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Understanding local patterns of genetic diversity in dipterocarps using a multi-site, multi-species approach: Implications for forest management and restoration

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ABSTRACT

The lowland tropical forests of Southeast Asia are dominated by a single family of canopy and emergent trees, the Dipterocarpaceae. The seeds of dipterocarps are gravity or gyration dispersed. Short distance and limited seed dispersal via these mechanisms result in the aggregation of related individuals and strong fine-scale spatial genetic structure (FSGS). In logged and fragmented forests, where gene flow may be disrupted, tree species with strong FSGS are predicted to exhibit increased inbreeding, which consequently can erode genetic diversity, fitness and might limit the potential for natural regeneration of dipterocarps. Developing a set of indirect operational indicators for FSGS provides a solid basis for informing conservation and management of forest genetic resources in logged forests. Our main objective was to use an information theoretic approach to identify these indicators of FSGS in dipterocarps. We quantify FSGS in 19 dipterocarp species across four forest sites in Malaysian Borneo, India and the Seychelles. We detected FSGS in 15 (79%) of our study species, most of which displayed significant inbreeding. Our results suggest that wood density and flower size offer useful indicators of FSGS. We propose some simple guidelines to allow forest managers to account for FSGS when planning approaches to maintain genetically diverse stands in logged dipterocarp forests. The integration of improved understanding of genetic processes is essential for conserving forest tree genetic resources and ensuring the resilience of logged forests.

1. Introduction

Southeast Asia and especially the island of Borneo includes some of the most diverse forest tree communities in the world (Davies et al., 2003), yet this region has been exposed to suffer among annual rates of forest loss and degradation that are among the highest across the tropics (Sodhi et al., 2010; Miettinen et al., 2011; Gaveau et al., 2014). The lowland forests are dominated by a single tree family, the Dipterocarpaceae, which are the major canopy and emergent species in these forests. Dipterocarps contribute substantially to the global trade in tropical round wood logs, accounting for 80% of timber exports from Southeast Asia and 25% of global consumption of tropical hardwoods in 2006 and 2007 (ITTO, 2008). To achieve sustainable tropical forest management requires a detailed understanding of both the ecological and genetic processes that underpin natural regeneration. Our understanding of local patterns of genetic diversity and especially fine scale spatial genetic structure (FSGS, as the spatial distribution of genotypes) and mating system in dipterocarps remain poorly resolved, despite the importance of these factors for mitigating the negative genetic consequences of selective logging and habitat fragmentation (Kettle et al., 2012; Jalonen et al., 2014).

Many factors including seed dispersal, pollen flow and mating system together shape fine-scale spatial genetic structure (FSGS) in tropical trees (Vekemans and Hardy, 2004). The dipterocarps

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are typified by their winged fruits or "nuts" with zero to five wings, and are generally poorly dispersed by gravity or gyration (Suzuki and Ashton, 1996). This limited seed dispersal coupled with restricted pollen dispersal by small insects is likely to create conditions for high FSGS in many dipterocarp species. Variations in the functional morphology of fruits, coupled with canopy height and local topography, may lead to differential dispersal potential across species (Seidler and Plotkin, 2006), and hence variation in the intensity and scale of FSGS is expected across species. Secondary seed dispersal is unlikely to play a significant role in species dispersal as dipterocarp seeds are highly recalcitrant and germinate rapidly after reaching the forest floor (Li and Pritchard, 2009).

Dipterocarps are insect pollinated and different species display a variation of flower size that is correlated with pollinator body sizes. On the other hand, species with tiny flowers are predominately pollinated by thrips, while those with larger flowers may be pollinated by large and mobile bees such as *Apis dorsata* (Appanah, 1985; Kettle et al., 2011b). Empirical research has confirmed that flower size is a good predictor of pollinator size in dipterocarps and has suggested that the smaller pollinators of species are less mobile and results in shorter average pollen dispersal (Kettle et al., 2011b). These patterns suggest that smaller flower size may be a predictor of greater FSGS across dipterocarp species (Kettle et al., 2011a).

