous K-functions (solid red line) and homogeneous K-functions (solid black line) for each of the 28 species of Dipterocarpaceae with abundance ≥25 in the 160 ha plot in the Sepilok Forest Reserve. The hypothetical K function generated by a poisson process (CSR) is given by the dotted line and its associated 95% confidence bands by the grey shading.
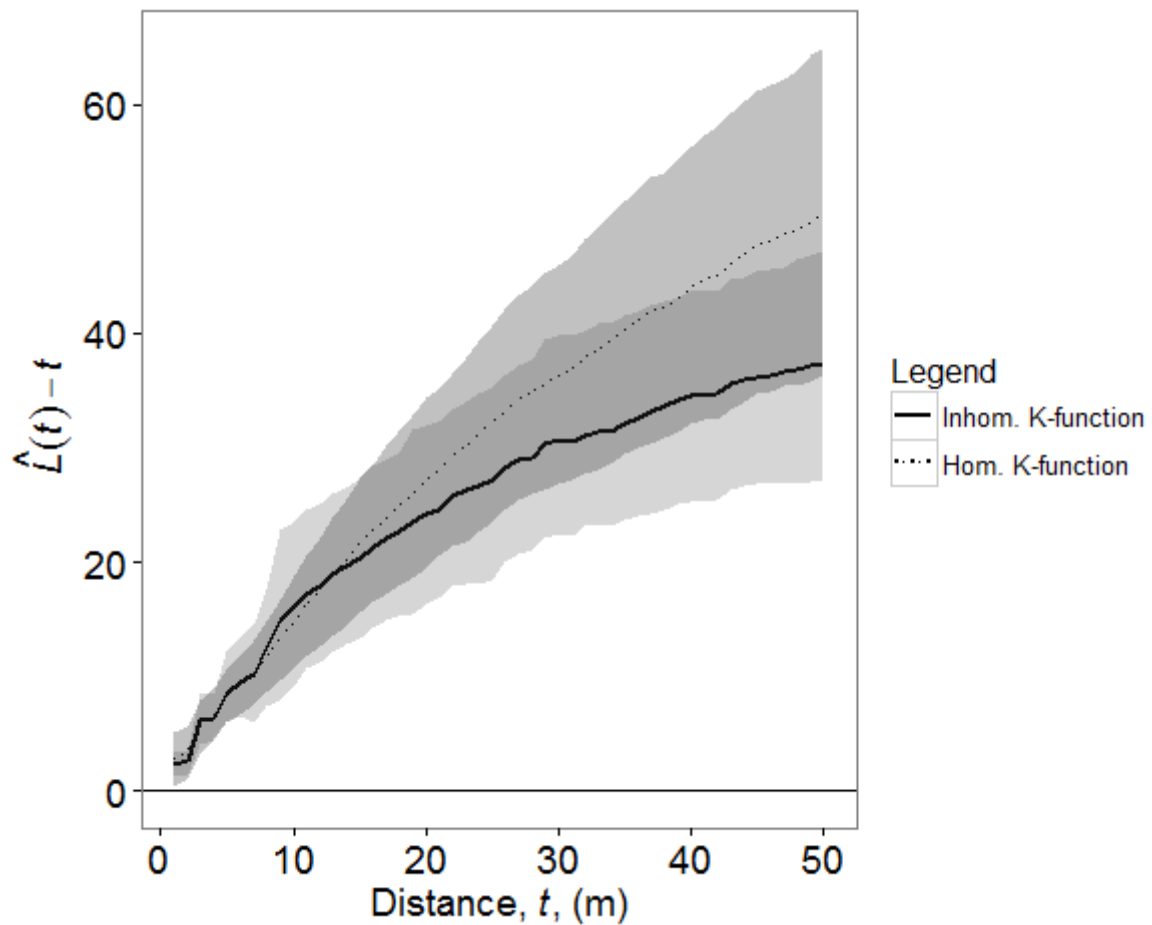
Figure 4. Mean homogeneous K-function (dotted black line) and inhomogeneous K-function (solid black line), as predicted from the RPP linear models, plotted following transformation to L-functions. Associated 95% confidence bands for both lines are given in grey shading. The horizontal black line at y = 0 is the theoretical number of trees predicted at distance t from a poisson process.
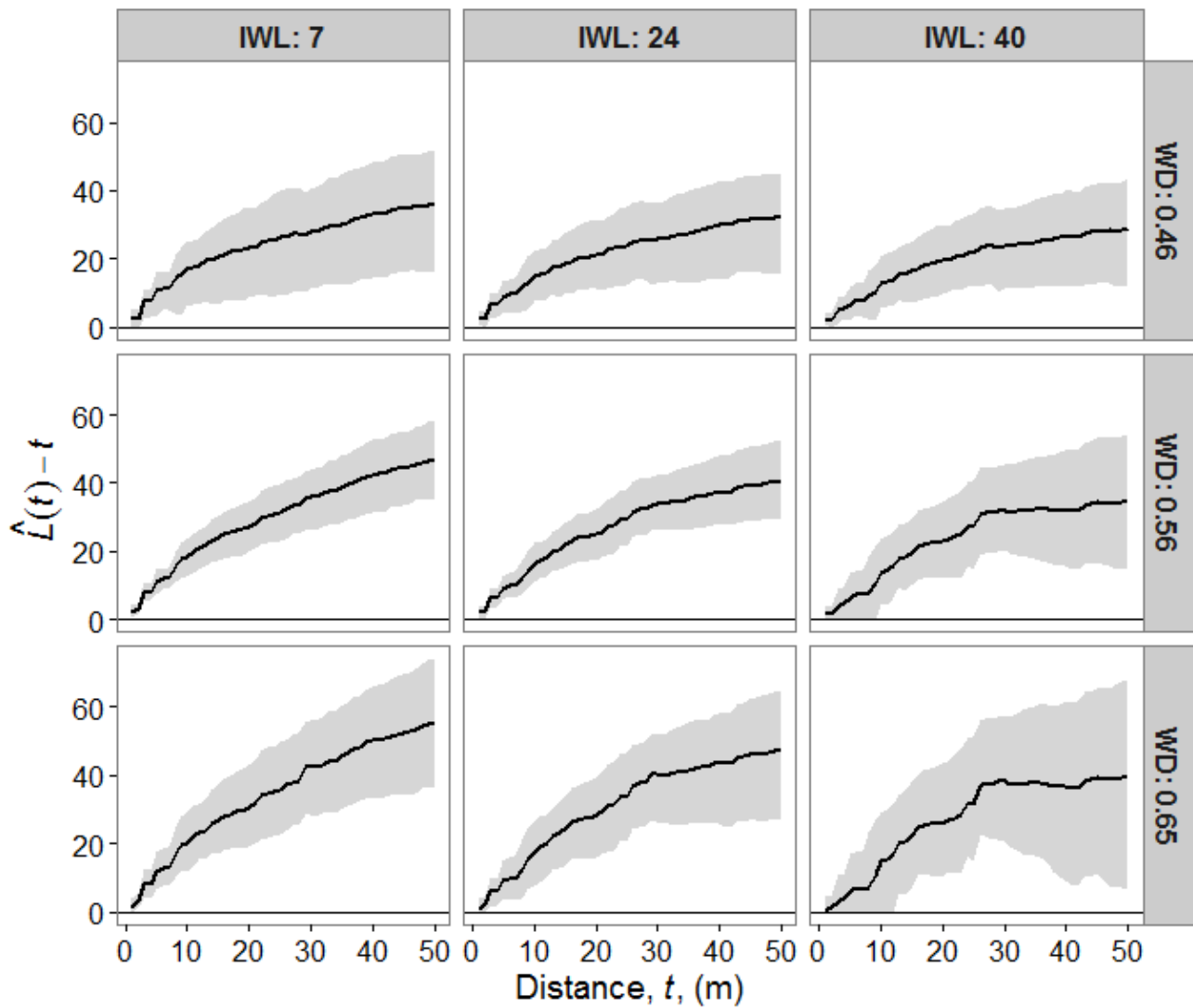
Figure 5. Panel plot showing predicted L-function (plus 95% confidence bands) from the RPP LM using inhomogeneous K-functions. Columns from left to right show an increase in dispersal potential (given by the 0.25, 0.5 and 0.75 quantiles of IWL), and wood density increases from top to bottom by row (given by the 0.25, 0.5 and 0.75 quantiles of wood density).

DISCUSSION

Our results show that adult individuals in over 90% of dipterocarp species present in Sepilok are more spatially aggregated than predicted under complete spatial randomness. The degree of spatial aggregation was reduced in 79% of these species once topographic covariates were incorporated in the analysis, highlighting that the majority of dipterocarps possess specific habitat associations. We found no evidence for increasing spatial aggregation with decreasing seed dispersal potential within the Dipterocarpaceae. These results suggest that variation in spatial aggregation patterns observed among seed dispersal syndromes (Condit et al. 2000, Seidler and Plotkin 2006) does not appear to extend to variation within the dispersal syndrome (gyration) in this study. Wood density, often considered a proxy for regeneration strategy, also had no significant influence on spatial aggregation patterns. Our results therefore provide no evidence that species traits are correlated with degree of spatial aggregation of adult trees. The persistence of spatial aggregation in cohorts of mature canopy sized trees, independent of habitat associations, implies that negative density dependent processes are not strong enough to overcome the pronounced spatial aggregation exhibited in the seedling cohorts produced by dispersal limitation in this family.

The majority of tropical tree species are spatially aggregated, and this study in addition to the work of others (Condit et al. 2000) suggests the Dipterocarpaceae are particularly aggregated. Such a large proportion of species exhibiting non-random spatial aggregation patterns suggests strong intrinsic or extrinsic processes drive the aggregation of conspecific individuals. In edaphically and topographically heterogeneous environments, species aggregate in particular habitats due to niche partitioning and environmental filtering (Valencia et al. 2004, John et al. 2007, Kraft et al. 2015). Such habitat associations explained much of the initial non-random distributions of dipterocarp species in Sepilok — controlling for habitat using intensity surfaces predicted using PPMs significantly reduced the inhomogeneous K-functions, the degree of spatial aggregation, compared to the homogeneous K-functions in 19 species (67%). In six of these species there was no significant difference between the inhomogeneous K-functions and CSR indicating that all spatial aggregation in these species was driven by habitat associations alone.

The percentage of species exhibiting habitat association in Sepilok, 67%, is similar to results from other Bornean forests. In a lowland dipterocarp forest in Kalimantan, 81% of dipterocarp species were observed to exhibit positive or negative associations with soil substrate (Paoli et al. 2006). In Lambir Hills National Park, 51–62% of dipterocarps exhibited specific habitat associations to topographic range (Itoh et al. 2010). A recent study by (Margrove et al. 2015) analysed habitat

associations for the 15 most abundant dipterocarp species in a subsection (68 ha) of the Sepilok 160 using a torus shift translation (Harms et al. 2001, Comita et al. 2007), allowing us to compare the consistency of species habitat associations assigned by both approaches. Margrove et al. (2015) observed all but two of the 15 species to express positive or negative associations to the alluvial, mudstone or sandstone habitats. Two species were associated to sandstone (*S. beccariana* and *S. multiflora*), six species were associated to mudstone hills (*D. kerrii*, *P. malaanonan*, *S. macroptera*, *S. mecistopteryx*, *S. parvifolia* and *S. xanthophylla*), and three to the alluvial plains (*P. tomentella*, *S. johorensis* and *S. leprosula*). These habitat associations are highly consistent with the surface intensities predicted for these species from the PPM models (Fig. 1; SI2), providing confidence that our point process models using elevation as an environmental covariate accurately account for habitat associations. Whilst the PPM models do not formally test for significant associations to habitats, elevation is highly correlated to habitat in this system.

Accounting for habitat significantly reduced the degree of spatial aggregation. Yet aggregation remained significantly higher than that expected by complete spatial randomness and the null expectation controlling indicating that intrinsic factors, including species traits and life-history strategies, shape patterns of spatial aggregation in addition to habitat associations. We hypothesized that dipterocarps with poor seed dispersal potential and high wood density would be more spatially aggregated than those with high seed dispersal potential and low wood density. There was, however, no significant effect of seed dispersal potential (IWL), wood density or their interaction on species inhomogeneous L-functions (Fig. 5). Significant increases in spatial aggregation with decreased seed dispersal was observed among dispersal syndromes by Seidler and Plotkin (2006), with a similar trend observed by Condit et al. (2000). Our method does not appear to distinguish similar trends of increasing aggregation with decreasing dispersal potential (Smith et al. 2015, Smith et al. 2016) within mature trees from a single dispersal syndrome, in this case, gyration (Ashton 2004).

A lack of an apparent relationship between dispersal potential and adult aggregation might be attributed to post-dispersal density-dependent processes such as intra-specific competition and density-dependent mortality. The spatial position of mature trees is determined not only by the locations of seed deposition but also their ability to survive. Whilst we controlled for habitat associations (though not in the *sensu stricto* terms of Kraft et al. 2015), on the assumption that these were driven by a post-dispersal habitat filtering process driven by abiotic factors correlated to elevation, biotic post-dispersal processes, including density-dependent effects on seed and seedling mortality, were not incorporated into the analysis.

The Dipterocarpaceae produce fruit episodically but synchronously during general flowering events hypothesized to satiate mobile mammalian seed predators (Ashton 1988, Curran 1999, Sakai 2002, Brearley et al. 2007, Sun et al. 2007). These mast fruiting events are a community wide phenomenon and thus predator satiation occurs at a community level (Curran and Leighton 2000, Curran and Webb 2000, Maycock et al. 2005, Sun et al. 2007). Seed survival is therefore positively density-dependent with seed recruiting in highly aggregated small clumps, in close proximity to mother trees (Itoh et al. 1997, Maycock et al. 2005). Despite some evidence for negative density-dependence among dipterocarp seedlings (Blundell and Peart 1998, Webb and Peart 1999, Blundell and Peart 2004, Stoll and Newbery 2005, Webb et al. 2006, Bagchi et al. 2010) this does not seem to be sufficiently strong to overcome the extreme clumping of seedlings around the mother tree (Itoh et al. 1997, Plotkin et al. 2002, Suzuki et al. 2009). Advanced regeneration is therefore likely to remain highly aggregated, resulting in increased adult recruitment probability of the particular species in the event of gap formation. As conspecific adults recruit into the canopy adult distributions become increasingly aggregated, leading to positive feedbacks as more conspecific trees in the same neighbourhood recruit ever more seedlings in the immediate locality due to positive density-dependent seed survival during fruiting events (Curran and Leighton 2000, Curran and Webb 2000, Maycock et al. 2005). An interesting question, therefore, is whether conspecific aggregations of dipterocarps are able to locally exclude other dipterocarp species. If not, then are dipterocarps co-evolved to minimize competition through niche segregation at fine scale to allow for overlapping aggregations among species. If species do have mutually exclusive aggregations, then a further question is how competition and recruitment among dipterocarp species unfolds at aggregation boundaries.

Our result might also indicate that the Dipterocarpaceae do not adhere to a strict trade-off between competition and colonization, one mechanism of species-coexistence with experimental support. The competition-colonization trade-off posits that light-demanding species need to locate their seeds into canopy gap sites, as their seedlings are short-lived under shade. As gaps environments are spatially and temporally ephemeral and patchy, such trees benefit from a wide seed dispersal which maximizes the chance that at least some seeds are dispersed into favourable environments. Shade tolerant species gain no such benefit, and indeed can suffer from competition with faster growing light demanding species in high light conditions (Whitmore and Brown 1996). We expected this competition-colonization trade-off to be expressed across dipterocarp species that show a wide range of wood density values (from 0.35 to more than 1 g.cm^{-3}) which acts as a proxy for shade tolerance (Wright et al. 2010). That we did not find such a relationship might be because dispersal for all dipterocarps is local despite species differences (Suzuki and Ashton 1996, Osada et al. 2001, Smith

et al. 2015, Smith et al. 2016). Most fruit regularly fail to disperse much beyond the mother tree's crown and is constrained to 20–40 m in most species (Tamari and Jacalne 1984, Itoh et al. 1997, Osada et al. 2001, Smith et al. 2015). Moreover, all dipterocarps also seem to show some degree of shade tolerance (Philipson et al. 2012), even if this is highly variable among species appears to show no clear trade-off against growth or mortality rate (Philipson et al. 2014).

CONCLUSION

The majority of dipterocarps in Sepilok exhibit clear habitat associations, leading to the non-random and highly aggregated distribution of adult individuals at the landscape scape. Once habitat associations are controlled for, mature dipterocarps continue to show fine-scale spatial aggregation suggesting that intrinsic factors influence patterns of aggregation. However, this study found no evidence that low seed dispersal or high wood density generated more aggregated distributions of adult individuals at the fine-scale. This suggests that negative density dependent mechanisms acting at the seedling stage are not sufficiently strong to overcome the high spatial aggregation of seedlings driven by positive density dependent survival during mast fruiting events, underpinned by the consistently limited seed dispersal potential among species despite variation in fruit morphology.

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SUPPLEMENTARY INFORMATION

SI1

Non-parametric bootstrap test of difference between the observed inhomogeneous K-function and CSR

To test whether the observed inhomogeneous K-values differed significantly from CSR, for each species we simulated 99 poisson point processes with the same intensity as the observed point pattern for the species using the "rpoispp" function from 'spatstat' (Baddeley and Turner 2005) R package. For each of the 99 simulated point process patterns we calculated the homogeneous K-function for distances 0–50 m. From each of the 99 simulated random point processes we calculated the mean and the variance of the K-function for each distance between 0 and 50 m. Under the null hypothesis that there is no significant difference between the inhomogeneous K-function and CSR, the difference in the observed inhomogeneous K-function and the mean simulated CSR K-function should be 0 for each distance between 0 and 50 m. We generated the test statistic T proposed by (Henrys and Brown 2009), whereby the deviations between the observed inhomogeneous K-function and the mean CSR homogeneous K-function are summed for distances 0 to 50 m and divided by the standard deviation of the mean CSR homogeneous K-function, and compared this to the T statistic for each of the individual simulated random poisson point processes. Approximate p-values were then calculated as the proportion of T statistics from the random simulated homogeneous K-functions greater than the T of the observed inhomogeneous K-function.

Non-parametric bootstrap test of difference between the observed inhomogeneous K-function and observed homogeneous K-function

A very similar approach was taken as above. However, as there are no variance estimates for the two observed K-functions we randomly subsampled 80% of the individuals from the species' point pattern process 99 times. For each of these 99 subsamples we calculated both a new homogeneous K-function, and, using the original species PPM model, a new inhomogeneous K-function. The null hypothesis for this test is that there is no difference between the homogeneous and inhomogeneous K-

functions per species. Therefore the difference between each iteration of the subsampled inhomogeneous K-function and the mean subsampled homogeneous K-function should be equal to the difference between each iteration of the subsampled homogeneous K-function and the mean subsampled homogeneous K-function, over distances 0 to 50 m. We generated the test statistic T (Henrys and Brown 2009) for the subsampled inhomogeneous K-functions by calculating the deviations between each iteration of the 99 subsampled inhomogeneous K-functions and the mean subsampled homogeneous K-function over distances 0 to 50 m, and dividing by the standard deviation of the mean subsampled homogeneous K-function. The mean was then calculated for each distance and summed, to generate a mean T statistic for the 99 subsampled inhomogeneous K-functions. This then compared to the T statistic for each of the individual subsampled homogeneous K-functions, calculated as above. Approximate p-values were then calculated as the number of times the T of the subsampled inhomogeneous K-functions was greater than the T's of the 99 subsampled homogeneous K-functions.

SI2

Plots of the predicted surface intensities per species, generated using the point process models (PPMs) modeling the intensity of individuals as a function of topography, latitude and longitude (in UTM units). Intensity at a given X and Y coordinate is shown by the scale on the right hand side of the plots. Tree positions are plotted on the intensity surfaces in black circles.
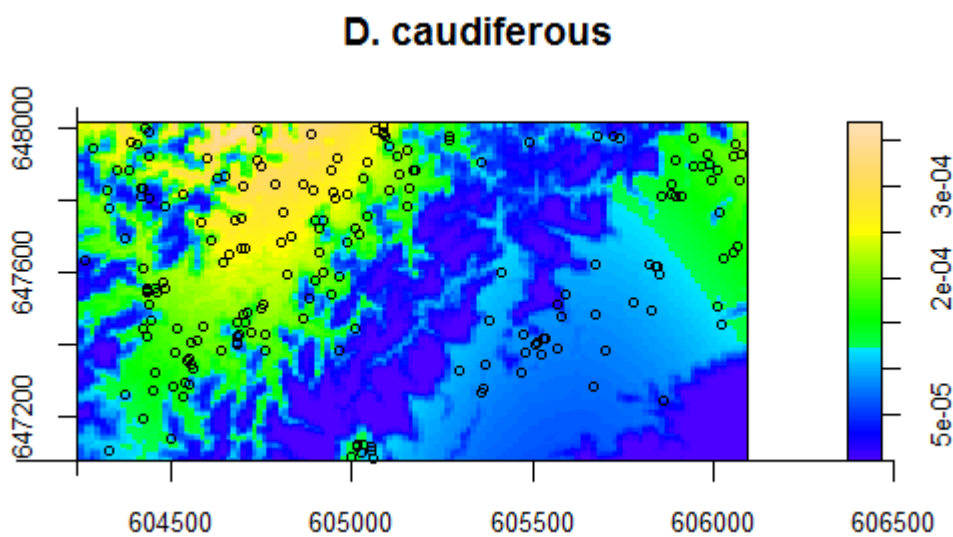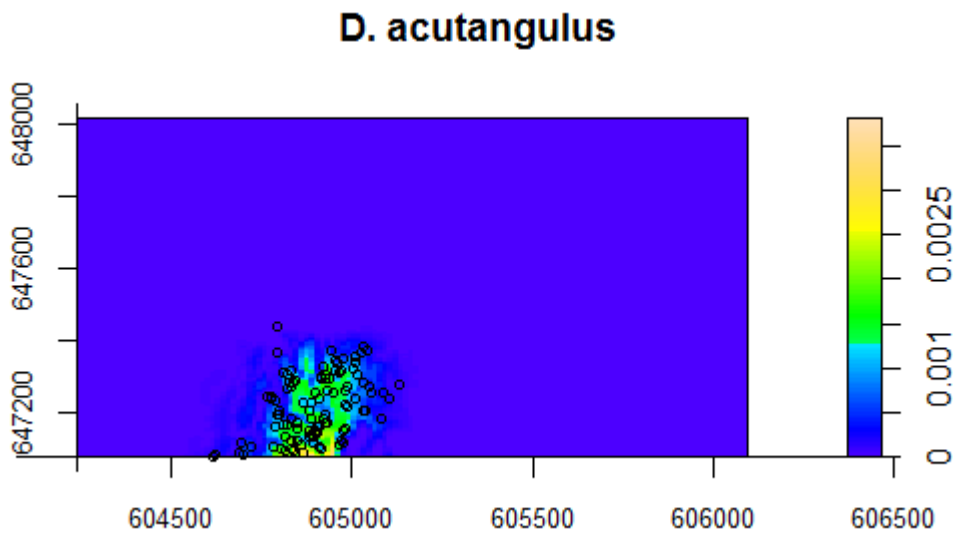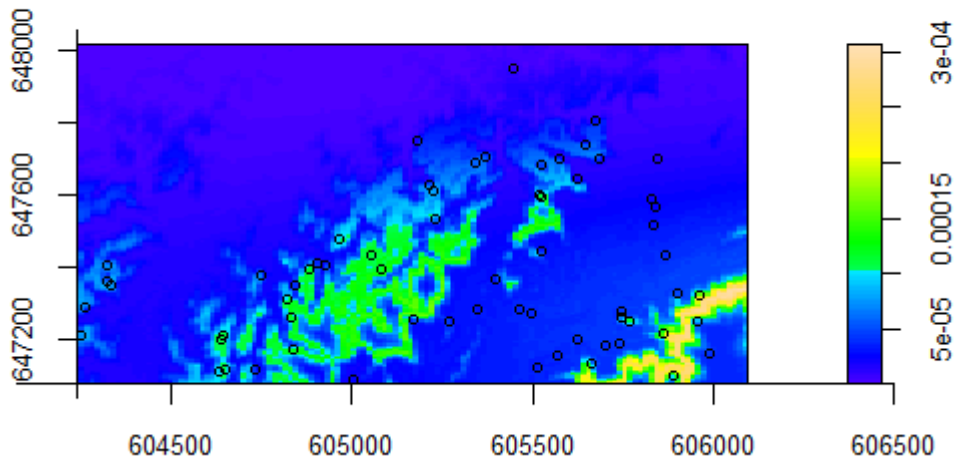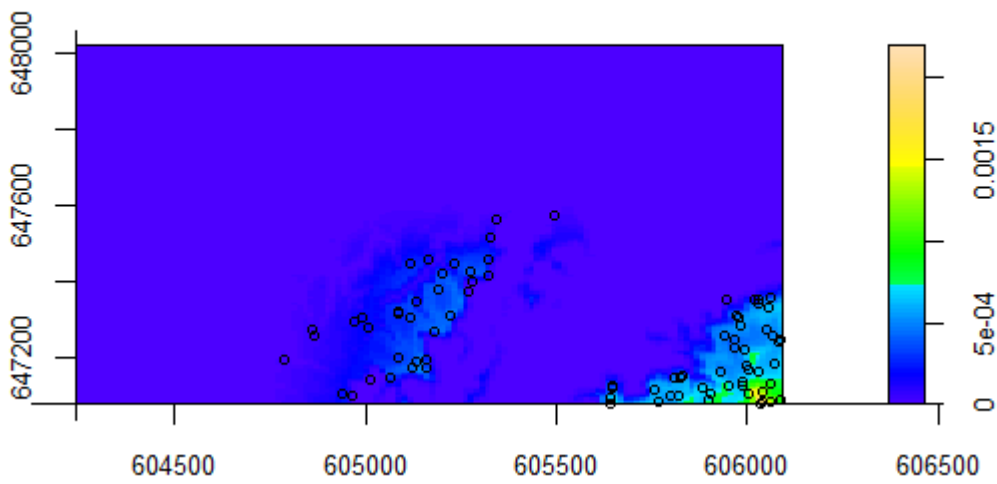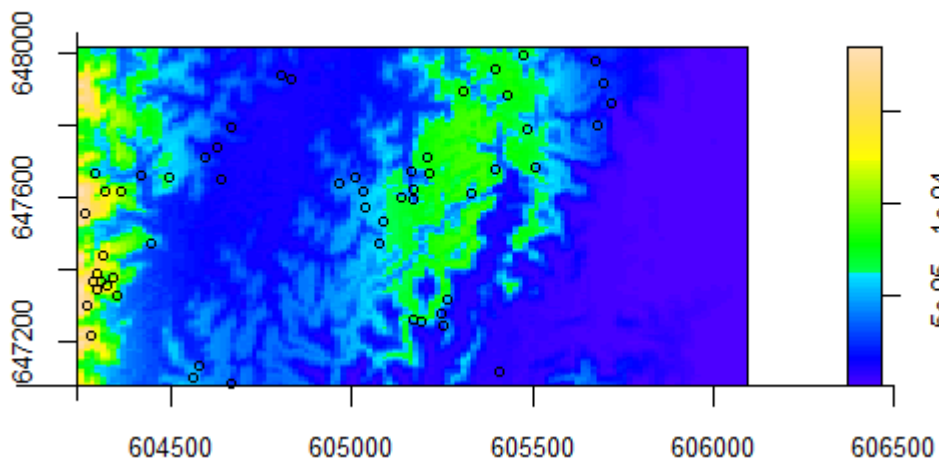
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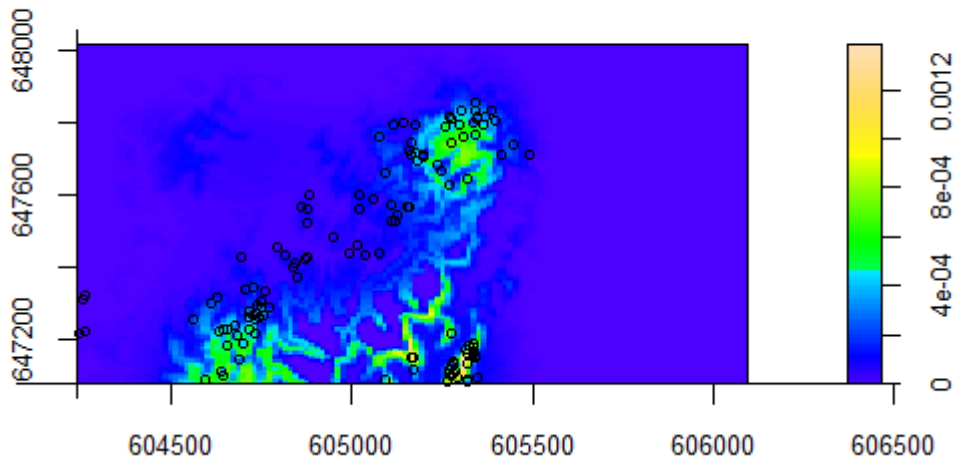
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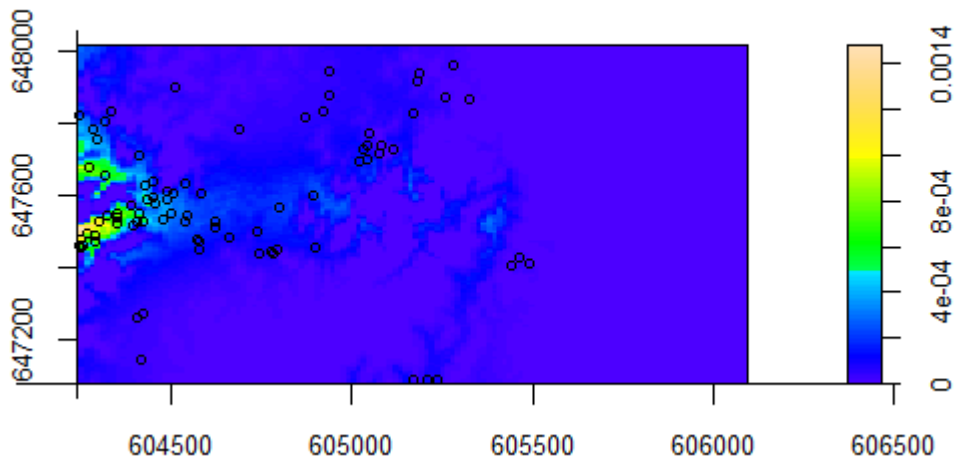
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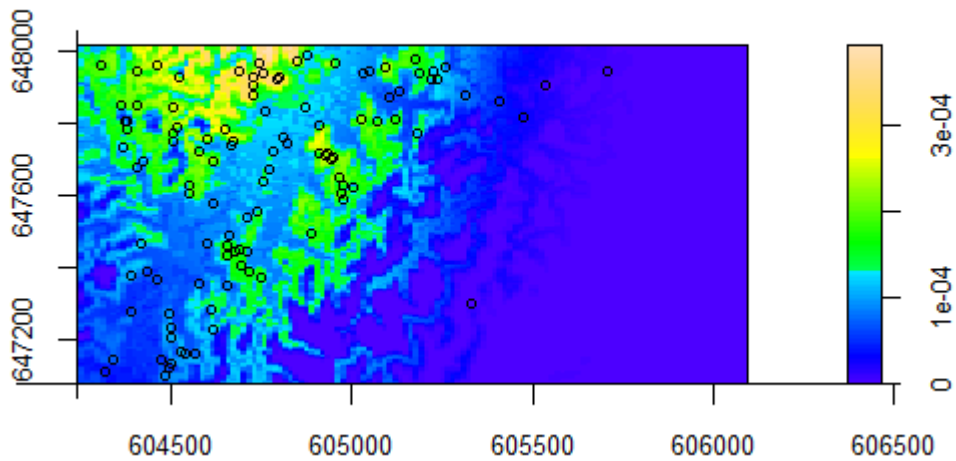
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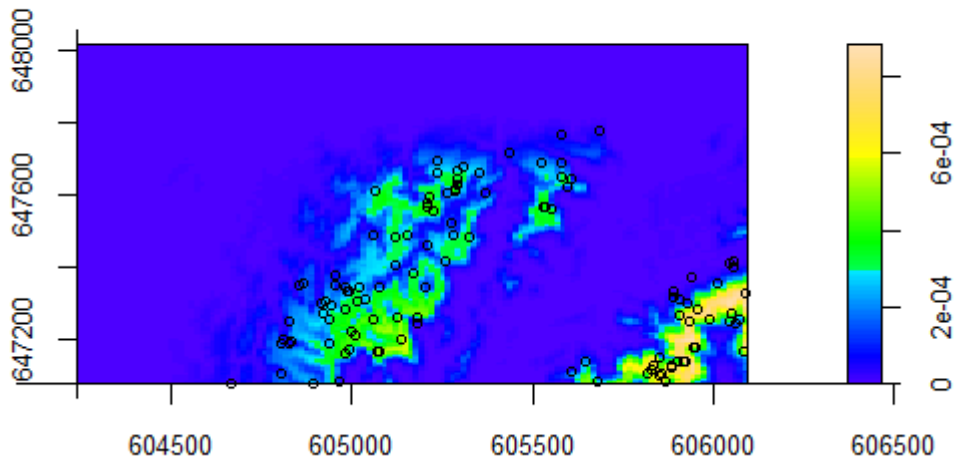
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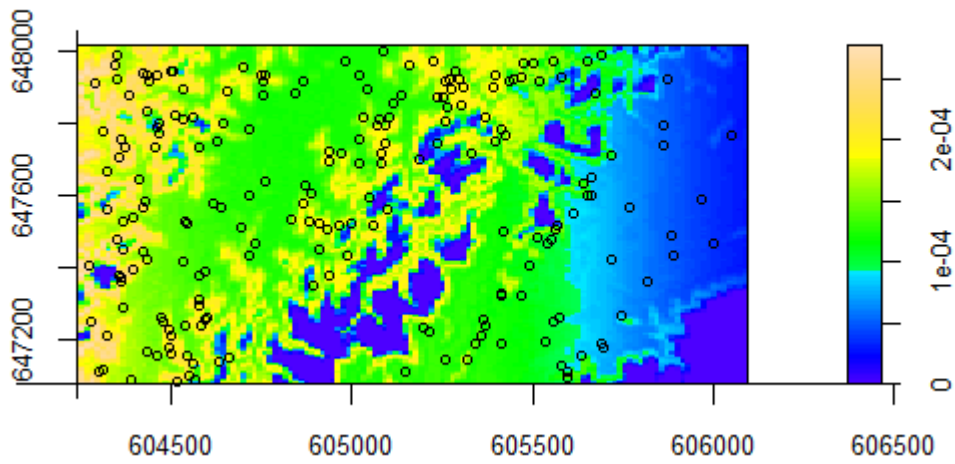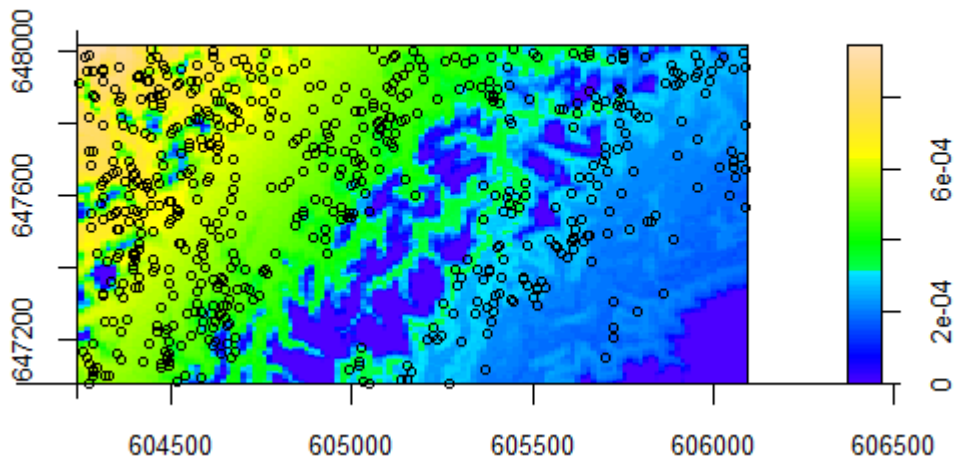
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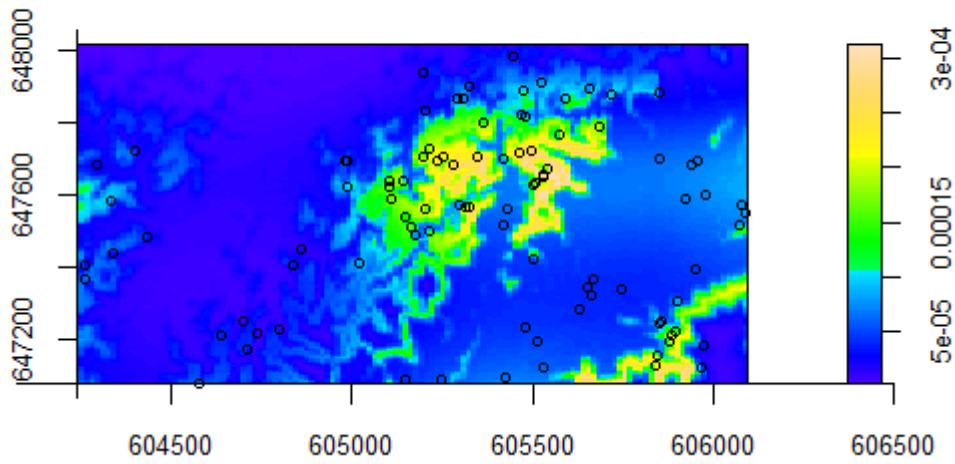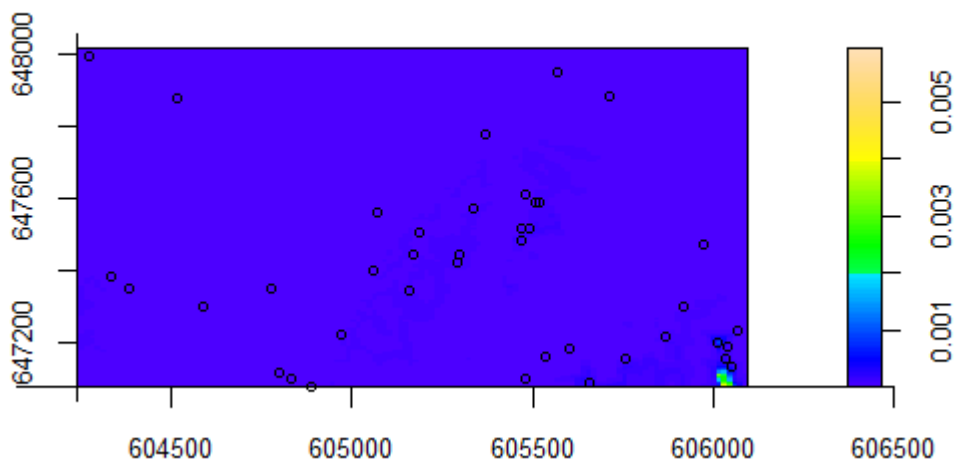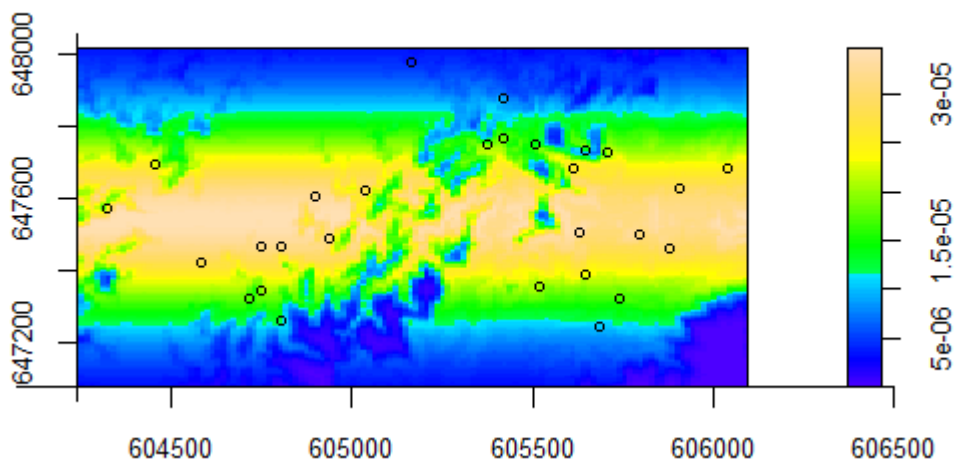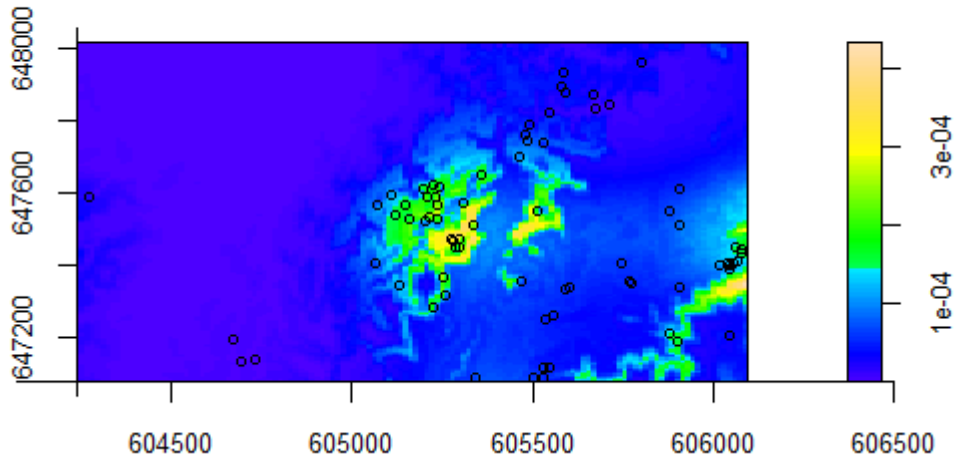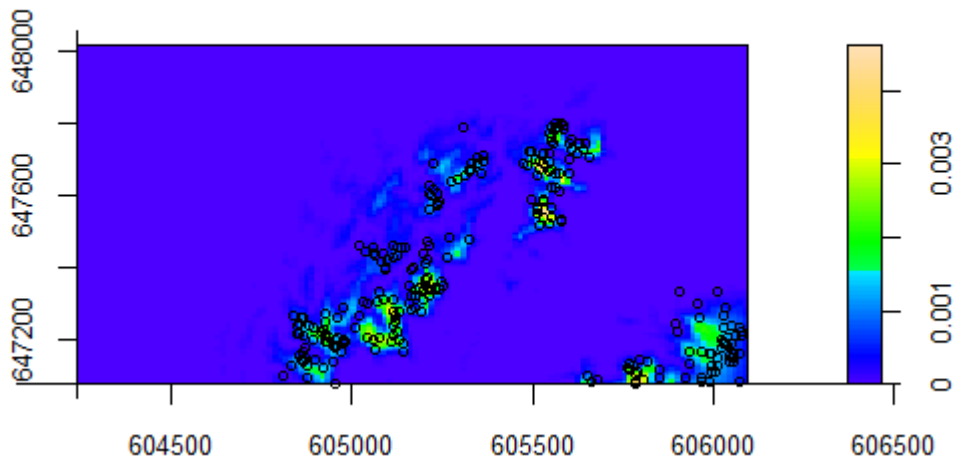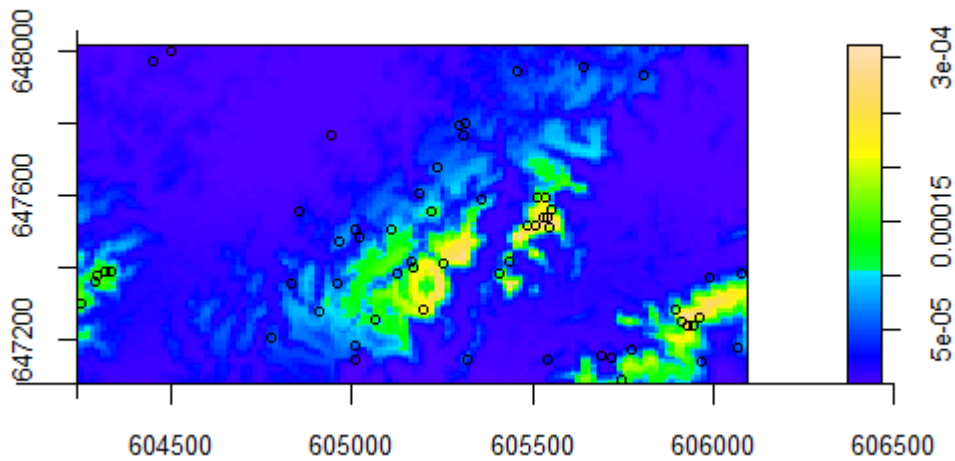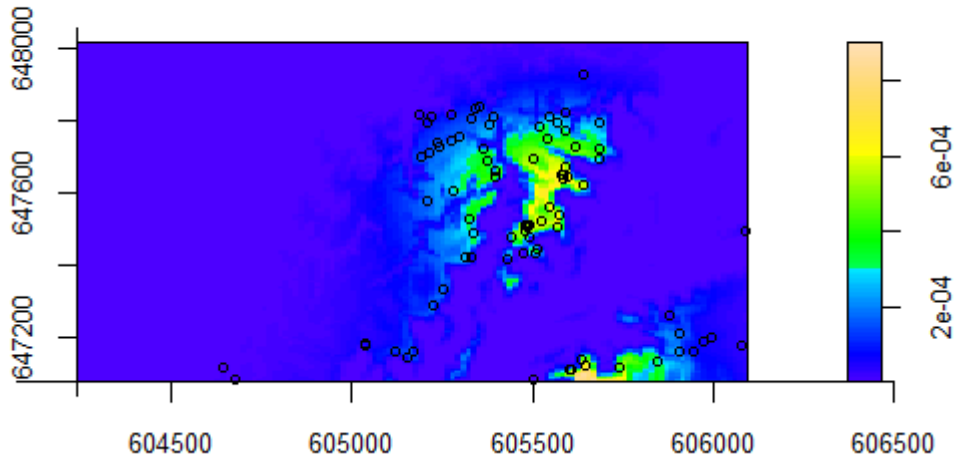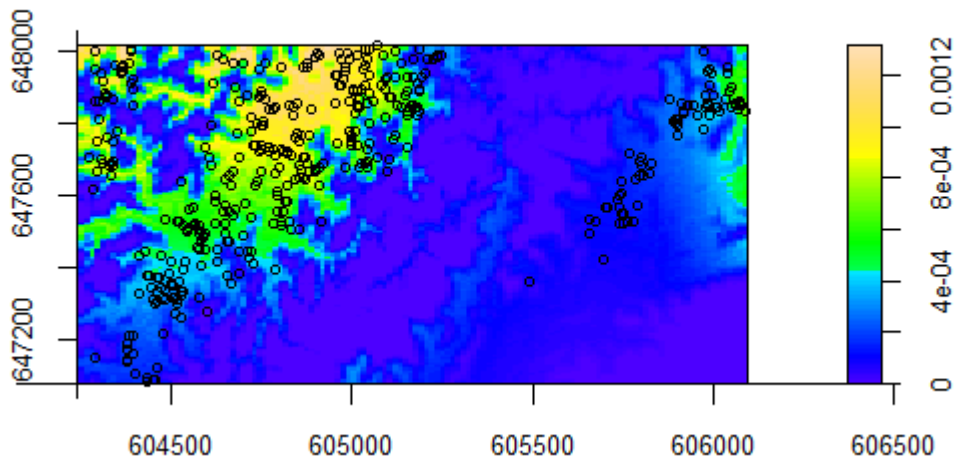
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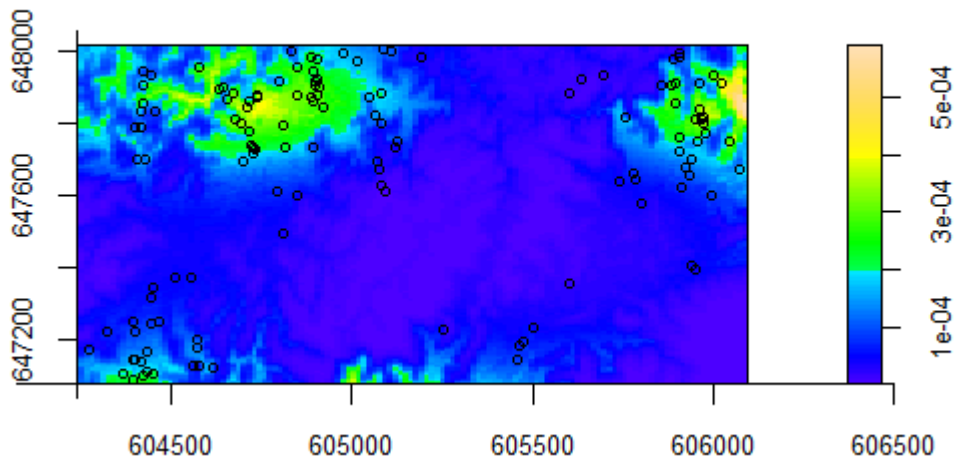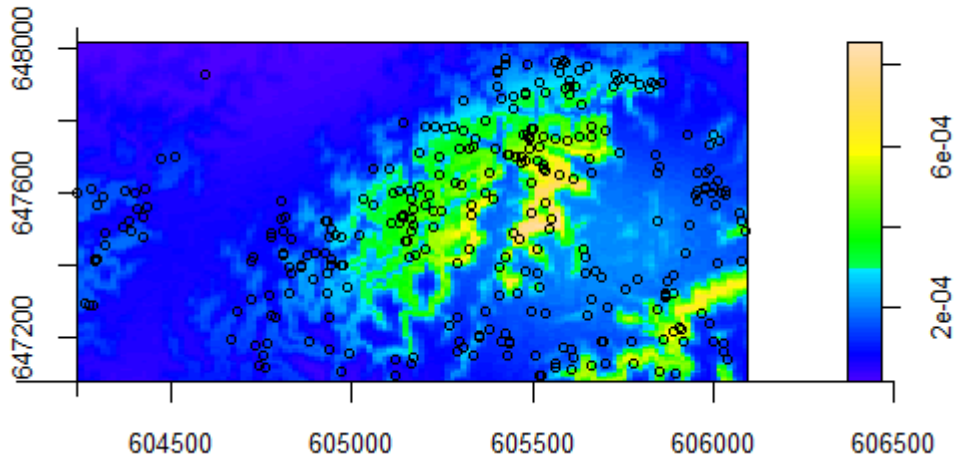
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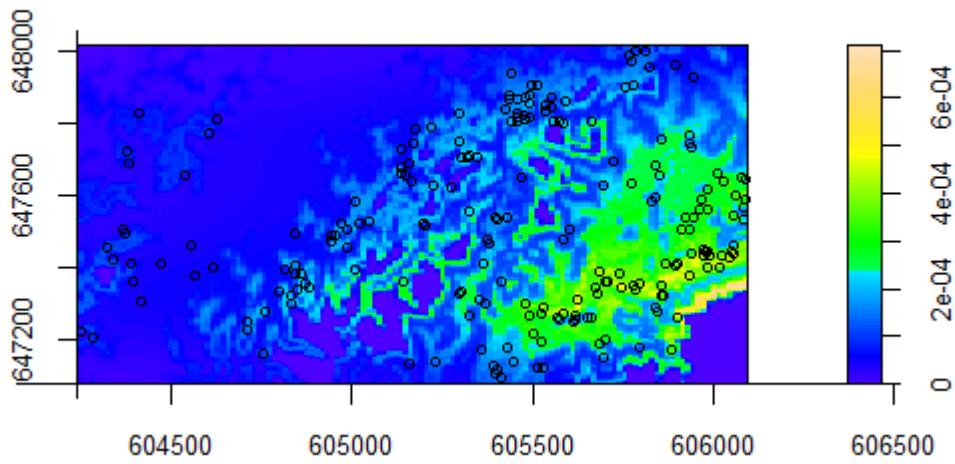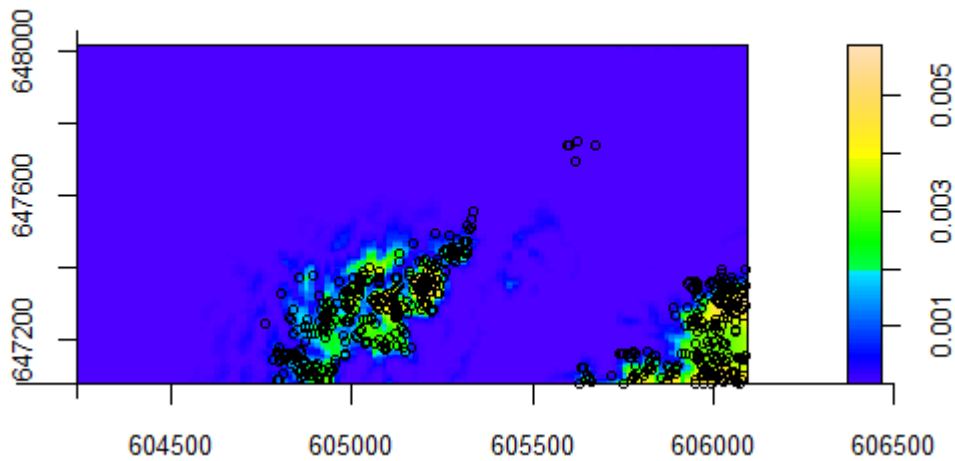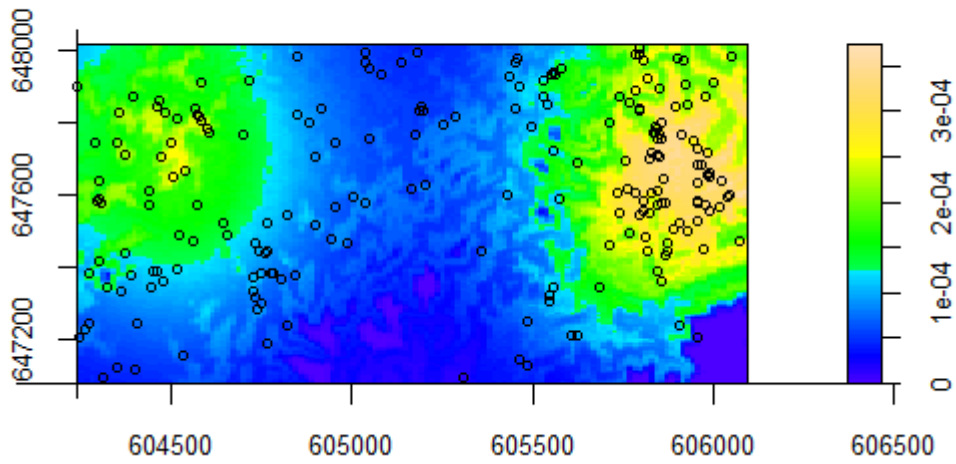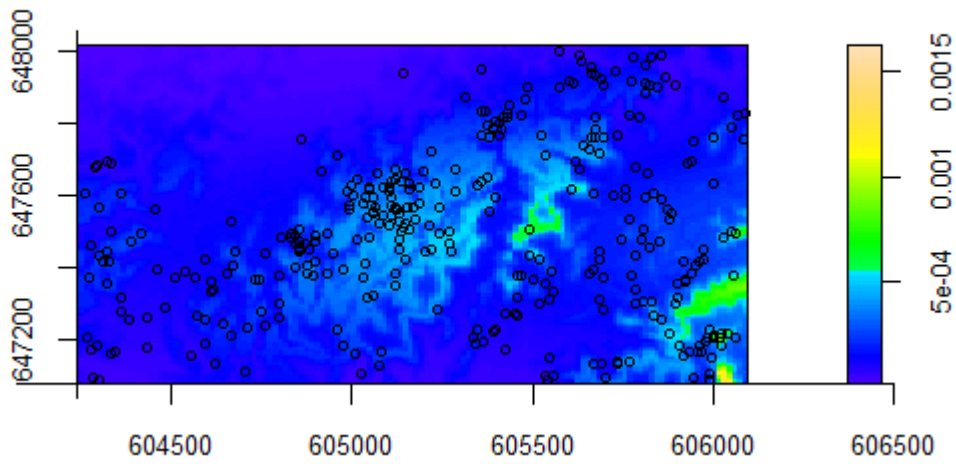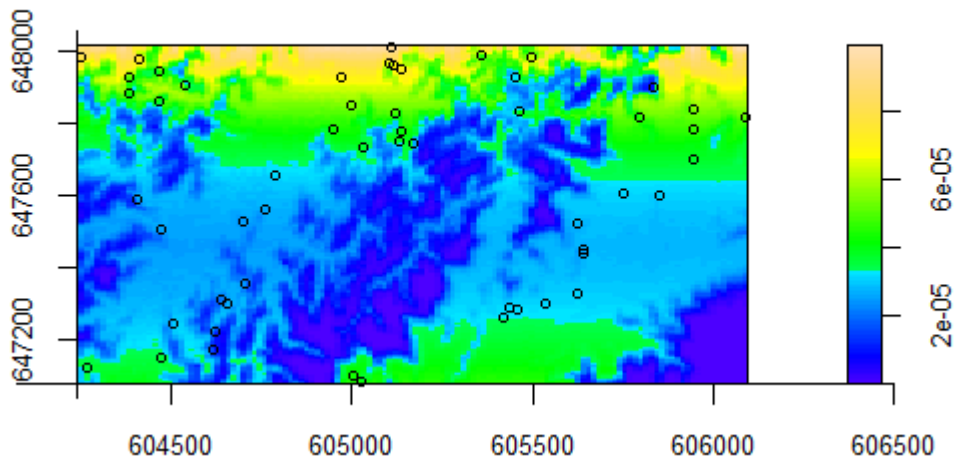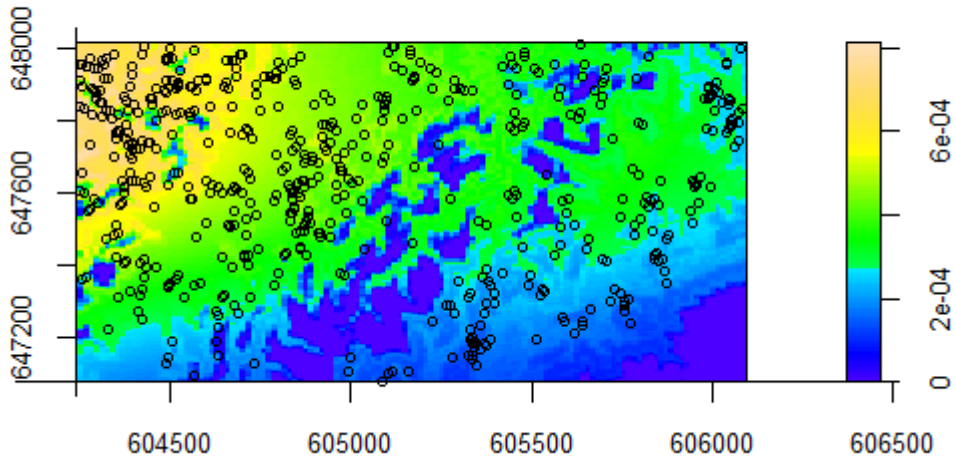
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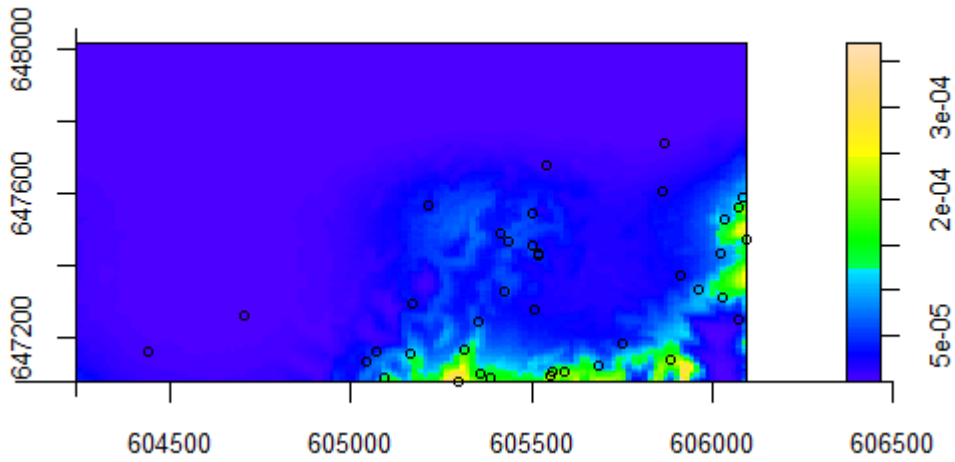
Are patterns of fine-scale genetic structure consistent between sites within Dipterocarp species?

with Jaboury Ghazoul, David Burslem, Eyen Khoo & Chris Kettle

ABSTRACT