Mating systems are highly variable across dipterocarps, which include species that display high proportion of selfed progeny, species with a mixed mating strategy, and species that are almost exclusively outcrossed (self-incompatible). Plant genetic theory predicts that species that are predominately outcrossed will be more vulnerable to restricted gene flow, and consequently inbreeding, because deleterious recessive genes have not been purged, as would be the case with highly selfing species (Charlesworth and Charlesworth, 1987; Aguilar et al., 2006). Thus species that have high FSGS and are highly outcrossed might be expected to be more vulnerable to logging and fragmentation than species which are highly selfed (Finger et al., 2012). Comparing inbreeding (coefficients) between seedlings and adults is thus useful, as it provides insights into how the mating system and selection against inbred individuals within dipterocarp species may influence patterns of genetic diversity at different ontogenetic stages.

As forests become fragmented, either by conversion or logging, trees may become reproductively isolated within smaller habitat patches (Vekemans and Hardy, 2004; Ghazoul, 2005; Dick et al., 2008; Kramer et al., 2008). Increased mating between related individuals has been shown to reduce fitness in some tropical tree species (Stacy, 2001; Reed and Frankham, 2003; Breed et al., 2012; Ismail et al., 2014). Studies have previously examined the patterns of FSGS in individual species of dipterocarps at single sites (Takeuchi et al., 2004; Ng et al., 2004, 2006), individual species sampled from multiple sites (Finger et al., 2012; Ismail et al., 2014) and multiple species at a single site (Kettle et al., 2011a; Harata et al., 2012). We currently, however, lack a detailed comparative study to understand patterns across species and sites which would enable generalizations of the implication of FSGS for the management of dipterocarp trees in the context of logging and habitat restoration (Jennings et al., 2001; Jalonen et al., 2014).

In this paper we provide a comparative evaluation of patterns of FSGS among multiple species of dipterocarps sampled across multiple sites in Borneo, in India and in the Seychelles (Table 1, Fig. 1). The particular strength and novelty of this study is that we compare complete data sets (spatial and molecular data) of the intensity of FSGS among 19 dipterocarp species in a single analysis. This enables us to account for spatial scale, molecular marker variation, and clustering of individual trees, which are all important variables for patterns of FSGS. Specifically, we compare levels of genetic diversity and patterns of inbreeding across all 19 species, intensity of FSGS indicated by the *Sp*-statistics and scales over which this is significant. In 10 of the species we compare these metrics between adult and seedling stages. The study species represent a wide range of flower sizes, population densities, life history traits, and fruit morphologies. Using this comparative approach across species

Table 1
Study sites of our study species. Numbers of trees sampled (N); Number of loci (Loci); Study sites; Publications references. New data*: new unpublished data from adults and seedlings of four species (*S. accuminatissima*, *S. argentifolia*, *S. gibbosa* and *S. smithiana*) and new seedlings data from three species (*D. grandiflorus*, *P. tomentella* and *S. xanthophylla*).