Many tropical tree species show pronounced fine-scale genetic structure (FSGS), the non-random distribution of genotypes across the landscape. FSGS is generated where seed and pollen dispersal is limited. This can lead to mating between related individuals and is particularly intense when species are spatially clustered in the landscape due to habitat associations or dispersal limitation. The ranges of many tropical tree species can be expansive and local environmental conditions may vary considerably between sites, potentially impacting species' spatial aggregation patterns and gene flow. Documenting the scale and intensity of FSGS, and the processes that shape it, is critical to the sustainable management of forest genetic resources in timber tree species. Logging and forest fragmentation are likely to disrupt gene flow and may lead to an erosion of genetic diversity especially in species with significant FSGS. Using nuclear microsatellite markers, we assessed patterns of FSGS among different forest sites but within species in three species of Dipterocarpaceae (*Parashorea tomentella*, *Shorea leprosula* and *Shorea parvifolia)*. We compared each species using identical methods at two different lowland tropical forest sites in Malaysia varying widely in their topographic heterogeneity (Danum Valley, Lambir, Pasoh and Sepilok). Results on the consistency of FSGS within species between sites were mixed, with little variation in the intensity and scale of FSGS in *S. leprosula* and *S. parvifolia* between sites, despite substantial variation in elevation between sites. Conversely, the intensity of FSGS for *P. tomentella* was much greater in the Sepilok than Danum, and a significant difference in the overall pattern of FSGS was detected between sites using a non-parametric heterogeneity test. Confirming consistency in species' FSGS amongst sites is an important step in managing timber tree genetic diversity as it provides confidence that species specific

management recommendations based on species reproductive traits can be applied across a species'
range. Our results suggest that management of genetic diversity in the Dipterocarpaceae might need to
be considered on not only a species–by–species trait basis, but on a species–by–site basis given the
inconsistency of FSGS observed in *P. tomentella*.

INTRODUCTION

Many forest tree species possess high levels of intraspecific genetic diversity maintained by large effective population sizes, long life spans with over-lapping generations, and typically high gene flow (Hamrick 2004, Dick et al. 2008). Genetic diversity is not, however, evenly distributed within a species. At the landscape scale genetic structure develops between subpopulations. Within subpopulations occupying contiguous local habitats, fine-scale spatial genetic structure (FSGS) may develop. FSGS is the non-random distribution of alleles through a population, and is typically observed as a negative relationship between genetic similarity and geographic distance between individuals (Hardy et al. 2006).

An understanding of the processes that generate and maintain FSGS in tropical trees has direct relevance for forest managers and resilience of forest landscapes as genetic diversity affects species' reproductive ecology, fitness and adaptive potential (Dick et al. 2008, Kettle et al. 2011b). One family of tropical trees where knowledge of the processes generating FSGS is of applied value is the Dipterocarpaceae (Kettle 2009, Kettle et al. 2011a). The dipterocarps are predominantly canopy and emergent tree species, found in high diversity in the lowland tropical forests of SE Asia (Ashton 1988). With typically tall, cylindrical, branch-free boles, dipterocarp timber is a valuable forest resource, and has been rapidly exploited over the last century as a prelude to agricultural expansion (Sodhi et al. 2010, Miettinen et al. 2011, Reynolds et al. 2011, Gaveau et al. 2014).

FSGS has been investigated in the Dipterocarpaceae by a number of authors (Takeuchi et al. 2004, Kettle et al. 2011b, Harata et al. 2012, Tito de Morais et al. 2015). Most recently, Tito de Morais et al. (2015) collated data on FSGS on 19 dipterocarp species from six genera to analyze which reproductive and ecological traits underpinned the spatial scale and intensity (strength of the correlation between geographic and genetic distance) of FSGS. Species with larger flowers had limited or weaker FSGS compared to smaller-flowered species, consistent with the hypothesis of long distance pollen dispersal by larger insect pollinators (Kettle et al. 2011b). Additionally, FSGS was positively correlated with wood density, a relationship attributed to the accumulation of half-sib progeny under mother trees in species with high wood density, a trait associated with shade tolerance and, by association, slow growth, low mortality, and physiological mechanisms to tolerate abiotic stress (Chave et al. 2009). Whilst seed dispersal (determined via the proxy trait 'inverse wing-loading' (IWL), Smith et al. (2015)) had no significant effect on the intensity of FSGS, the scale of FSGS increased as seed dispersal potential decreased (Tito de Morais et al 2015). Their study corroborates the observation of Harata et al. (2012) that FSGS in adult dipterocarp populations is determined by the

interplay of multiple traits, but with seed dispersal driving FSGS at smaller scales (<100 m), and pollen dispersal and spatial structure driving FSGS at larger scales (>100 m).

While Tito de Morais et al. (2015) were able to assess general patterns of FSGS in relation to species traits based on their extensive multi-species, multi-site analysis, no datasets were available to compare FSGS of the same species at different sites. Cross-site analyses are relevant as local factors including, topography, soil substrate, and disturbance dynamics, could alter the scale and intensity of FSGS. Variation in these site specific factors, could potentially generate contrasting patterns of FSGS at different sites within the same species by influencing cluster size (potentially driven via soil associations or gap-phase regeneration) (Denslow 1987, John et al. 2007), population density and, reproductive traits (Hardy et al. 2006), such as pollen dispersal distances (Ghazoul et al. 1998, Ghazoul 2005). The species range of many common dipterocarps is extensive, with some species in the genus *Shorea*, for example *S. leprosula* and *S. parvifolia*, possessing distributions spanning much of the Sundaland floristic region including southernmost peninsula Thailand, peninsular Malaysia, Sumatra and Borneo (Ashton 1983, Newman et al. 1996). Hence there is potential for FSGS patterns to vary widely across ranges that encompass a multitude of soil types, local climatic conditions, and forest community compositions. Analysing FSGS at across sites that vary in environmental conditions within the same species allows us to investigate the effect that site conditions might have on patterns of FSGS and, the corollary of this, the extent to which FSGS can be reliably generalizable within species across sites. Such work is not only of theoretical interest but also has applied relevance as forest managers and conservationists increasingly recognize the importance of maintaining genetic diversity in forest tree populations and aim to integrate patterns of FSGS into management recommendations (Jalonen et al. 2014, Thomas et al. 2014, Tito de Morais et al. 2015).

Our aim was to assess whether patterns of FSGS are consistent within species between sites. We hypothesize that if species traits rather than site environmental conditions are the primary determinant of FSGS then patterns of FSGS will be identical between different sites for the same species. We used nuclear microsatellite markers to genotype four species of common dipterocarp (*Parashorea tomentella*, *Shorea leprosula*, *Shorea parvifolia*, *Shorea pauciflora*) in a 50 ha CTFS Forest Dynamics Plot (FDP) located in Danum Valley, Malaysian Borneo. Published microsatellite genotype and coordinate datasets for three of these species located in other large-scale forest inventory plots in Borneo (*P. tomentella*, Sepilok (Kettle et al. 2011b); *S. parvifolia*, Lambir (Harata et al. 2012)) and Peninsula Malaysia (*S. leprosula*, Pasoh (Ng et al. 2009b)) were analyzed using identical methods, allowing us to assess the consistency in scale and intensity of FSGS patterns within three pairs of species, and investigate systematically the role site plays on influencing FSGS patterns.

METHODS

Study species

The Dipterocarpaceae is a pan-tropical family of mainly canopy and emergent trees. Dipterocarps flower on an inter-annual periodicity of roughly 2–10 years, participating in forest-wide 'general flowering' events (Ashton 1988, Ashton et al. 1988, Sakai 2002, Brearley et al. 2007). Flowers are hermaphroditic but vary in size, pollinated by a range of insects from thrips, beetles, moths, and a variety of bees, including the giant Asian honey bee (*Apis dorsata*) (Ashton 1983, Momose et al. 1998, Sakai 2002, Kettle et al. 2011c). Dipterocarp fruit bear two to five elongated fruit sepals which act as wings to disperse the fruit via gyration, although fruits of some species are wingless (Suzuki and Ashton 1996). Dipterocarp fruit dispersal is primarily local, often failing to disperse beyond the crown of the mother tree (Suzuki and Ashton 1996, Itoh et al. 1997, Osada et al. 2001, Smith et al. 2015), although convective storms can distribute fruit much further (Webber 1934). There is no substantial secondary seed dispersal.

Over 30 dipterocarp species have been identified from the Danum 50 ha plot. All but six are found at densities of < 1 individual ha^{-1} in DBH size class ≥ 30 cm (J. R. Smith, *personal observation*), which is too low to analyse FSGS with accuracy at the scales available due to the limited number of pair-wise comparisons at lower distance classes. Of the six common species, *Parashorea tomentella* (Symington) Meijer, *Shorea leprosula* Miq. and *Shorea parvifolia* Dyer have previously been sampled for FSGS in other large-scale forest plots and were therefore included to allow comparisons of paired populations at two different sites for three species. *Shorea pauciflora* King (Ashton 1983) was also genotyped although no comparator data are available from other populations.

All four study species are emergent trees with the potential to reach over 60 m in height (Ashton 1983) (Table 1). *Shorea parvifolia*, *S. leprosula* and *S. pauciflora* are members of the *Shorea* red meranti timber group. *Shorea parvifolia* and *S. leprosula* (Section *Mutica*, sub. section *Mutica*) are considered among the most common dipterocarp species in mixed dipterocarp forests below 700 m, particularly on clay soils, with distributions encompassing peninsular Thailand, Peninsula Malaysia, Sumatra and Borneo (Ashton 1983, 2004). *Shorea pauciflora* (Section Brachypterae) is widespread and locally common in Borneo below 700 m, with a similar geographic range to *S. leprosula* and *S. parvifolia*, though absent from Thailand (Ashton 1983, 2004). *Parashorea tomentella* is endemic to Borneo and abundant below 200 m on fertile clay and alluvial soils (Ashton 2004).

Table 1. The four emergent Dipterocarpaceae study species sampled from 50 ha FDP at Danum Valley, Malaysian Borneo, and selected traits.

Species	Maximum DBH (cm)[a]	Maximum height (m)[a]	$\sqrt{\text{wing-loading}}$ $((mg \cdot cm/s^2)/cm^2)$[b]	Wood density (g/cm³)[c]	Calyx width (mm)[d]
Parashorea tomentella	200	65	317.0	0.42	4.2
Shorea leprosula	150	60	208.7	0.46	2.2
Shorea parvifolia	200	65	175.0	0.40	2.3
Shorea pauciflora	220	60	190.3	0.58	2.5

[a] Data from Ashton (2004)

[b] Data from (Smith et al. 2016) (Data for *P. tomentella*, *S. leprosula* and *S. parvifolia* are observed values. The value for *S. pauciflora* is a prediction based on fruit morphology)

[c] Mean for each species compiled from (Burgess 1966, Lee et al. 1979, Oey 1990, Basuki et al. 2009, Saner et al. 2012)

[d] Data from Kettle et al. (2011c) (Data for *S. pauciflora* is unavailable therefore we use the value for *S. johorensis* — a phylogenetically closely related species with similar flower bud size, Ashton (1983))

Table 2. A comparison of plot climates. This table is adapted from Anderson-Teixeira et al. (2015) with the inclusion of data from a plot in the Sepilok Forest Reserve which is not part of the CTFS-ForestGEO forest dynamic plot network.

Site		Plot size (ha)	Elevation (m)[a]	MAT (°C)	MAP (mm yr⁻¹)
Danum Valley Conservation Area	(DVCA)	50	202–318	26.7	2282
Lambir Hills National Park	(LHNP)	52	104–244	26.6	2664
Pasoh Forest Reserve	(PFR)	50	70–95	27.9	1788
Sepilok Forest Reserve	(SFR)	50	13–40	27.3[b]	3136[b]

[a]Elevation data was obtained from digital elevation models (DEMs) of Danum and Sepilok, and from the original survey data from grid intersections for Lambir and Pasoh.

[b]Data from Margrove et al. (2015)

Study sites

This study compares FSGS of four dipterocarp species located in sites in SE Asia: Danum Valley Conservation Area (DVCA) and Sepilok Forest Reserve (SFR) in Sabah, Malaysian Borneo; Lambir Hills National Park (LHNP) in Sarawak, Malaysian Borneo; and Pasoh Forest Reserve (PFR) in Peninsula Malaysia.

Individuals were sampled from the 50 ha forest dynamics plots (FDP) at Danum Valley, Lambir Hills and Pasoh (Ng et al. 2009b, Harata et al. 2012). These three plots are integrated within the CTFS–ForestGEO global network of forest plots (Anderson-Teixeira et al. 2015). *Parashorea tomentella* sampled from Sepilok Forest Reserve by Kettle et al. (2011b) followed a stratified sampling approach over a much larger spatial scale (to a maximum distance of 3 Km between individuals) than the CTFS plots, and additionally sampled almost three times as many individuals than are present on the Danum 50 ha plot. Greater genetic diversity is expected in larger populations (due to the accumulation of rare alleles) sampled over a wider spatial scale. To explicitly compare genetic diversity and FSGS between plots we subsampled this larger dataset by restricting the individuals included in our analysis to those located within a 50 ha plot of equal dimensions to the other three (500 x 1000 m), delineated within the existing 160 ha plot in which all mature dipterocarps (DBH 30 cm) have been identified and coordinates recorded. Surface elevation plots with individuals sampled from each species are presented in the supplementary information (SI2).

Climatic conditions are similar across the four plots (Table 2). Mean annual temperatures range 26.6–27.9°C and mean annual precipitation is >2000 mm except at Pasoh (1788 mm p.a.). No site experiences an annual dry season. Vegetation is broadleaf evergreen forest (Anderson-Teixeira et al. 2015) under the 'mixed lowland dipterocarp forest' classification, and all plots lie upon an ultisol soil substrate. The plots differ primarily in their topographical heterogeneity. Pasoh Forest Reserve is the least topographically heterogeneous, with the 50 ha FDP plot from which *S. leprosula* was sampled situated on an alluvial plain ranging only 70 to 95 m in elevation (Manokaran et al. 2004, Ng et al. 2009b), followed by the 50 ha FDP at Danum Valley Conservation Area which ranges 201 to 317 m.a.s.l. The Lambir Hills National Park plot (52 ha, sampled for *S. parvifolia*) is the most topographically and edaphically heterogeneous, comprising a number of ravines and steep escarpments ranging 100 to 244 m elevation (Lee et al. 2004a), followed by Sepilok Forest Reserve, which can be subdivided into periodically flooded low-lying alluvial areas with low mudstone hills between 15–30 m elevation, and sandstone hills reaching 100 m elevation (Fox 1973).

Sampling and DNA extraction

We sampled all individuals of the four study species in the Danum plot with DBH > 30 cm, consistent with the sampling regime of the three comparison populations. Tree coordinates were recorded using a handheld GPS (Garmin GPSmap 60CSx), and cambium samples were taken using a 2 cm diameter leather punch and hammer following the procedure of Colpaert et al. (2005). Samples were desiccated in silica gel and then stored at -4°C prior to DNA extraction. DNA was extracted from roughly 0.025g of lyphosized sample using Qiagen DNeasy™ 96-well-plate extraction system, after first milling samples to a fine powder using a Qiagen Mixer-Mill™. Details of sampling and DNA extraction from LHNP, PFR and SFR are described in the original papers (Ng et al. 2009b, Kettle et al. 2011b, Harata et al. 2012).

Microsatellite Genotyping

The genotype of each individual was determined at six (*P. tomentella*) (Ng et al. 2009a, Kettle et al. 2011b), eight (*S. leprosula* (Lee et al. 2004b, Ng et al. 2009a) and *S. pauciflora*) and ten (*S. parvifolia*) (Lee et al. 2004b) nuclear microsatellite loci (Table S1). PCR amplifications were performed on peltier thermo cyclers (Sensoquest Labcycler and Dyad Biorad). For *S. leprosula*, *S. parvifolia* and *S. pauciflora* each PCR reaction consisted of 1 µL of DNA template, 2 µL of 5x GoTaq reaction buffer (Promega), 0.6 µL of $MgCl^2$ (25 mM), 0.2 µL dNTP mix (10 mM), 0.4 µL M13 labelled forward primer (2 mM), 1.6 µL reverse primer (2 mM), 1.6 µL of FAM labeled M-13 fluorescent dye (2 mM), 0.18 µL BSA (10 mg/mL), 0.05 µl *Taq* Polymerase (Promega) (5 U/µL) and 2.37 µL of ddH_20. The touchdown PCR amplification protocol for these three species consisted of an initial denaturation at 94°C for 5 minutes, followed by eight cycles of 94°C for 30s, 58°C for 45s with a reduction of 1°C each cycle, and 72°C for 30s. This was followed by 20 cycles of 94°C for 30s, 50°C for 45s, and 72°C for 30s to provide stable annealing temperatures. The protocol finished with a final eight cycles of 94°C for 30s, 53°C for 45s, and 72°C for 30s, ending with a final extension of 72°C for 10 minutes. The *P. tomentella* markers were labeled and hence a modified PCR reaction and amplification protocol was used. Each PCR reaction consisted of 1 µL of DNA template, 2 µL of 5x GoTaq reaction buffer (Promega), 1.2 µL of $MgCl^2$ (25 mM), 0.2 µL dNTP mix (10 mM), 2.5 µL forward primer (2 mM), 2.5 µL reverse primer (2 mM), 0.18 µL BSA (10 mg/mL), 0.05 µl *Taq* Polymerase (Promega) (5 U/µL) and 0.37 µL of ddH_20. The touchdown PCR amplification protocol for *P. tomentella* markers consisted of an initial denaturation at 95°C for 2 minutes, followed by 10 cycles of 95°C for 30s, 65°C for 30s with a reduction of 1°C each cycle, and 72°C for 30s. This was followed by 30 cycles of 95°C for 30s, 55°C for 30s, and 72°C for 30s to provide stable annealing

temperatures. The protocol finished with a final extension of 72°C for 30 minutes. Fragment analysis was performed on ABI 3730xl capillary sequencer (Applied Biosystems). Genotypes were scored using GeneMarker® software version 2.6.0 (SoftGenetics, PA, USA) against a LIZ 500 HD size standard. Details of microsatellite genotyping for species sampled in LHNP, PFR and SFR are described elsewhere (Ng et al. 2009b, Kettle et al. 2011b, Harata et al. 2012).

Analysis of genetic diversity and inbreeding

For each locus we calculated the number of alleles (*Na*), and observed (*Ho*) and expected (*He*) heterozygosity using GenAlEx 6.4 (Peakall and Smouse 2006). Allelic richness (*Ae*) and the inbreeding coefficient (F_{IS}) were calculated using FSTAT (Goudet 1995). Allelic richness is sensitive to the sample size (El Mousadik and Petit 1996, Leberg 2002) and thus we used 42 randomly selected samples per species, our lowest overall sample size, to allow direct comparisons to be drawn (El Mousadik and Petit 1996, Leberg 2002). Null allele frequencies were calculated using GenePop 4.2.1 (Raymond and Rousset 1995). All loci were highly polymorphic enabling comparison between the species (Table 1). For species with an $F_{IS} > 0.15$, indicating a mixed mating system, we calculated the selfing rate (*s*), $s = (2F_{IS})/(1 + F_{IS})$, for each species (Allard and Adams 1969).