Species	N	Loci	Study site	Publications
Dipterocarpus crinitus	23	7	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Dipterocarpus globulus	289	6	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Dryobalanops aromatica	375	10	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Dryobalanops lanceolata	26	10	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea acuta	144	7	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea amplexicaulis	27	10	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea beccariana	115	10	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea curtisii	50	16	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea ovata	36	7	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Shorea parvifolia	42	9	Lambir National Park, Sarawak, Borneo	Harata et al. (2012)
Dipterocarpus grandiflorus	192	6	Sepilok Forest Reserve, Sabah, Borneo	Kettle et al. (2011a)
Seedlings	96			New data*
Parashorea tomentella	177	6	Sepilok Forest Reserve, Sabah, Borneo	Kettle et al. (2011a)
Seedlings	95			New data*
Shorea accuminatissima	91	8	Sepilok Forest Reserve, Sabah, Borneo	New data*
Seedlings	713			New data*
Shorea argentifolia	77	8	Sepilok Forest Reserve, Sabah, Borneo	New data*
Seedlings	735			New data*
Shorea gibbosa	97	10	Sepilok Forest Reserve, Sabah, Borneo	New data*
Seedlings	731			New data*
Shorea smithiana	339	8	Sepilok Forest Reserve, Sabah, Borneo	New data*
Seedlings	617			New data*
Shorea xanthophylla	170	6	Sepilok Forest Reserve, Sabah, Borneo	Kettle et al. (2011a)
Seedlings	96			New data*
Vateria indica	240	12	Western Ghat, Kodagu, India	Ismail et al. (2014)
Seedlings	236			Ismail et al. (2014)
Vateriopsis seychellarum	116	10	Seychelles archipelago	Finger et al. (2012)
Seedlings	317			Finger et al. (2012)

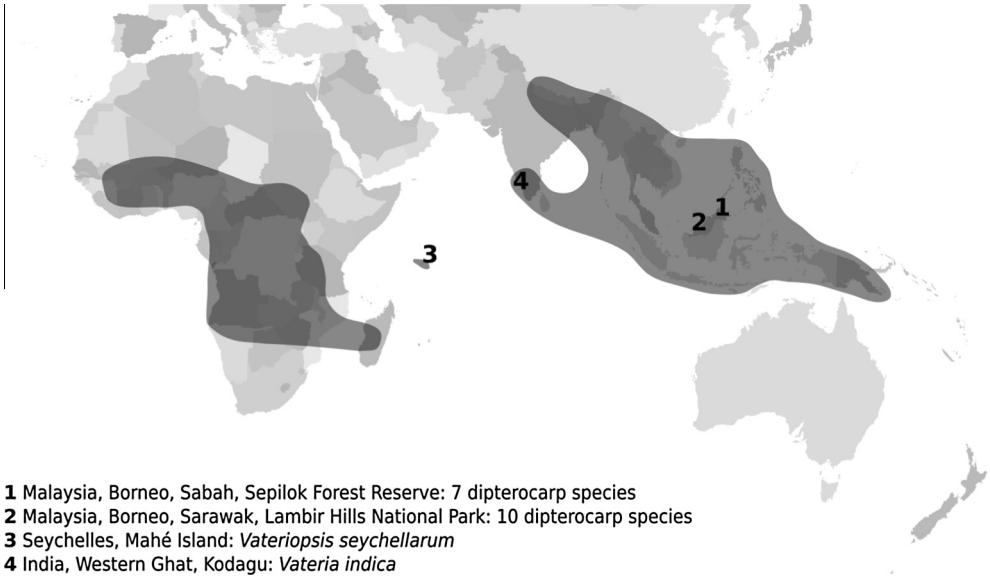

Fig. 1. Localization of the study sites. In grey is shown the geographical range of Dipterocarpaceae family excluding the South American subfamily Pakaraimoideae.

and sites, we test the following hypotheses. (A) Flower size (proxy for pollen dispersal) is presented as an observable indirect factor inversely correlated with FSGS intensity and scale. Large flowers attract large and more mobile pollinators, which are predicted to undermine FSGS. (B) Adult tree density is inversely correlated with FSGS intensity and scale. A large number of pollen donors and large seed shadow is predicted to decrease FSGS. Additionally, species which are highly clumped (mean clump radius variable) are expected to exhibit FSGS over short distances. (C) Inverse wing loading (mean total wing area divided by mean total fruit weight, which is a proxy for seed dispersal) is inversely correlated with FSGS intensity and scale. We expect species with large inverse wing loading (IWL) to have greater seed dispersal and thus to exhibit less intense FSGS. Finally (D) Wood density is inversely correlated to FSGS patterns. We predict that species with high wood density values exhibit weaker FSGS than species with low wood density. Wood density is a predictor of growth rates among tropical trees and correlated to variation among species in regeneration across light environments (King et al., 2005, 2006; Kraft et al., 2010). Species that persist and grow slowly in shaded understory environments may display reduced population level synchronicity in recruitment than fast growing species that are dependent on spatially isolated gaps for recruitment (Kettle et al., 2011a). Ultimately, we use this comparative approach to develop feasible and operational guidelines for forest managers to account for the vulnerability of dipterocarp species to genetic erosion and inbreeding as a consequence of strong FSGS. Adopting practices which include a better understanding of these processes is relevant for the long term conservation and management of forest in Southeast Asia.