Characterisation of fine-scale genetic structure

The following steps were conducted for all sample datasets from the four study sites. To elucidate FSGS, the spatial autocorrelation between paired samples at multiple distance classes was calculated using the relatedness coefficient (r) and kinship coefficient (F) (Loiselle et al. 1995) with GenAlEx (Peakall and Smouse 2006) and SPAGeDi respectively (Hardy and Vekemans 2002). Eleven distance classes were used. We defined four classes of 25m in the first 100m; four classes of 50m between 100 and 300m; two classes of 200m between 300 and 700m; and finally one class of 300m between 700 and 1000m. To compare the relative intensity of FSGS between species we calculated the *Sp* statistic, $Sp = -\hat{b}_F/(1 - \hat{F}_{(1)})$, where $-\hat{b}_F$ is the regression slope of the kinship coefficient and $\hat{F}_{(1)}$ is the mean kinship coefficient, at the nearest distance class (here 25m) (Vekemans and Hardy 2004). The scale of FSGS for each species was defined as the maximum distance at which the kinship coefficient differed from zero (*DistF*). A nonparametric heterogeneity test (Smouse et al. 2008) was applied using GenAlEx 6.4 (Peakall and Smouse 2006) to test for significant differences in FSGS between species present at Danum across distance classes. A sequential Bonferroni correction (Rice 1989) was applied to the *P* values, which were subsequently considered significant if $P < 0.01$ (Banks and Peakall 2012).

Two tests were applied to test for statistical differences in the pattern of FSGS observed for the paired site comparisons per species. First, a paired *t*-test (pairing within species from the different sites), was applied to test for statistical differences in the intensity of FSGS as observed via the *Sp* statistics. Second, nonparametric heterogeneity tests (Smouse et al. 2008) were applied to test whether the slopes of the spatial decay in the relatedness coefficient (r) differed significantly between sites on a species by species basis.

Site environmental heterogeneity

Given the difficulty in generating a robust measure of environmental heterogeneity that encapsulates the complexity of edaphic, climatic, floristic, and topographic factors at the plot level we chose plot topographical range as a proxy for environmental heterogeneity. Topographical heterogeneity has been associated with variation in light availability, microclimate, underlying bedrock, soil type, and soil water availability (Itoh et al. 2003, Brown et al. 2013, Born et al. 2014). Dipterocarp species show positive or negative associations with particular soil substrates (Itoh et al. 2003, Palmiotto et al. 2004, Paoli et al. 2006, Itoh et al. 2010, Itoh et al. 2012, Sukri et al. 2012), which in many lowland forest plots is correlated with elevation. We calculated the 95th percentiles of species' elevation range at each plot, using DEMs (Danum and Sepilok) (Tan et al. *submitted*) and topographic maps (Lambir and Pasoh) (Lee et al. 2004a, Manokaran et al. 2004) to interpolate individual tree elevations, and used this species 'realized' elevation range as a proxy of habitat heterogeneity. Nevertheless, such an approach might not be applicable to other research sites, where habitats do not differentiate along an altitudinal gradient. In such cases soil maps or alternative factors encapsulating habitat variability would be preferable.

RESULTS

Genetic diversity and inbreeding

The microsatellite loci used for analysis of the *Shorea* species sampled from Danum were highly polymorphic, with number of alleles per locus ranging 7–24 in *S. leprosula*, 6–15 in *S. parvifolia*, and 6–24 in *S. pauciflora*. Mean allelic richness (*Ae*) was correspondingly high with values of 14.23, 9.80 and 12.03 for *S. leprosula*, *S. parvifolia* and *S. pauciflora* respectively (Table 3, Table S1). *P. tomentella* loci were less polymorphic, ranging from 6 to 11 alleles per locus, and the mean allelic richness of 3.347 was substantially lower than the *Shorea* species. Gene diversity (*He*) was highest in *S. leprosula* (0.79 ± 0.040) and S. *pauciflora* (0.780 ± 0.029), intermediate for *S. parvifolia* (0.632 ± 0.045) and lowest for *P. tomentella* (0.571 ± 0.063). All four species were significantly inbred (Table 3), though the inbreeding coefficient (F_{IS}) varied considerably from 0.108 (± 0.034) and 1.116 (± 0.22) in *S. parvifolia* and *S. leprosula* to 0.285 (± 0.430) and 0.273 (± 0.041) in *P. tomentella* and *S. pauciflora*. *Parashorea tomentella* and *S. pauciflora* had F_{IS} values > 0.15 and selfing rates (*s*) of 0.44 and 0.43 respectively. Genetic diversity and inbreeding statistics are additionally given in Table 3 and S1 for the three comparison populations.

Table 3. Summary statistics of genetic diversity and inbreeding coefficients for the dipterocarp species *Parashorea tomentella*, *Shorea leprosula*, *Shorea parvifolia* and *Shorea pauciflora* from the 50 ha FDP at Danum Valley and comparison plots, ± indicates the standard error (± SE); number of samples (N); mean density per hectare (N ha^{-1}); number of loci (Loci); mean number of alleles (A); allelic richness (Rt); observed heterozygosity (Ho); expected heterozygosity (He); inbreeding coefficient (Fis) and significance; selfing rate (s) following Allard and Adams (1969). Allelic richness (Rt) is calculated on a random sample of 42 individuals per species.

Species	Site	N	N ha^{-1}	Loci	A (± SE)	Rt	Ho (± SE)	He (± SE)	Fis	*s*
P. tomentella	DVCA	81	1.6	6	6.67 ± 1.43	5.48	0.416 ± 0.07	0.571 ± 0.06	0.285**	0.44
	SFR[a]	85	1.7	6	8.50 ± 1.57	6.57	0.580 ± 0.08	0.575 ± 0.10	-0.001	–
S. leprosula	DVCA	87	1.7	8	14.38 ± 1.94	11.81	0.708 ± 0.05	0.792 ± 0.04	0.116**	–
	PFR	154	3.1	7	13.57 ± 2.89	10.39	0.667 ± 0.05	0.736 ± 0.07	0.064**	–
S. parvifolia	DVCA	137	2.7	10	10.30 ± 1.04	6.86	0.561 ± 0.04	0.632 ± 0.05	0.108**	–
	LHNP	42	0.8	9	15.00 ± 2.66	15.00	0.749 ± 0.05	0.819 ± 0.03	0.098**	–
S. pauciflora	DVCA	83	1.7	8	12.25 ± 2.29	10.43	0.577 ± 0.05	0.779 ± 0.03	0.273**	0.43

[a] Data from the 50 ha subsample of the 160 ha plot at SFR.

Fine scale genetic structure at Danum

In all four species a significant correlation of *r* against geographic distance was observed, confirming fine scale genetic structure in the Danum 50 ha FDP (Peakall and Smouse 2006) (Table 3). The slopes of the regressions of *r* against the null hypothesis $r = 0$ were significant (nonparametric heterogeneity test statistic ω) for *S. leprosula* ($\omega = 90.92$, $P < 0.001$), *S. parvifolia* ($\omega = 129.88$, $P < 0.001$), *S. pauciflora* ($\omega = 108.60$, $P < 0.001$) and additionally *P. tomentella* ($\omega = 101.46$, $P < 0.001$). Significant differences in pair-wise kinship *F* (Loiselle et al. 1995) calculated using SPAGeDi were detected to a *DistF* of 25m in *S. leprosula* and *S. parvifolia* ($P < 0.05$), and 100m for *S. pauciflora* ($P < 0.05$) (Table 4, Fig. 1). At the nearest distance class, 0–25m, kinship values ranged from $F = 0.058$ in *S. leprosula* to $F = 0.213$ in *S. pauciflora*. Despite a significant correlation of *r* against geographic distance over the full correlogram, no significant difference in *F* was observed for *P. tomentella* at any distance class, though a consistent trend of a reduction in *F* with distance was observed (Fig. 1). The intensity of the FSGS also varied between species. The intensity of FSGS was greatest for *S. pauciflora* ($Sp = 0.070 \pm 0.012$), then *S. leprosula* ($Sp = 0.015 \pm 0.004$), *P. tomentella* ($Sp = 0.012 \pm 0.005$) and weakest for *S. parvifolia* ($Sp = 0.009 \pm 0.002$) (Table 4).

The heterogeneity test between species pairs indicated a significant difference in FSGS patterns between *S. pauciflora* and the other three species (*P. tomentella*: $\omega = 82.43$, $P < 0.001$; *S. leprosula*: $\omega = 85.33$, $P < 0.001$; *S. parvifolia*: $\omega = 96.79$, $P < 0.001$), complementing the large *DistF* and high *Sp* value in this species compared to the others (Table 4). A significant difference was observed between *S. parvifolia* and *P. tomentella* ($\omega = 39.73$; $P < 0.05$); however significance was lost after applying the Bonferroni correction with a 1% significance threshold ($P < 0.01$) (Rice 1989, Banks and Peakall 2012). No difference was observed in pair-wise comparisons between *S. leprosula* and *P. tomentella* or *S. parvifolia*.

Table 4. Summary statistics of fine-scale spatial genetic structure (FSGS) for *P. tomentella*, *S. leprosula*, *S. parvifolia* and *S. pauciflora* from Danum Valley and the three comparison sites, ± indicates the standard error (± SE); number of samples (N); *F*1, mean pairwise kinship coefficient *F* among individuals at the shortest distance class (25m); *DistF*, geographic distance (m) to which *F* deviates significantly for 0; bLd, slope of the regression of pairwise kinship *F* on ln(dij), the natural logarithm of the geographic distance between pairs of individuals; ω, multi-class test criterion for null hypothesis $r = 0$; *Sp*, the intensity of FSGS, following Vekemans and Hardy (2004); and species elevation range (m) observed at the site (0.05–0.95 percentile).

Species	Site	N	*F*1 (± SE)	DistF	bLd (± SE)	ω	*Sp* (± SE)	Elev. range
P. tomentella	DVC	81	0.094 ± 0.06	–	-0.011 ± 0.005	43.38 **	0.012 ± 0.005	242–293
	SFR	85	0.083 ± 0.04	25	-0.023 ± 0.008	106.90 ***	0.025 ± 0.009	14–29
S. leprosula	DVC	87	0.058 ± 0.02	25	-0.014 ± 0.004	89.73 ***	0.015 ± 0.004	235–291
	PFR	154	0.053 ± 0.02	50	-0.011 ± 0.003	90.29 ***	0.012 ± 0.003	73–85
S. parvifolia	DVC	137	0.072 ± 0.02	25	-0.008 ± 0.002	134.87 ***	0.009 ± 0.002	242–293
	LHNP	42	-0.001 ± 0.04	–	-0.010 ± 0.004	42.03 –	0.010 ± 0.004	139–200
S. pauciflora	DVC	83	0.213 ± 0.04	100	-0.055 ± 0.010	106.41 ***	0.070 ± 0.012	236–292
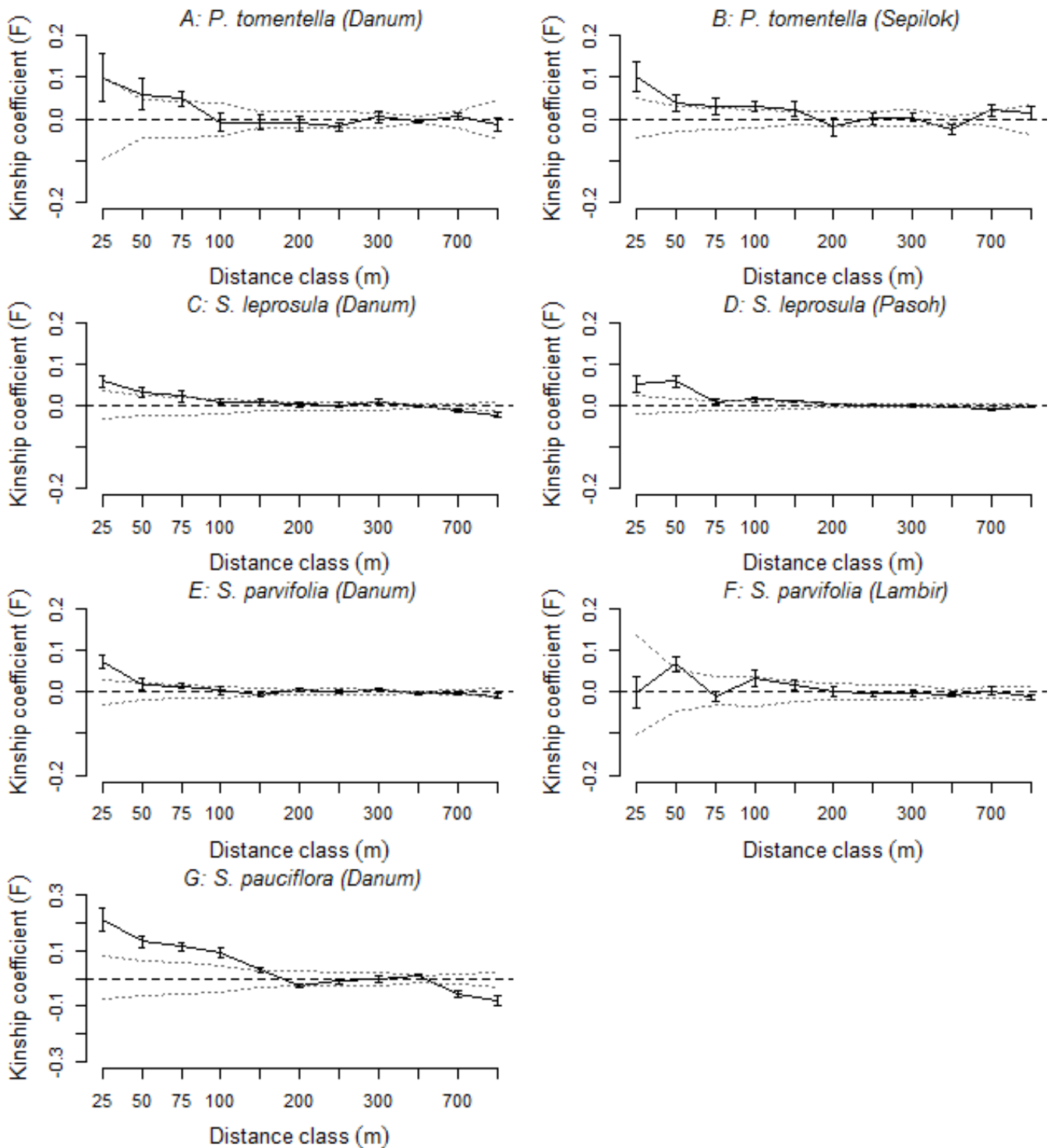
Figure 1. Fine-scale genetic structure of the four dipterocarp species *P. tomentella*, *S. leprosula*, *S. parvifolia* and *S. pauciflora*. Plots show the Kinship coefficient *F* (Loiselle et al. 1995) (solid line, ± standard error) plotted against distance class (m). Random spatial genetic structure at is given by the dashed line, and the 95% confidence intervals around the random spatial genetic structure by the dotted lines.

Fine scale genetic structure comparisons among sites

The scale and intensity of FSGS was similar for *P. tomentella*, *S. leprosula* and *S. parvifolia* between the Danum and comparison plots. A paired *t*-test comparing the intensity of FSGS in the Danum populations to the comparison populations using the *Sp* statistic was non-significant ($t = -0.670$, $P = 0.572$). The scale and intensity of FSGS in *S. leprosula* at Pasoh and *S. parvifolia* at Lambir were both consistent with the results obtained from the Danum populations. Significant FSGS was observed in *S. leprosula* at both Danum and Pasoh. The scale of FSGS was greater in Pasoh, with a *DistF* of 50 m compared to 25 m at Danum. The intensity of FSGS was also slightly stronger at Pasoh (*Sp* value of 0.012) than at Danum (0.015, Table 4). Nevertheless the heterogeneity test on the slope of *r* observed no significant difference between the two populations ($\omega = 11.38$, $P = 0.301$). Similarly, levels of genetic diversity including the mean number of alleles, allelic richness, observed and expected heterozygosity and inbreeding coefficients were extremely close in value at the two sites (Table 3).

Significant though weak FSGS was observed in *S. parvifolia* to a *DistF* of 25 m in Danum, but no FSGS was observed in *S. parvifolia* at Lambir. However, the *Sp* values measuring the intensity of FSGS were highly consistent between populations (0.009 and 0.010 respectively), and the heterogeneity test on the slope of *r* was non-significant ($\omega = 9.64$, $P = 0.491$). Levels of genetic diversity were however higher at Lambir than Danum, with greater allelic richness, mean number of alleles, and observed heterozygosity (Table 3).

The results for *Parashorea tomentella* at Danum and Sepilok were less consistent. Populations from both plots exhibited significant FSGS but the intensity of FSGS was much lower for the Danum population (*Sp* value of 0.012) than the Sepilok plot population (*Sp* value of 0.025, Table 4). *Parashorea tomentella* at Sepilok also exhibited a significant difference in pair-wise kinship *F* (Loiselle et al. 1995) calculated using SPAGeDi to a *DistF* of 25 m, while no significant difference was observed at Danum. A non-parametric heterogeneity test on the relatedness coefficient (*r*) across distance classes confirmed a significant difference in the pattern of FSGS between the Danum and Sepilok plots for *P. tomentella* ($\omega = 40.03$, $P < 0.01$). Additionally, the Danum population was significantly inbred, with a selfing rate of $s = 0.44$ whereas the Sepilok population was not significantly inbred (Table 3).

DISCUSSION

Using nuclear microsatellites loci we genotyped all mature trees (DBH ≥30 cm) from four dipterocarp species located in a 50 ha FDP in Danum Valley, Malaysian Borneo. We compared the scale and intensity in FSGS observed in three of these species to the same species in Lambir Hills National Park, Pasoh Forest Reserve and Sepilok Forest Reserve to assess the consistency of FSGS patterns within species in different plots. At Danum, all four study species, *P. tomentella*, *S. leprosula*, *S. parvifolia* and *S. pauciflora*, displayed significant FSGS. Results on the consistency of FSGS within species between plots were mixed, with little variation in the intensity and scale of FSGS in *S. leprosula* and *S. parvifolia* between plots (Danum with Pasoh and Lambir respectively), as confirmed by non-significant heterogeneity tests on the slope of the relatedness coefficient (*r*) against geographic distance between sites. Conversely, the intensity of FSGS was much greater in the Sepilok plot than Danum plot for *P. tomentella*, and a significant difference in the overall pattern of FSGS was detected between plots using a non-parametric heterogeneity test. Below we interpret our results on the FSGS of species present at Danum within the wider context of FSGS in the Dipterocarpaceae and discuss the abiotic factors that might promote or prevent consistent patterns of FSGS within our study species.

Our results on the scale and intensity of FSGS in *S. leprosula* and *S. parvifolia* at Danum were highly consistent with those obtained using populations from Pasoh and Lambir respectively. For *S. leprosula* significant kinship using Loiselle's *F* was observed to a *DistF* of 25 m at Danum, and 50 m at Pasoh (Fig. 1). There was no significant difference in the intensity of FSGS with *Sp* values of 0.015 (± 0.004) and 0.012 (± 0.003) (Table 4). *Shorea parvifolia* showed significant kinship *F* to distances of 25 m at Danum Valley but no significant *DistF* at Lambir. However, *S. parvifolia* is present at lower densities in the 52 ha Lambir plot (N = 42) than in Danum (N = 137) (Table 4) for trees ≥30 cm DBH (Harata et al. 2012), and hence errors around the estimates of *r* and *F* are wider at the nearest distance classes (25–50 m) (Fig. 1). Nevertheless, a trend of weak FSGS limited to the nearest distance class is congruent between the two sites for *S. parvifolia*, and is supported by the nearly identical *Sp* values (0.009 ± 0.009 and 0.010 ± 0.004; Table 4) and the lack of a significant difference in the slope of the relatedness coefficient (r) from the heterogeneity test.

Results from the genus *Shorea* suggest that patterns of FSGS are consistent within species between sites. Beyond assessing the consistency of species' FSGS patterns, our initial aim was to assess the relative influence site environmental heterogeneity on generating FSGS. We used each plot's elevation range as a simple proxy for environmental heterogeneity. The plot at Danum ranges

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116 m in elevation (202–318 m) compared to both a greater range in elevation of 140 m (104–244 m) at the more heterogeneous plot at Lambir and a much lower elevation range of 25 m (70–95 m) for the relatively homogeneous Pasoh plot. Yet despite these differences in plot elevation ranges, our proxy for site heterogeneity, there were no significant differences in either the intensity of FSGS or the slope of the regression between genetic relatedness and geographic distance between these species across a pair of sites.