2. Material and methods

Genetic and spatial coordinates data analyzed in this study combines previously published datasets on 15 species (Kettle et al., 2011a; Finger et al., 2012; Harata et al., 2012; Ismail et al., 2014) and new data from adults and seedlings (young plants, less than 10 cm height) of four species (*Shorea accuminatissima*, *Shorea argentifolia*, *Shorea gibbosa* and *Shorea smithiana*) and genotypes for seedlings from three species (*Dipterocarpus grandiflorus*, *Parashorea tomentella* and *Shorea xanthophylla*), all sampled in Sepilok Forest Reserve Sabah. Previously published data are clearly indicated in Table 1.

Study sites: In total, we combine spatial and molecular data from 19 dipterocarp species located across four sites in three countries (Table 1, Fig. 1). Seventeen species were sampled in two protected forest sites in Borneo: seven in Sepilok Forest Reserve in east Sabah, and ten species in Lambir Hills National Park in Sarawak. Another species, *Vateria indica*, was sampled from Kodagu district, Karnataka State, India. Finally, we include *Vateriopsis seychellarum*, an endemic to Mahé island, Seychelles. In contrast to the Bornean sites, tree populations from India and Seychelles were sampled in fragmented forest patches rather than in continuous forest.

Study species: The 19 species encompass six genera, including 11 *Shorea*, one *Parashorea*, three *Dipterocarpus,* two *Dryobalanops*, one *Vateria* and one *Vateriopsis* (Table 1). All study species have hermaphrodite insect pollinated flowers and gravity or gyration dispersed seeds. The species differ in their seed dispersal potential, defined by inverse wing loading, (IWL): mean total wing area divided by mean fruit weight, (Augspurger, 1986; Osada et al., 2001; Smith et al., 2015), flower size as a surrogate of pollinator size and pollen dispersal (Newman et al., 1996, 1998; Ashton, 2004), population density (Kettle et al., 2011a; Finger et al., 2012; Ismail et al., 2014), wood density (Chave et al., 2009; Zanne et al., 2009) and spatial patterns (Table 2, Tables S2 and S3). Further details of the field locations and species traits are available in the Supplementary information.

DNA sampling, extraction and genotyping: All trees were mapped with a GPS (Garmin 60CSx, accuracy of five meters). Cambium (adult trees) or leaf tissues (seedlings) were collected from each tree or seedling for genetic analysis (see original papers for details). For the new collections of seedlings in Sepilok Forest Reserve (*S. accuminatissima*, *S. argentifolia*, *S. gibbosa* and *S. smithiana*) we used two different sampling strategies. In the first method we sampled 10 seedlings in each distance classes (0–5 m/10–15 m/20–25 m/30–35 m) along transects extending from each of six mother trees yielding 40 seedling sampled per mother tree and 240 seedlings overall. In the second method, we randomly sampled 25 seedlings within a 10 m radius of each 20 mother trees. Seedlings of *S. xanthophylla*, *P. tomentella* and *D. grandiflorus* seedlings were sampled randomly around mother trees.