Habitat associations in dipterocarps are thought to be maintained by niche partitioning and habitat filtering mechanisms, which are likely active throughout a tree's lifespan but are particularly intense at the juvenile stage (Palmiotto et al. 2004, Paoli et al. 2006, Dent and Burslem 2009, Suzuki et al. 2009). Such habitat associations can lead to spatially aggregated, or clumped, distributions of adult trees on their preferred substrate irrespective of seed dispersal potential (Chapter 4). Analysing patterns of FSGS in reference to the elevation range of the full plots might therefore not represent the habitat heterogeneity experienced by the species. This might, instead, be considered relatively homogeneous if a species' realized niche constrains its position to specific areas or elevations within the plots. This might reduce the area of each plot suitable for the study species, and thus alter the pattern of FSGS via reduced density, sub-division of population spatially within the plot (via ridges and valleys), and influence spatial aggregation patterns and cluster size. Despite the greater plot level topographic heterogeneity at Lambir compared to Danum, the heterogeneity (expressed as elevation range) experienced by *S. parvifolia* within plots was similar, with 51 m (242–293 m) at Danum and 61 m (139–200 m) at Lambir. Conversely, despite observing no significant difference in the slope of the relatedness coefficient (*r*) for *S. leprosula* between Danum and Pasoh, the topographic heterogeneity experienced by *S. leprosula* differed substantially between sites, with 56 m (235–291 m) elevation range at Danum but only 12 m (73–85 m) at Pasoh. Our results from the genus *Shorea* therefore indicate that site plays a minor role in influencing patterns of FSGS in *S. leprosula* and *S. parvifolia*. On this basis, recognizing that we have data from only a limited number of sites, our data suggest that FSGS within species may be relatively invariant to site. Such a prediction clearly warrants further empirical scrutiny. One caveat is that the results might differ at the edge of the species' altitudinal ranges, which is 700–800 m a.s.l., where individuals might be more isolated due to lower population densities.

In contrast to the high degree of consistency in our results between sites for the two *Shorea* species, our results for *P. tomentella* were less consistent between Danum and Sepilok. Significant FSGS was observed to a *DistF* of 25 m at Sepliok, but no significant *DistF* was observed at Danum. Fine-scale genetic structure was more intense at Sepilok than at Danum, with an *Sp* value of 0.025

compared to 0.012 (Table 4), and a significant difference between the patterns of FSGS at the two sites was confirmed via a non-parametric heterogeneity test. Contrary to the situation observed in *Shorea*, the significant difference in the FSGS in *P. tomentella* between Sepilok and Danum might in part be attributed to the contrasting habitat heterogeneity between the plots. The 50 ha plot within the Sepilok forest reserve encompasses a much more restricted total elevation range than Danum (37 versus 116 m), and indeed *P. tomentella* is restricted to a much narrower elevation range of 15 m (14–29 m) within the plot, one third that of the elevation range for this species on the 50 ha plot at Danum (51 m; 242–293 m). This constricted elevation range within the Sepilok plot might therefore restrict *P. tomentella* to lower elevation areas of the Sepilok Forest Reserve divided by sandstone ridges, potentially generating a clumped spatial aggregation pattern, and driving the development of more intense FSGS in this species. Interestingly, evidence in support of this scenario for *P. tomentella* within the Sepilok Forest Reserve is provided by Kettle et al. (2011b), who observed three distinct genetic clusters within this species despite a transect length of only 3 km, and mean pollen dispersal distance of 400 m. Given the increased intensity of FSGS in *P. tomentella* within a plot with a much more restricted elevation band, we therefore discount the null hypothesis that species traits are the primary drivers of FSGS, and deduce that, for some species in certain sites, environmental covariates may well influence patterns of FSGS.

The results of our study highlight more fundamental concerns regarding future analyses of FSGS in the Dipterocarpaceae, and late-successional tropical tree species more generally. Despite focusing our sampling strategy at Danum to exhaustively sample all mature individuals (DBH >30 cm) in the large-scale forest plots, our population sizes were still somewhat too small for analyses at the nearest distance classes, which tend to lack sufficient pairwise comparisons to distinguish FSGS signals from the null hypothesis. In future studies of FSGS in the Dipterocarpaceae it would be interesting to reduce the threshold of adult size classes from 30 cm DBH to 20 or 25 cm DBH to increase the number of individuals sampled. Whilst 30 cm DBH is typically considered the cut-off between immature and mature trees in this family, few datasets are available to support this notion. Anecdotal evidence suggests that at least some individuals flower and fruit at DBH sizes of as little as 20 cm (U. Ilstedt, *pers. comm.*).

The data presented in this study are from a limited number of plots, and yet they are consistent with the notion that habitat heterogeneity is an important factor shaping patterns of FSGS within species. Statistically significant differences in FSGS were observed in *P. tomentella* between Danum and Sepilok, while FSGS for *S. leprosula* and *S. parvifolia* remained consistent across Danum, Lambir and Pasoh. This has potentially important implications for the management of genetic diversity of

these commercially valuable timber species. Tito de Morais et al. (2015) propose a number of recommendations to maintain genetic diversity in the Dipterocarpaceae. These include planning the spatial distribution of retained seed trees at distances beyond that at which species display significant FSGS, to prevent the development of intense FSGS post-logging. To implement management recommendations based on species specific traits as suggested by Tito de Morais et al. (2015) it is necessary to confirm that patterns of FSGS within the same species are consistent across multiple sites throughout the species range. Our results suggest that the policy recommendations suggested by Tito de Morais et al. (2015) might need to be considered on not only a species–by–species basis, but additionally on a species–by–site basis given the inconsistency of FSGS observed in *P. tomentella*.

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SUPORTING INFORMATION

Table S1. Primers details for all loci of the four dipterocarp species at Danum, together with *P. tomentella* data from Sepilok (Kettle et al. 2011b), *S. leprosula* from Pasoh (Ng et al. 2009b), and *S. parvifolia* from Lambir (Harata et al. 2012). Number of samples (N); Locus name; allele size range (bp); observed number of alleles (N_a); allelic richness (Ae); observed heterozygosity (H_o); expected heterozygosity (H_e); inbreeding coefficient (F_{is}) and frequency of null alleles. Na, Ho, He were calculated with Genalex 6.5, Ae and F_{is} with FSTAT 2.9.3.2 and frequency of null alleles with Genepop 4.2.1 (** *p*-value<0.01, **p*-value < 0.05)

Species	N	Locus	Size range (bp)	Na	Ae	Ho	He	Fis	Null alleles
Parashorea tomentella	81	Dip2[a]	202-240	11	10.524	0.408	0.659	0.386**	0.162
(Danum)		Dip3[a]	133-139	3	2.968	0.416	0.513	0.196	0.534
		Dip4[a]	158-172	6	5.893	0.432	0.693	0.382**	0.172
		Dip5[a]	178-186	5	4.988	0.383	0.416	0.087	0.099
		Sle003[c1]	162-180	4	4.000	0.175	0.385	0.552**	0.187
		Sle009[c1]	193-224	11	10.795	0.684	0.759	0.105	0.066
		Mean		6.667	3.347	0.416	0.571	0.277**	0.203
		SE		1.430	1.830	0.066	0.063	0.430	0.410
Shorea leprosula	87	Sle003[c1]	153-206	14	13.829	0.635	0.755	0.164**	0.092
(Danum)		Sle004[c1]	170-187	7	6.967	0.674	0.721	0.070	0.172
		Sle007[c1]	195-254	20	20.000	0.827	0.914	0.102	0.062
		Sle079[c2]	178-246	24	23.735	0.938	0.919	-0.013	0.003
		Sle105[c2]	148-174	10	9.935	0.500	0.598	0.169**	0.103
		Sle280[c2]	121-171	15	14.922	0.766	0.864	0.120**	0.077
		Sle303[c2]	160-193	14	13.697	0.733	0.853	0.147	0.106
		Sle475[c2]	141-169	11	10.742	0.595	0.708	0.166	0.085
		Mean		14.38	14.228	0.708	0.792	0.111**	0.087
		SE		1.936	1.927	0.049	0.040	0.022	0.017
Shorea parvifolia	137	Sle118[c2]	115-206	15	14.335	0.678	0.865	0.220**	0.103
(Danum)		Sle280[c2]	121-151	13	12.777	0.528	0.568	0.075	0.012
		Sle392[c2]	186-204	8	7.899	0.623	0.696	0.109	0.106
		Sle475[c2]	152-167	11	10.919	0.580	0.743	0.225**	0.096
		Spar07[b]	132-199	15	13.536	0.538	0.584	0.083	0.043
		Spar11[b]	104-126	6	5.182	0.515	0.469	-0.095	0.000
		Spar12[b]	193-229	9	9.000	0.820	0.823	0.007	0.032
		Spar13[b]	116-146	6	6.000	0.438	0.522	0.167**	0.130
		Spar19[b]	232-262	9	8.441	0.441	0.463	0.050	0.071
		Spar20[b]	186-233	11	9.919	0.449	0.586	0.239**	0.105
		Mean		10.3	9.801	0.561	0.632	0.116**	0.070
		SE		1.044	0.980	0.038	0.045	0.034	0.014
Shorea pauciflora	83	Sjoh_2[b]	212-252	12	11.717	0.538	0.737	0.275**	0.122
(Danum)		Sjoh_3[b]	221-298	20	20.000	0.696	0.880	0.217**	0.115
		Sjoh_6[b]	168-251	24	23.055	0.805	0.908	0.120	0.053

		Sjoh_9[b]	156-190	12	11.682	0.543	0.803	0.329**	0.130
		Spau_13[b]	206-227	7	6.885	0.468	0.693	0.331**	0.145
		Sjoh_19[b]	142-170	9	8.972	0.695	0.786	0.122	0.071
		Sjoh_20[b]	187-203	6	5.991	0.470	0.689	0.324**	0.140
		Sjoh_21[b]	194-210	8	7.940	0.398	0.738	0.466**	0.202
		Mean		12.25	12.030	0.577	0.779	0.266**	0.122
		SE		2.289	2.213	0.050	0.029	0.041	0.016
Parashorea tomentella	85	Dip02	207-248	14	13.578	0.763	0.861	0.123	0.066
(Sepilok)		Dip03	132-146	4	3.977	0.395	0.374	-0.051	0.087
		Dip04	152-180	11	10.170	0.733	0.723	-0.006	0.023
		Dip05	172-188	7	5.657	0.507	0.419	-0.205	0.000
		Pt05	109-119	5	4.678	0.306	0.307	0.011	0.035
		Sld19	178-205	10	10.000	0.776	0.764	-0.005	0.028
		Mean		8.50	8.010	0.580	0.575	-0.001	0.040
		SE		1.565	1.555	0.084	0.096	0.044	0.013
Shorea leprosula	154	Shc01	132-212	22	21.701	0.604	0.911	0.340**	0.014
(Pasoh)		Shc02	135-153	7	7.000	0.797	0.603	-0.320	0.000
		Shc03	121-131	5	5.000	0.586	0.578	-0.011	0.050
		Shc04	80-124	19	19.000	0.828	0.906	0.090**	0.047
		Shc07	129-183	23	22.940	0.758	0.911	0.171**	0.093
		Shc09	170-196	12	11.880	0.636	0.803	0.211**	0.106
		Shc17	65-89	7	6.945	0.458	0.441	-0.034	0.015
		Mean		13.57	13.495	0.667	0.736	0.097**	0.069
		SE		2.894	2.873	0.050	0.073	0.081	0.022
Shorea Parvifolia	42	Dra215	259-318	28	28.00	0.881	0.942	0.076**	0.034
(Lambir)		Shc03	129-135	4	4.00	0.643	0.721	0.121	0.173
		Shc09	187-215	12	12.00	0.857	0.789	-0.074	0.000
		Shc111a	129-158	17	17.00	0.714	0.885	0.205	0.110
		Sle280	100-183	21	21.00	0.881	0.924	0.059	0.043
		Sle290	174-219	19	19.00	0.548	0.739	0.270**	0.117
		Sle392	180-197	8	8.00	0.714	0.701	-0.007	0.005
		Sle475	123-139	6	6.00	0.595	0.751	0.218	0.149
		Sle605	112-177	20	20.00	0.905	0.923	0.032	0.018
		Mean		15.00	15.00	0.749	0.819	0.098**	0.072
		SE		2.661	2.661	0.045	0.033	0.038	0.022

[a] Primers from Lee et al. (2006) redesigned by Kettle et al. (2011b)

[b] Newly developed microsatellite primers

[c] Published primers (1) Ng et al. (2009a); (2) Lee et al. (2004b)

SI2

Topographic maps of the four research plots including the coordinates of sampled individuals (Figs SI2a–d)
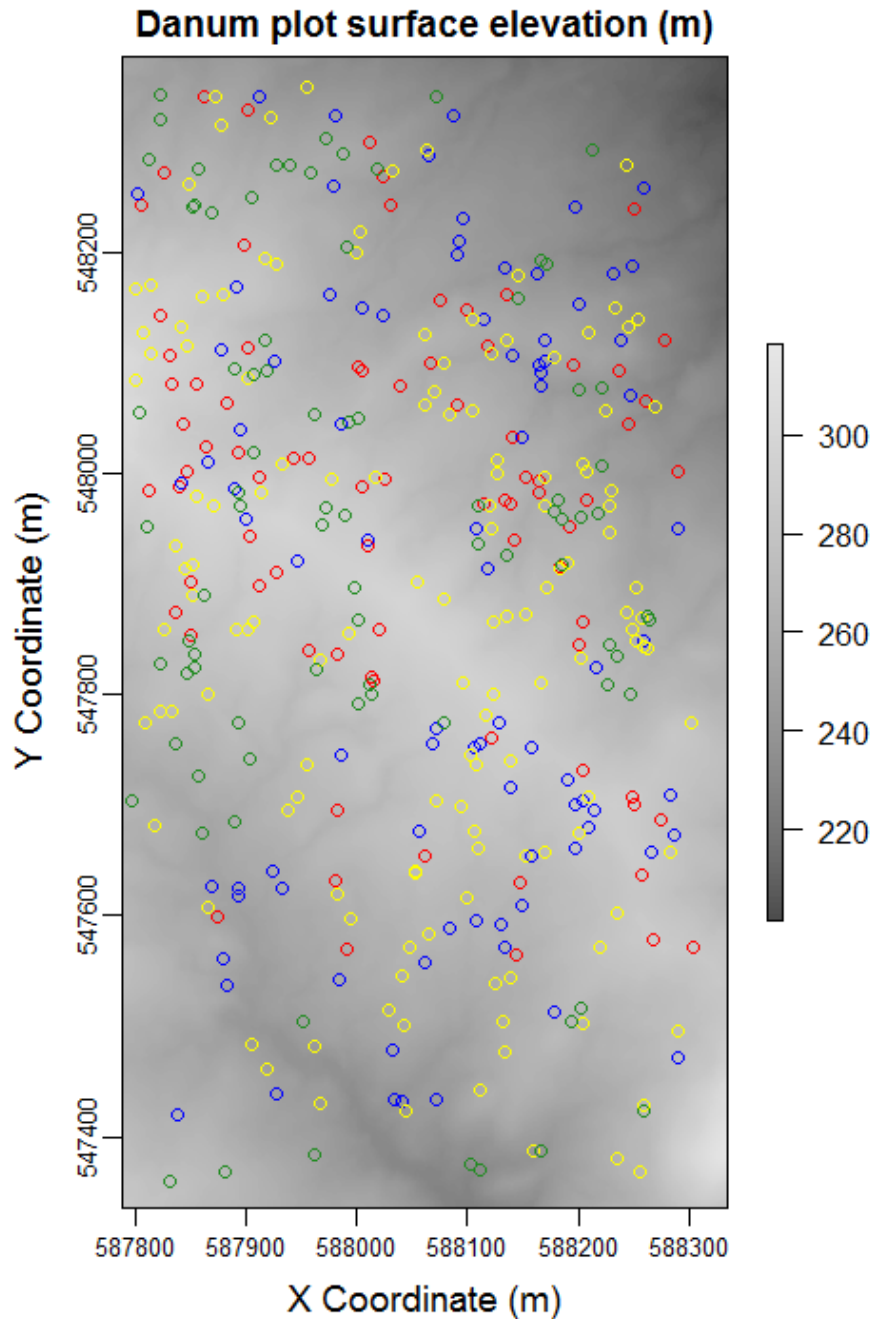
Fig SI2a. Topographic map (digital elevation model from Tan et al., *Submitted*) of the Danum Valley Conservation Area 50 ha FDP, with individual positions of sampled trees from *P. tomentella* (red), *S. leprosula* (blue), *S. parvifolia* (yellow) and *S. pauciflora* (green).
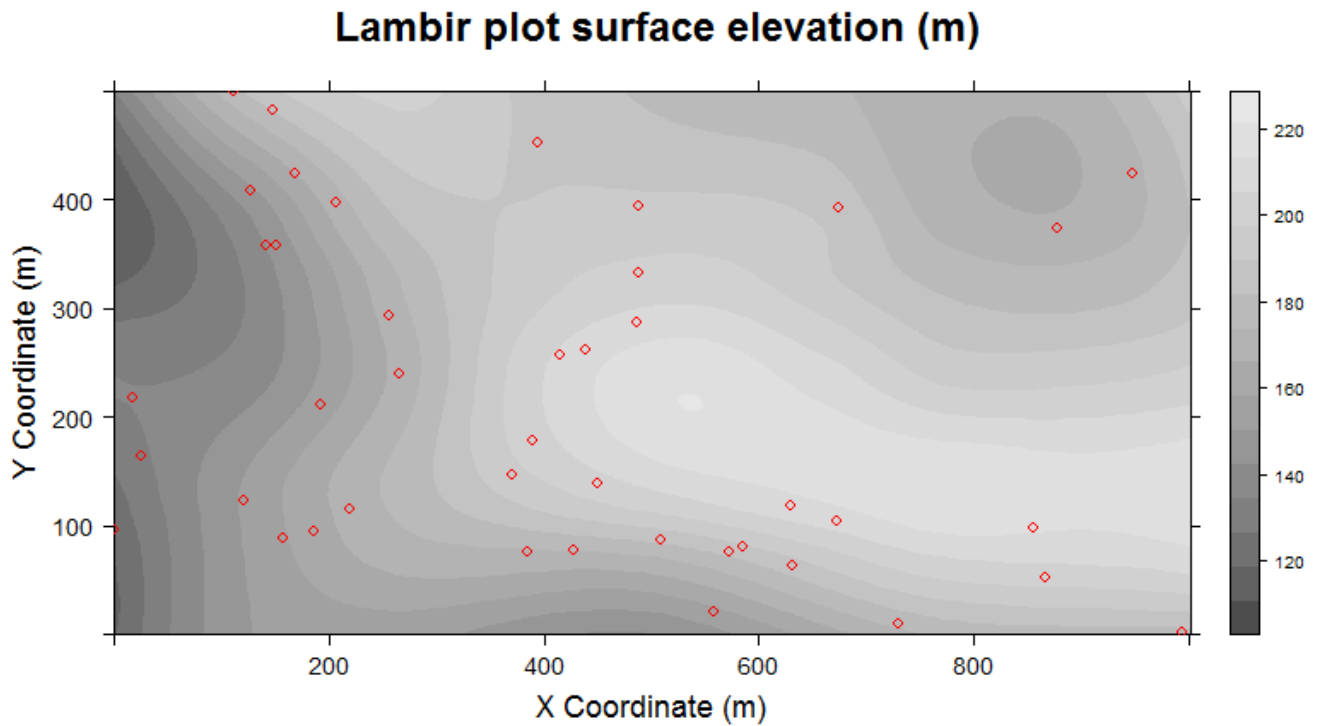
Fig SI2b. Topographic map of the Lambir Hills National Park 50 ha FDP (interpolated from quadrat elevations), with positions of *S. parvifolia* individuals sampled (red).
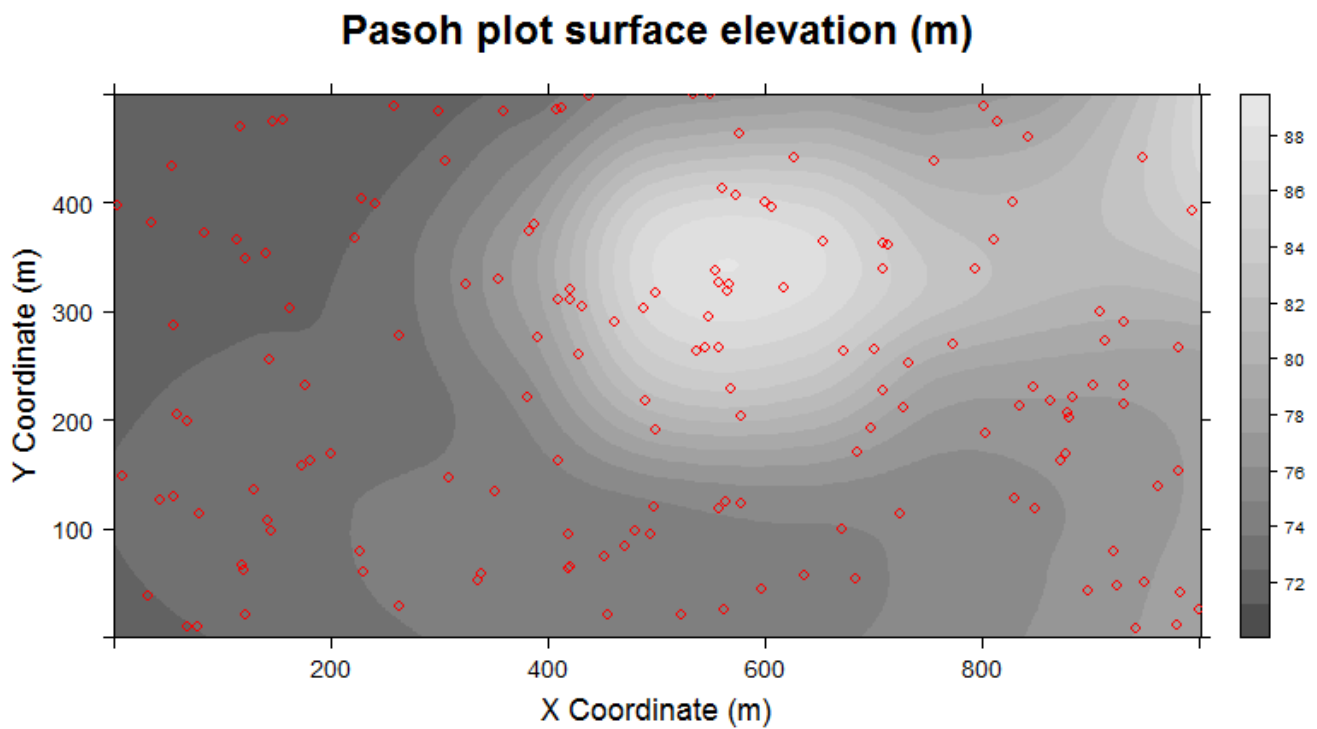
Fig SI2c. Topographic map of the Pasoh Forest Reserve 50 ha FDP (interpolated from quadrat elevations), with positions of *S. leprosula* individuals sampled (red).
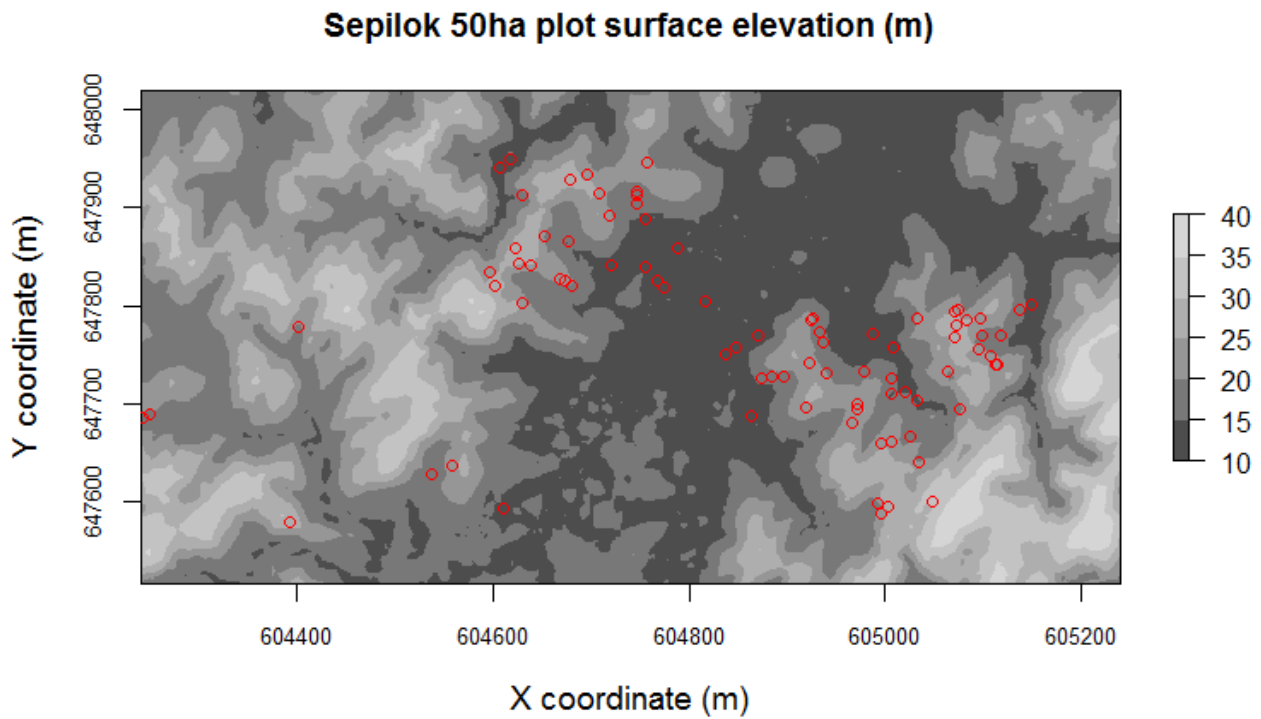
Fig SI2d. Topographic map (digital elevation model from Tan et al., *Submitted*) of the Sepilok Forest Reserve 50 ha subsampled plot, with positions of *P. tomentella* individuals sampled (red).

General Discussion

Thesis aims:

The aims of this thesis were to quantify seed dispersal in the Dipterocarpaceae and explore how inter-specific variation in this trait impacts upon other aspects of dipterocarp ecology, including patterns of spatial aggregation and fine-scale spatial genetic structure. The Dipterocarpaceae are found in high abundance and diversity in the lowland forests of Southeast Asia. These forests have been subject to high rates of timber extraction and deforestation driven by agricultural expansion and therefore have become fragmented and degraded. Quantifying seed dispersal is of applied value in understanding the potential impacts of habitat fragmentation on the connectivity and gene flow between remnant populations, providing insights into the long term viability of such populations and their vulnerability to loss of genetic diversity. Fruit production and seed dispersal is of theoretical importance to understanding the dynamics of natural regeneration and species distributions in primary forests, and thus is considered in many model of plant species coexistence. In this general discussion we outline the key results of the thesis before discussing, first, their relevance to forest fragmentation, and second, their relevance to species coexistence and community structure.

Key findings:

The elongated sepals of dipterocarp fruit form 'wings', causing the fruit to gyrate once abscised from the mother tree. There is variation in fruit morphology, both in nut mass and the number of wings, which ranges from zero to five depending on the genus. Suzuki and Ashton (1996) inferred that fruit above a threshold wing area to nut volume were gyration dispersed, with those falling below this threshold dispersed by gravity. Chapters two and three extended these initial investigations by analyzing how interspecific variation in the ratio of fruit wing area to nut mass influenced dispersal potential.

In Chapter two, we measured the distance individual fruits dispersed after releasing them from a canopy tower. The phenomenological model developed allowed the generation of dispersal kernels for each species. Fruit morphology had a significant effect on dispersal potential; species with large wing areas in relation to fruit mass, termed the 'inverse wing-loading' (IWL), dispersed greater

distances. There was also a positive interaction with wind speed, such that species with higher IWLs dispersed significantly longer distances with increasing wind speed. Nevertheless, fruit dispersal was primarily local with 90% of fruit dispersing <10 m.

In Chapter three, we measured the terminal velocity of dipterocarp fruit by individually releasing fruit from a canopy tower and recording the length of time each fruit remained in the air column. Again there was a significant interspecific variation in fruit terminal velocity which was directly correlated to fruit morphology, specifically the square-root of wing-loading (nut mass over wing area). Fruit with larger square-root wing-loading had higher terminal velocities, which ranged 1.22–5.39 m/s. Under normal atmospheric conditions dispersal distances of 16–77 m were predicted from a ballistic model of seed dispersal using the observed terminal velocities from the species experimentally released.

In Chapter four, the spatial aggregation patterns of 28 dipterocarp species were analysed. We observed that over 90% of species were more spatially aggregated than random. The degree of spatial aggregation decreased in most species after controlling for topography, suggesting that habitat associations are prevalent in this family and contribute to spatial aggregation. There was no effect of seed dispersal potential, wood density or their interaction on the residual patterns of spatial aggregation after controlling for habitat, suggesting that negative density dependent mechanisms are insufficiently strong to overcome the extreme aggregation of seedlings around the mother tree in all species driven by dispersal limitation.

In the fifth Chapter, we analysed the fine-scale genetic structure of three dipterocarp species from a 50 ha plot at Danum Valley and compared our results to those obtained from datasets on the same three species at different lowland dipterocarp forest plots. Significant FSGS was observed in all species studied at Danum Valley, consistent with a body of literature showing that the Dipterocarpaceae regularly exhibit pronounced FSGS due to limited seed and pollen dispersal. However, results for the within species between site comparisons were mixed, with two species showing consistent and one species showing inconsistent results. This importantly suggests that patterns of FSGS are not determined by species reproductive traits in isolation but that habitat factors play a role in patterns of FSGS.

Research Implications:

Fragmentation and implications for population viability

The results of Chapters two and three confirm that there are significant intraspecific differences in seed dispersal within the Dipterocarpaceae, and that these are underpinned mechanistically by variation in fruit morphology, specifically the ratio of fruit wing area to nut mass. The results of Chapter three, a strong correlation between fruit morphology and terminal velocity, mechanistically explain the increased dispersal distances of fruit with high IWLs in Chapter two. Fruit with high IWLs will have a corresponding low terminal velocity. High IWL fruit are therefore in the air-column for a greater length of time than low IWL fruit and are dispersed greater distances laterally, generating the positive interaction term with wind speed observed.

These Chapters highlight the critical role of wind in dipterocarp dispersal. The gyration generated by the fruit sepals is an adaptation to reduce the fruit terminal velocity, as the gyrating motion itself does not cause lateral movement of the fruit. Under normal atmospheric conditions and in the relatively still air within the forest canopy and understory, fruit dispersal is constrained to the near vicinity of the mother tree (Tamari and Jacalne 1984, Itoh et al. 1997, Osada et al. 2001). However, during periods of high and turbulent wind speeds, particularly during extreme weather events, fruit with large ratios of wing area to mass and hence low terminal velocities are able to take advantage of such conditions for long distance dispersal over hundreds of meters. This observation is key to explaining the discrepancy between the dispersal distances observed in Chapter two and the estimates of dispersal distance in Chapter three, and the anecdotal evidence that dipterocarp fruit can disperse distances of many hundreds of meters (Webber 1934).

Based upon the results of Chapters two and three, we would predict that under normal climatic conditions there will be extremely limited dispersal between forest fragments in human-dominated agricultural landscapes (McEuen and Curran 2004, 2006, Montoya et al. 2008). The oil palm and paper and pulp plantations that constitute the majority of the agricultural matrix between fragments in SE Asian landscapes are normally many hundreds if not thousands of hectares in area (Carlson et al. 2013), and consequently inter-fragment distances are typically measured in kilometers not hundreds of meters (Scriven et al. 2015). Dipterocarp dispersal distances under normal atmospheric conditions fall well short of this. A large proportion of the Dipterocarpaceae will be precluded from inter-fragment dispersal, even in extreme wind conditions, due to low IWLs (Chapter two). Nevertheless, the potential for dispersal between forest fragments remains during extreme weather events (Webber 1934, Whitmore 2006, Corlett 2009), with the likelihood of inter-fragment dispersal increasing with

increasing IWL (Chapter two). Further research should therefore explore both the physical and temporal scale at which such long distance dispersal events occur. The strong correlation between square-root wing loading and terminal velocity (Chapter three) can be used in mechanistic models of seed dispersal coupled to high resolution climate data to accomplish this goal (Hanski and Gilpin 1991, Tackenberg 2003, Bohrer et al. 2005, Katul et al. 2005, Nathan et al. 2008, Nathan et al. 2011). Documenting the frequency at which such long-distance dispersal events occur is critical to understanding the vulnerability of dipterocarps to fragmentation.

It must be stressed that the results observed are constrained by the species used in the analyses. In Chapters Two and Three species were selected based on availability of ripe fruit during the masting events of 2010 and 2014. Whilst the 2010 event was far larger than 2014's (Kettle et al. 2010, Kettle et al. 2011a), fruiting in these years was primarily observed in canopy and emergent species from the genera *Dipterocarpus*, *Dryobalanops*, *Parashorea* and *Shorea*, with few species participating from the genera *Anisoptera*, *Hopea*, *Upuna* and *Vatica*. Fruit were considered mature when the full sepal area was desiccated (brown and stiff as opposed to green, red or yellow and 'fleshy' – thereby enabling them to gyrate), and the nut was judged to have a significant weight representative of a fully developed embryo (aborted and pre-dispersal predated fruit could easily be distinguished based on their low mass by hand). The results on seed dispersal are therefore constrained to primarily emergent and main canopy genera listed above. Yet all dipterocarps possess a conserved fruit morphology, and there is a clear relationship between species height at maturity and fruit dispersal potential in the Dipterocarpaceae, with the majority of understory, small trees (20 m height) possessing wingless fruit, or fruit with reduced wing areas compared to species in the canopy and emergent layer (40 m plus height) with large wing area to nut volumes (Suzuki and Ashton 1996). The results should therefore represent the dispersal potential of canopy and emergent tree species well, and capture the dispersal potentials of smaller statured species that disperse via gyration and gravity given that dispersal potential has been measured as a continuous variable. Species associated with riparian habitats in particular have the highest proportion of wingless or reduced sepal area fruit (Suzuki and Ashton 1996), for example *Vatica rassak* which possesses wingless fruits with a corky pericarp (Ashton 2004), considered an adaptation for dispersal by water. The dispersal potential of such species is not captured by these analyses.

The predicted dispersal distances from the mechanistic model using observed wing-loading presented in Chapter Two focused on seed dispersal in primary forests. The distance over which the lateral movement of air could disperse fruit was given as the mean canopy height at Sepilok, 45 m. Whilst the predicted dispersal distances were primarily local, ranging 17.5 to 77.4 m, they are

potentially over-estimates due to differences in wind conditions above and below the canopy, with a pronounced reduction in wind speed with increasing proximity to the forest floor (Whitmore 2006). Fruit abscised from emergent trees in primary forests therefore experience high wind speeds for the first 5–10 m for their descent, before entering the relatively still ambient air conditions below the canopy, within which lateral movement is predicted to be minimal. This is a further cause underlying the discrepancy between potential and realized dispersal in the Dipterocarpaceae in primary forests. By disrupting the canopy integrity of primary forests, management practices might influence fruit dispersal potentials. In selectively logged forests, tree crowns are more segregated and detached from the canopy layer, and are therefore subject to increased wind turbulence and potentially greater seed dispersal. Any reproductive trees remaining in destructively harvested forests, if able to produce fruit given allee effects (Ghazoul et al. 1998), would similarly possess much greater dispersal distances given crown isolation. Greatest dispersal might be achieved by emergent trees at forest margins, where the full distance between release height and ground is subject to gusts of wind. Establishment of offspring would nevertheless remain improbable unless dispersal was sufficiently long distance to cross the unsuitable establishment conditions of the agricultural matrix.

The Dipterocarpaceae are particularly vulnerable to the sub-division of their populations for a number of reasons. First, unlike many tropical rain forest tree species which reproduce every year, the Dipterocarpaceae produce fruit roughly every 2–10 years after forest wide 'general flowering' (GF) events (Ashton 1988, Ashton et al. 1988, Sakai 2002, Brearley et al. 2007). Opportunities for connectivity and gene flow between isolated fragments driven by seed dispersal are therefore constrained to two or three times a decade – and such long distance dispersal events are entirely dependent on climatic conditions as discussed previously. This suggests that the inter-fragment movement of fruit is likely to act on a highly infrequent decadal basis, however this is yet to be confirmed via observational, experimental or simulation studies and should be the focus of future work.

As late-successional trees, many dipterocarps are observed at low density even in primary forest. Fragmentation of the population could potentially lead to 'allee effects' (Ghazoul et al. 1998, Forsyth 2003, Feldman and Morris 2011), where the population density falls to such an extent that the reproductive output is disproportionately reduced as remaining reproductively mature individuals become pollen limited reducing fruit set. Further, in Chapter four we observed that most species were spatially aggregated, and in Chapter five we observed that all four species studied (*P. tomentella*, *S. leprosula*, *S. parvifolia* and *S. pauciflora*) possessed significant fine-scale genetic structure, as do vast majority of dipterocarps studied (Ng et al. 2004, Takeuchi et al. 2004, Kettle et al. 2011b, Harata et al.

2012, Tito de Morais et al. 2015). The Dipterocarpaceae are therefore likely to be vulnerable to the loss of genetic diversity following forest fragmentation. Fragmentation is predicted to exacerbate FSGS, as the smaller population sizes increase the rate at which genetic diversity is lost via genetic drift, and inbreeding rates increase as pollen dispersal occurs primarily between closely related neighbouring individuals (Stacy et al. 1996, Naito et al. 2005, Jones and Comita 2008, Naito et al. 2008, Ismail et al. 2012). Inbreeding not only reduces the fitness of offspring via decreased growth and survival rates (Ismail et al. 2014, Nutt et al. in revision), but it also compounds FSGS by generating increasingly intense and fine-scale genetic structure, further accelerating the loss of genetic diversity. Gene flow via pollen dispersal could buffer small populations from the rapid loss of genetic diversity (Kramer et al. 2008), though whether effective pollen dispersal occurs between fragments in SE Asian mosaic agricultural landscapes is unknown (although see Bacles et al. 2006, Ismail et al. 2012). Reduced genetic diversity in the seed also reduces the ability of the next generation to adapt to a changing climate.

Seed dispersal does not equate to successful recruitment as a number of other processes impact whether a seed will establish and reach maturity (McEuen and Curran 2004, 2006). These processes depend both on the abiotic and biotic environments, both of which are impacted by forest fragmentation in a manner which might retard dipterocarp regeneration and thus impede fragment connectivity even with seed travelling many kilometers. First, forest fragmentation creates forest edges. Forest edges lead to an opening of the forest canopy and thus allow light and arid tropical air to penetrate into the forest understory altering the microclimate by increasing temperature and decreasing humidity (Kapos 1989, Murcia 1995, Laurance et al. 2011). These conditions favour the recruitment of pioneer species rather than dipterocarp seed which are unable to tolerate desiccation and germinate rapidly in the dark and humid forest understory (Tompsett 1998, O'Brien et al. 2013). Forest fragmentation and the composition of the surrounding agricultural matrix also changes the composition of the local biotic community (Terborgh et al. 2001). Studies have observed substantial increases in wild pig populations in fragmented landscapes compared to contiguous forest as they are supported by high yielding oil palm crops in the agricultural matrix (Ickes 2001, Luskin et al. 2014). This has the potential to create a spill-over effect (Rand et al. 2006), whereby the wild pigs predate heavily on the already reduced dipterocarp fruit crop in smaller fragments, which combined with reduced fruit production and altered microclimates might prevent natural regeneration. Recent evidence suggests that these processes are leading to complete reproductive failure of dipterocarps in small fragments <250 ha (Yeong 2015). Increased pre-dispersal seed predation by insects might

further lead to a reduced seed crop in small, fragmented populations, exacerbating this effect (Toy 1991, Nakagawa et al. 2003).