Across all studies, each individual tree or seedling was genotyped at a minimum of six nuclear microsatellite loci (Table S1). We collected new adults and seedlings genetic data for seven Shorea species. All tissues were lyophilized with silica gel before storage at −25 °C. Before extraction all tissues were ground into

Table 2
Descriptions of species traits. Number of trees sampled (N); Density of tree per hectare (D^{ha})[1]; Number of loci genotyped (Loci); Flower sizes (FS, L = large, M = medium, S = small)[2]; Inverse Wing loading (IWL, $cm^2\ g^{-1}$)[3]; Wood density ($g\ cm^{-2}$)[4]; Mean clump radius (m).

Species	N	Loci	D^{ha}	FS	IWL	Wood density	Mean clump radius (m)
Dipterocarpus crinitus	23	7	0.46	M	13.20	0.745	18.50
Dipterocarpus globulus	289	6	7.4	L	3.50	0.700	122.40
Dryobalanops aromatica	375	10	7.62	M	6.60	0.620	106.20
Dryobalanops lanceolata	26	10	0.5	L	5.90	0.620	45.00
Shorea acuta	144	7	3.69	M	8.40	NA	186.70
Shorea amplexicaulis	27	10	0.56	L	6.40	0.440	29.30
Shorea beccariana	115	10	2.92	M	4.20	0.470	53.70
Shorea curtisii	50	16	1	S	13.50	0.527	19.80
Shorea ovata	36	7	0.75	S	20.00	0.640	20.00
Shorea parvifolia	42	9	0.84	S	23.80	0.405	248.60
Dipterocarpus grandiflorus	192	6	1.4	L	3.50	0.670	62.85
Parashorea tomentella	177	6	5.48	L	9.42	NA	99.53
Shorea accuminatissima	91	8	0.63	S	17.37	0.390	132.78
Shorea argentifolia	77	8	0.5	S	44.60	0.520	97.76
Shorea gibbosa	97	10	0.63	S	11.53	0.450	95.26
Shorea smithiana	339	8	2.2	L	20.95	0.355	100.49
Shorea xanthophylla	170	6	1.63	S	0.00	0.520	41.29
Vateria indica	240	12	NA	L	0.00	NA	25.56
Vateriopsis seychellarum	116	10	NA	L	0.00	NA	134.12

[1] Density of trees: Kettle et al., 2011a; Finger et al., 2012; Ismail et al., 2014.
[2] Flower sizes: Newman et al., 1996; Ashton, 2004,
[3] IWL: Ausperger 1986, Osada et al., 2001; Smith et al., in preparation.
[4] Wood densities: Chave et al., 2009; Zanne et al., 2009.

a fine powder using a Qiagen Mixer-mill™. All cambium samples were extracted with a CTAB method (Sambrook et al., 1989). *Shorea accuminatissima*, *S. argentifolia* and *S. smithiana* individuals were genotyped using eight microsatellites (Ujino et al., 1998; Kettle et al., 2011a; Lee et al., 2004). For *S. gibbosa,* the genotyping was conducted using 10 nuclear microsatellites (Lee et al., 2004; Kettle et al., 2011a). PCR fragment analysis was carried out on an ABI3730 capillary sequencer (Applied Biosystems) and scored relative to a LIZ 500 size standard with GeneMapper v.4.0 software (Applied Biosystems). See Supplementary information and previously published work (Kettle et al., 2011a; Finger et al., 2012; Harata et al., 2012; Ismail et al., 2014) for further details.

2.1. Analysing genetic diversity and inbreeding

Genetic diversity analysis of all species was conducted *de novo* using the raw genotype data. We reanalyzed all genotypic datasets to ensure comparability of allelic richness information between species. Moreover, this *de novo* analysis allowed us to use the same distance classes in the FSGS analysis to compare sites and species. Descriptive statistics at the multi-locus level for each species including number of alleles (A), observed heterozygosity (Ho) and expected heterozygosity (He) were calculated separately using Genalex 6.4 (Peakall and Smouse, 2006). Allelic richness (Rt, following Mousadik and Petit, 1996) and inbreeding coefficient (F_{IS}) were generated with FSTAT 2.9.3.2 (Goudet, 1995). The frequencies of null alleles were calculated with Genepop 4.2.1 (Raymond and Rousset, 1995) (Table S1, Table 3). For species with a mixed mating system ($F_{IS} > 0.15$; Table 3), following Allard and Adams (1969), we calculated the selfing rate (s) for each species, $s = (2F_{IS})/(1 + F_{IS})$. In all species microsatellite loci had high levels of polymorphism, thus ensuring comparability (Table S1).

2.2. Characterisation of intensity and the scale of fine scale genetic structure

Within species: Two analyses were performed to investigate fine scale spatial genetic structure. Spatial autocorrelation between pairs of samples at different distance classes using the relatedness coefficient (r) was calculated with Genalex 6.4 (Peakall and Smouse, 2006) and using the kinship coefficient (F) (Loiselle et al., 1995) calculated with Spagedi 1.4 (Hardy and Vekemans, 2002). Eleven distance classes up to 2400 m were used. Within the first 100 m we defined four intervals of 25 m; between 100 m and 300 m we defined four intervals of 50 m; and from 300 m we doubled the intervals until 2400 m.

Among species: To compare the intensity of FSGS among species we calculated $Sp = -b_F/(1 - F_{(1)})$ where b_F is the regression slope of the kinship coefficient and $F_{(1)}$ is the mean kinship coefficient between individuals for the first distance class following Vekemans and Hardy (2004). For each species the scale of FSGS was defined by the maximum distance (*DistF*) at which the kinship coefficient is (F) differed significantly from zero. From the relatedness coefficient (r) calculated with Genalex 6.4 (Peakall and Smouse, 2006) we only included in Table 4 "ω" the multi class criterion for the null hypothesis $r = 0$. This non-parametric test is used to detect significant FSGS patterns among species. We applied a sequential Bonferroni correction following Rice (1989), subsequently p-values were considered significant only if they were less than 0.001 (Banks and Peakall, 2012).

2.3. Spatial distribution pattern and clustering of adult trees within species

Ripley's K function and a Poisson Cluster model (Diggle, 2013) were used to determine the degree of spatial aggregation of each species. Ripley's K function describes the expected number of trees within a specified distance of an arbitrary point divided by the overall tree density (Ripley, 1976; Rowlingson and Diggle, 1993). The estimates of $K(d)$ are defined as $K(d) = n^{-2}A\sum\sum_{i\neq j} w_{ij^{-1}} I_d(u_{ij})$, where n is the number of trees in the plot, A is the area in m^2, I_d is a counter variable, u_{ij} is the distance between 2 trees i and j and $w_{ij^{-1}}$ is an edge corrector estimate. In Figs. S1–S4 we represent $K(d)$ against d with 95% intervals estimated by 100 randomizations. All calculations were performed with the *R* package "splancs" (Rowlingson and Diggle, 1993). The Poisson cluster model randomly locates the cluster center and place trees according to a two dimensional Gaussian distribution. This model has three parameters: ρ (density of clusters), m the mean number of trees in a cluster and $2\sigma^2$ the mean squared distance from a tree to

Table 3
Summary of genetic diversity parameters and inbreeding coefficients, ± indicates the standard error (± stderr); number of samples (N); number of loci (Loci); mean number of alleles (A); allelic richness (Rt); observed heterozygosity (Ho); expected heterozygosity (He); inbreeding coefficients (Fis) and significance; selfing rates (*s*, following Allard and Adams, 1969 for species with Fis > 0.15).