Combined, these observations suggest that Dipterocarpaceae will increasingly struggle to recruit in forest fragments. Seed dispersal is unlikely to allow effective connectivity between fragments to stave off the negative genetic consequences expected of small populations displaying FSGS. Evidence is emerging that increasingly supports this view. Similarly, infrequent reproduction with limited opportunity for long distance dispersal suggests that the pace of range-shift migration in response to climate warming may be limited. The long-term management of dipterocarp populations is likely to necessitate the use of large contiguous protected areas that span wide altitudinal gradients, with human assisted dispersal and regeneration within and between fragments.

Species coexistence and role of seed dispersal in shaping community structure

The results of the second Chapter confirm that dipterocarp dispersal is primarily limited, but also that there are significant interspecific differences in dispersal capability. Dispersal is classically considered a mechanism to deposit offspring to locations suitable for establishment where offspring will suffer reduced competition and predation and thus improving survival. Yet the results of the fourth Chapter confirmed that there was no significant difference in the patterns of spatial aggregation between species with high and low dispersal capacity. This runs contrary to our expectation that species with low seed dispersal potential will be more spatially aggregated as they possess adaptations allowing them to persist in the forest understory until released by a canopy gap. Similarly, large differences in fruit morphology generated relatively small differences in realized dispersal under normal atmospheric conditions. What, therefore, are the drivers of differential fruit morphology and seed dispersal in this family?

One mechanism for species coexistence with a substantial body of experimental support is the Janzen Connell (JC) hypothesis (Janzen 1970, Connell 1971), that predicts that seedlings establishing in close proximity to the mother tree or in high conspecific densities will suffer increased mortality as they are attacked by species-specific pathogens and predators (Harms et al. 2000, Bagchi et al. 2010). To avoid this negative density-dependent mechanism (NDD), trees should disperse their seed greater distances to increase their probability of survival. However, NDD effects are expected to be relatively weak in mast fruiting forest systems (Janzen 1974) as offspring survival is dependent on which seed escape pre-dispersal predation by insects (Toy 1991, Nakagawa et al. 2003) and post-dispersal predation by large mammals – which individual mother trees cannot influence in isolation since predator satiation occurs at the community scale (Curran and Leighton 2000, Curran and Webb 2000,

Sun et al. 2007). Seed survival during mast fruiting events is therefore a positive density-dependent mechanism where greater survival is observed in higher densities of conspecifics. Highly aggregated seedling 'carpets' establish as the recalcitrant fruit escape predation and germinate contemporaneously (Maycock et al. 2005). This mechanism may be self-reinforcing. First, if aggregations of seedlings successfully reach maturity then their high densities during future fruiting events will further increase the likelihood of offspring recruiting locally due to positive density-dependent effects. There are additional positive density-dependent effects in the production of fruit, with positive correlations between the number of flowering conspecifics and the percentage of trees with viable seed (Maycock et al. 2005). This is probably driven by more effective pollen dispersal and increased outcrossing rates when clustered trees flower synchronously; indeed, fruiting individuals of *Dryobalanops aromatica* were observed to be more spatially aggregated than the species generally (Itoh et al. 2003). Poor seed dispersal and highly clustered aggregations of mature individuals might therefore be advantageous in these systems.

Habitat associations generated non-random, aggregated distributions of the majority of species in the Sepilok plot at the landscape scale (Chapter four). Extremely limited seed dispersal and a high propensity for habitat associations is unlikely to be independent; indeed it is plausible that they interact. Species with particularly restrictive habitat associations, driven by strong environmental filtering (Engelbrecht et al. 2007, Kraft et al. 2015), face trade-offs in dispersing seed from the mother tree whilst ensuring they deposit in a site or substrate suitable for germination. On this basis we might expect that habitat restricted species prioritize the provisioning of individual fruit, to increase offspring competitive ability in the crowded forest understory (Westoby et al. 1992, Westoby et al. 1996), and promote establishment in environmental conditions they are adapted to, rather than risk complete reproductive failure by dispersing seed to unsuitable sites. Seed dispersal might therefore be under stabilizing selection for intermediate dispersal distances. Germination and growth experiments confirm that larger dipterocarp fruit grow more rapidly to larger sizes, imbuing fruit with a distinct competitive advantage to exploit limited light resources in temporally ephemeral canopy gaps (O'Brien et al. 2013). Larger fruit also germinate more rapidly under infrequent rainfall regimes, providing additional support in favour of the hypothesis that larger seeds are adaptions to a strategy of exploiting canopy gaps close to mother trees, as such sites are less humid that the forest understory (O'Brien et al. 2013). Empirical models of species coexistence confirm that limited seed dispersal coupled with highly competitive offspring can be a stable and successful life-history strategy (Bolker and Pacala 1999).

The above observations suggest that many dipterocarp fruit are adapted for regeneration in canopy gaps, with large fruited species monopolizing canopy gaps close to the mother tree and small fruited species having an advantage in establishing in distant canopy gaps. Yet up to 87 species of dipterocarp, with large differences in seed dispersal potential, may be present in a single 50 ha plot (Davies et al. 2005). The successful recruitment of smaller, better dispersed fruit requires extremely limited seed dispersal in the large fruiting species – which is observed – but also that large fruited species are spatially restricted and thus unable to disperse fruit into the majority of newly formed canopy gaps. This assumption is probably not tenable as seed dispersal is a continuous trait, and therefore even if small seeded fruit are not competing with the largest, most competitive seed, they are likely still competing with large seeded fruit from other species. Furthermore, it requires that tree-falls creating canopy gaps destroy all seedlings and pole size trees and therefore remove competition from taller established seedlings able to capture a large proportion of light. This is again highly unlikely and therefore newly establishing small seeded dipterocarps will be competing with taller, established seedlings from shade-tolerant species from previous mast fruiting events. Previously research confirms that seedling success in newly formed canopy gaps is determined both by relative height at gap creation and growth responses in relation to high light conditions (Brown and Whitmore 1992). Species with high dispersal potential and high growth rates in high light environments might therefore employ a strategy of dispersing fruit widely so their seedlings to germinate over a larger geographic area, increasing the opportunity that some small proportion of them are firmly established in the forest understory in readiness of gap creation. Canopy gaps are patchily distributed both spatially and temporally, and therefore these species might also reproduce more frequently than other dipterocarp species, participating in smaller 'minor' fruiting events (Maycock et al. 2005).

These combined observations (infrequent fruiting with the necessity to satiate large mammal predators, strong habitat associations, the positive reinforcement of high adult density to seed recruitment, and the low probability that tree falls destroy all understory trees) help interpret the observation that the majority of dipterocarps are shade-tolerant and do not show consistent responses to differences to light availability (Philipson et al. 2012, Philipson et al. 2014). The probability of a seed dispersing to a newly created canopy gap, in the absence of pre-existing larger dipterocarps or other pioneer competitors is low. All species must invest to some degree on adaptations that allow shade-tolerance to establish in the forest understory, however the maximum length of persistence varies along a continuous scale. The identity of species recruiting to the canopy and maturity is then determined by the relative juvenile sizes, species composition and inter-specific differences in growth rate under high light conditions (Brown and Whitmore 1992, Whitmore and Brown 1996, Brown et al.

1999). This mechanism has been proposed by (Brown et al. 1999) as a special form of dispersal limitation allowing for the species richness of the Dipterocarpaceae. Such a mechanism of regeneration is congruent with a) our observations of poor dispersal in the majority of dipterocarp species (Chapters two and three); b) of high density carpets of seedlings in species with high wing areas to fruit mass (Maycock et al. 2005); c) no relationship between seed dispersal or wood density and species spatial aggregation patterns (Chapter four); and d) the high intensity and frequent expression of fine-scale genetic structuring within dipterocarp populations (Chapter five).

Sustainable management of lowland dipterocarp forest

In addition, this series of observations on the natural regeneration of the Dipterocarpaceae is pertinent to sustainable management of lowland mixed-dipterocarp forests. Dipterocarp seedlings are shade-tolerant, with new adults entering the canopy layer recruiting from already established individuals in the abundant seedling or pole sized cohorts during gap canopy creation (Nicholson 1958, Brown and Whitmore 1992, Brown 1993, Brown et al. 1999), for example during wind-throw events. Management systems which remove the commercially valuable timber crop with minimal damage to the seedling bank and 'advanced regeneration' in the forest understory will in effective simulate the creation of canopy gaps and stimulate natural regeneration. Such an approach is taken by the Malayan Uniform System (MUS) (Wyatt-Smith 1963), which was introduced in 1948 (Appanah 1998) following the post-war observation that mixed-dipterocarp forests in which all mature trees had been harvested had substantial and adequate regeneration without human assistance (Wyatt-Smith 1963, Appanah 1998). The MUS, considered the only sustainable silvicultural method in tropical rain forests (P. Ashton, *pers. comm*) (for timber production but emphatically not conserving the full diversity of the community), prescribes a harvest of all commercial (primarily dipterocarp) trees above 45 cm DBH in lowland mixed-dipterocarp forests (it is not applicable to ridges and higher elevation areas where natural regeneration is patchy and limited), and poison girdling of non-commercial species and defective trees to 5 cm DBH (Wyatt-Smith 1963). Further 'release' treatments followed after 20, 35 and 55 years clear the understory and remove lianas (Wyatt-Smith 1963). This treatment allows the shade-tolerant yet light-demanding, late-successional dipterocarps to regenerate effectively, and generates a more-or-less even aged stand of commercially valuable dipterocarp timber harvestable on a logging rotation of 60–80 years. As regeneration in this system is primarily from established saplings and poles, as in primary forests, pioneer species are precluded and regeneration is not driven by post-disturbance seed fall (Nicholson 1958). In relation to dipterocarp seed dispersal in degraded forests, this suggests that even in areas where the adult cohort has been removed by logging the

species should recover given the large populations of remaining juvenile individuals relative to adult densities (Sist et al. 2003), and again, highlights the previously identified paradox in dipterocarp dispersal: that despite observing significant differences in dispersal potential between species, this appears to play a minor role in natural regeneration which is driven by satiation of post-dispersal seed predators and subsequent competitive interactions between established juveniles at the time of gap creation. Dispersal in this family is likely therefore a mechanism for distributing fruit widely in anticipation of gap creation. In such a system the retention of seed trees is of limited value, as fruit crops are unlikely to satiate seed predators, and thus emphasis must be placed on procedures that minimise damage to the forest understory (Pinard and Putz 1996, Pinard et al. 2000).

Future work

The results of this thesis highlight a range of interesting research avenues and we present a number of possible future studies below.

Non-random fruit abscission and dispersal

Wind dispersed fruit are dependent on high wind velocities, and preferably turbulent conditions for dispersal. Selective pressures for long distance dispersal should therefore generate active or passive mechanisms that allow for the release of fruit during wind speeds promoting long distance dispersal, as has been observed in a number of species (Bohrer et al. 2008, Soons and Bullock 2008, Greene and Quesada 2011, Maurer et al. 2013). Does abscission of dipterocarp fruit occur at higher wind speeds or during updrafts to increase the probability of dispersal? If so, what are the implications for the seed dispersal kernels presented and the potential for long distance dispersal in this family? Are there positive correlations between inverse wing loading and thresholds of fruit abscission?

Parameterizing models of fragment connectivity and migration rates

One of the most important results of this thesis is that both the dispersal distance and terminal velocity of dipterocarp fruit can be predicted based on fruit morphology (Chapters two and three). This has allowed us to predict the terminal velocity of all Dipterocarpaceae in the Malesia region from the fruit dimensions contained within Ashton (1983). This data is of applied use in parameterizing models of fragment connectivity in the fragmented agricultural landscapes of Southeast Asia (Hanski and Gilpin 1991, Hanski and Ovaskainen 2000, Tackenberg 2003, McEuen and Curran 2004, Bohrer et al. 2005, Montoya et al. 2008, McConkey et al. 2012). Fruit terminal velocity is a vital parameter in modeling long distance dispersal using mechanistic models, which additionally incorporate the effects of height

of diaspora release, wind speed and turbulence, and the effect of surrounding vegetation (Tackenberg 2003, Nathan et al. 2011, Thomson et al. 2011, Tamme et al. 2014). Combined with high resolution climate data and forest cover maps generated using remote sensing technologies (Asner and Martin 2012, Asner et al. 2012, Hansen et al. 2013, Scriven et al. 2015) our data will allow simulation models to determine rates of seed movement across the fragmented landscapes. Such models are necessary to identify those species with no or limited potential for connectivity and gene flow between fragments, and between fragments and large contiguous protected areas, relevant to climate driven range shifts (Colwell et al. 2008, Corlett 2011). Similar studies have been conducted on butterflies in Borneo (Scriven et al. 2015). The maximum rate of tree migration is determined by the maximum long distance dispersal event per generation. Coupled to data on growth rates, size at maturity and age of first reproductive event, our data on fruit terminal velocities can be used to estimate the rate of migration for each species (Corlett 2009).

Modeling changes in community composition over time

Remote sensing techniques have become increasing accessible to ecologists in the past two decades, and can be used to map forest topography and canopy height in addition to many chemical properties of the forest canopy (Asner and Martin 2012, Asner et al. 2012). Such projects have been recently completed in both Sepilok and Danum, the field sites used in this thesis (Tan et al. *submitted*). From these studies canopy gaps can be identified due to their low canopy height. Combining data available from forest inventoried plots (Tree species identification, diameter at breast height, latitudinal and longitudinal coordinates) with fruit dispersal models presented in this thesis we can generate high resolution seed shadow maps, allowing for quantitative predictions on how many seed from which species will arrive at each canopy gap. These predictions can be ground-truthed, to compare predicted versus observed dispersal. More challenging but rewarding is to integrate recent results of studies on dipterocarp growth and mortality rates under different light regimes (Philipson et al. 2012, Philipson et al. 2014), soils substrates (Dent and Burslem 2009, Born et al. 2014) and micro-topographic sites (Born et al. 2015) to model which seed will succeed in the newly created gap. Similarly such data can be used to parameterize existing simulation models of forest growth, for example the FORMIX3 model of Huth and Ditzer (2000), to simulation potential changes in forest composition over successive generations.

Pollen dispersal in fragmented landscapes

In combination with models of connectivity via seed dispersal, it is important to understand the dynamics of pollen dispersal in fragmented, human-dominated landscapes, as pollen dispersal can maintain gene flow between fragments in the absence of seed dispersal (Kramer et al. 2008). Pollen dispersal distances are frequently higher than seed dispersal distances (Dick et al. 2008), as is observed in the Dipterocarpaceae (Kettle et al. 2011b). Mean pollen dispersal distances in the Dipterocarpaceae within contiguous forest ranges between 100–500 m depending on the identity of the pollinator (Kettle et al. 2011b, Kettle et al. 2011c). Pollen dispersal might therefore buffer small remnant dipterocarp populations from the rapid loss of genetic diversity via drift and inbreeding. The Asian giant honey bee (*apis dorsata*), which pollinates some larger flowered dipterocarps, is able to migrate long distances and could potentially disperse pollen between fragments. Small insects can be carried great distances by the wind (Harrison 2003, Ahmed et al. 2009), and thus small flowered dipterocarp species could potentially maintain high rates of gene flow between fragments. For example, in a highly fragmented agricultural landscape in the Western Ghats, long distance pollen dispersal between fragments with small, remnant tree populations has been observed at scales of ~5 km or greater (Ismail et al. 2012).

Dispersal and spatial aggregation patterns

In Chapter four we observed no correlation between seed dispersal or wood density and the spatial aggregation patterns of mature adult dipterocarps. A natural extension to Chapter four would be to expand the study to include dipterocarps from a number of other forest dynamic plots in the Malesia region, for example the 50 ha CTFS-ForestGEO plots located in Danum Valley, Lambir Hills and Pasoh Forest Reserve. The greater statistical power generated by including a larger number of species should increase the precision of model results and help elucidate any influence of seed dispersal and wood density on spatial aggregation patterns in the Dipterocarpaceae. An added benefit of such an approach is that spatial aggregation in both juvenile and adult cohorts could be analysed, which might better elucidate the role of dispersal limitation in patterns of fine-scale spatial aggregation, and confirm the generality of NDD mortality at the seedling stage (Harms et al. 2000, Bagchi et al. 2011).

The consistency of FSGS between sites

Our results from Chapter five indicate that habitat is an important factor shaping local patterns of fine-scale genetic structure in tropical trees, and we concluded that patterns of FSGS must be viewed on a species-by-site basis given that we did not observe consistent patterns of FSGS across the three focal

species. Nevertheless, our study is only an initial indication as it was restricted to three species and additionally was not fully factorial as the three comparison populations to Danum came from different sites varying in their heterogeneity. However, *S. leprosula* and *S. parvifolia* are both present in all four of the plots used in the study (Danum Sepilok, Pasoh and Lambir Hills) (and there is substantial overlap in other dipterocarp species too) and therefore we could rapidly build upon this initial study by sampling and genotyping both of these species at each of the four sites. As mentioned in Chapter four, future analyses should also reduce the diameter size threshold for inclusion in studies from 30 cm DBH to 20 cm DBH, to increase the number of individuals per plot and therefore the precision of the estimates of genetic relatedness.

Habitat effects on individual tree fitness

Chapter four used point process models to fit cubic splines to tree locations, using elevation as a covariate, to predict intensity surfaces for each species. These predicted surface intensities served well as surrogate habitat association maps, as confirmed via their consistency with the species habitat associations observed by Margrove et al. (2015). Plotting the location of individual trees from each species on their respective density surface can identify individuals located in positions at the edge of their associated habitats; *i.e.* in positions they are less well adapted too. Census data through time might allow us to analyse the relative effect of positioning on a less suitable substrate or at the edge habitats for each species on individual tree performance, and in particular growth, mortality and fecundity (fruit production).

The relationship between seed dispersal potential and fruiting phenology

General flowering events and the mast fruitings that follow vary in their intensity, with infrequent 'major' events interspersed with 'minor' events in which a lower percentage of species and individuals participate (Maycock et al. 2005, Sun et al. 2007). In Chapter four we observed that species aggregation patterns were not correlated with wood density or seed dispersal. This was despite an expectation that low seed mass, high dispersing species with low wood densities should be at a competitive disadvantage to larger, poorer dispersing fruit when establishing in the forest understory and thus should preferentially disperse and establish in canopy gaps reducing spatial aggregation. Yet significant differences in wood density and seedling shade tolerance are observed in the Dipterocarpaceae, with some species markedly more light demanding (Whitmore and Brown 1996). However, if recruitment to maturity is dependent on their persistence in the shaded forest understory until gap creation, less shade-tolerant species are likely to be filtered out much more rapidly than the

seedlings of more shade-tolerant species due to their higher mortality rate (Philipson et al. 2014). As canopy gaps are extremely patchily distributed both spatially and temporally less shade-tolerant species might overcome this limitation by fruiting more frequently, in 'minor' events, thereby distributing seed widely in the forest understory in preparation for gap formation.

Competition–colonization trade-off

Previous research has observed no correlation between seed mass and wood density in the Dipterocarpaceae (Philipson et al. 2014). However seed mass is a less accurate measure of dispersal potential than either fruit inverse wing-loading (Chapter two) or terminal velocity (Chapter three). Additionally, we observed significant differences in seed dispersal potential based on fruit morphology, which implies that dispersal is an important process in the regeneration of many species. Given that all Bornean dipterocarps are shade-tolerant to a lesser or greater extent (Swaine and Whitmore 1988, Whitmore 1989), and that their fruit cannot tolerate desiccation (Tompsett 1985, Tompsett 1998), this is likely related not to dispersal to recently formed canopy gaps but rather an adaptation to disperse fruit widely, thereby increasing the probability that some small proportion of fruit receive high light conditions following the subsequent creation of a canopy gap. Further research should therefore investigate whether a trade-off between dispersal ability and wood density and/or growth rate is observed in this family.

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APPENDIX: ARCHIVED DATA

All data collected and analysed in this thesis are stored in the Ecosystem Management Group's Archived Data folder on the public server, found at the following location:

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