Species	Life stage	N	Loci	A (±stderr)	Rt	Ho (±stderr)	He (±stderr)	Fis		*s*
Dipterocarpus crinitus	Adults	23	7	6.57 ± 1.288	6.57	0.689 ± 0.082	0.673 ± 0.076	−0.002	NS	
Dipterocarpus globulus	Adults	289	6	28.66 ± 4.688	28.67	0.798 ± 0.048	0.843 ± 0.043	0.056	**	
Dryobalanops aromatica	Adults	375	10	14.50 ± 3.603	14.50	0.589 ± 0.065	0.640 ± 0.069	0.081	**	
Dryobalanops lanceolata	Adults	26	10	6.75 ± 1.114	6.75	0.591 ± 0.071	0.601 ± 0.067	0.036	NS	
Shorea amplexicaulis	Adults	27	10	11.50 ± 1.500	11.50	0.589 ± 0.069	0.739 ± 0.065	0.221	**	0.36
Shorea acuta	Adults	144	7	14.14 ± 2.219	14.14	0.772 ± 0.043	0.806 ± 0.045	0.046	**	
Shorea beccariana	Adults	115	10	18.00 ± 2.255	18.00	0.660 ± 0.055	0.792 ± 0.055	0.170	**	0.29
Shorea curtisii	Adults	50	16	5.06 ± 0.628	5.06	0.545 ± 0.056	0.521 ± 0.054	−0.035	NS	
Shorea ovata	Adults	36	7	10.43 ± 1.288	10.43	0.794 ± 0.048	0.774 ± 0.051	−0.011	NS	
Shorea parviflora	Adults	42	9	15.00 ± 2.661	15.00	0.749 ± 0.045	0.819 ± 0.032	−0.011	**	
Dipterocarpus grandiflorus	Adults	192	6	15.83 ± 1.470	15.11	0.635 ± 0.028	0.683 ± 0.049	0.074	**	
	Seedlings	96		10.83 ± 0.654		0.587 ± 0.078	0.686 ± 0.038	0.153	**	
Parashorea tomentella	Adults	214	6	11.00 ± 1.983	10.68	0.572 ± 0.072	0.606 ± 0.092	0.059	**	
	Seedlings	95		5.83 ± 0.945		0.426 ± 0.092	0.553 ± 0.074	0.234	**	
Shorea accuminatissima	Adults	90	8	6.12 ± 0.990	6.70	0.375 ± 0.086	0.440 ± 0.086	0.153	**	0.27
	Seedlings	713		8.37 ± 1.487		0.358 ± 0.073	0.479 ± 0.067	0.254	**	
Shorea argentifolia	Adults	77	8	7.37 ± 1.322	6.95	0.638 ± 0.103	0.686 ± 0.05	0.080	**	
	Seedlings	735		8.87 ± 1.684		0.698 ± 0.094	0.702 ± 0.048	0.006	NS	
Shorea gibbosa	Adults	97	10	8.10 ± 1.169	7.66	0.442 ± 0.057	0.638 ± 0.052	0.318	**	0.48
	Seedlings	731		10.50 ± 1.600		0.416 ± 0.047	0.606 ± 0.052	0.315	**	
Shorea smithiana	Adults	339	8	11.75 ± 1.346	9.01	0.629 ± 0.059	0.692 ± 0.031	0.094	**	
	Seedlings	617		11.62 ± 1.413		0.588 ± 0.059	0.666 ± 0.038	0.119	**	
Shorea xanthophylla	Adults	170	6	8.83 ± 1.536	8.07	0.616 ± 0.066	0.659 ± 0.059	0.069	*	
	Seedlings	96		6.67 ± 1.429		0.436 ± 0.099	0.505 ± 0.114	0.142	**	
Vateriopsis seychellarum	Adults	116	12	4.22 ± 0.236	12.28	0.621 ± 0.031	0.561 ± 0.022	0.346	**	0.51
	Seedlings	317		10.90 ± 1.224		0.466 ± 0.041	0.772 ± 0.050	0.397	**	
Vateria indica	Adults	240	10	6.87 ± 0.515	8.48	0.608 ± 0.039	0.633 ± 0.034	0.044	**	
	Seedlings			6.87 ± 0.501		0.613 ± 0.034	0.655 ± 0.030	0.067	*	

** *p*-value < 0.01, * *p*-value < 0.05, NS non-significant.

Table 4
Summary table of statistics for fine-scale genetic structure (FSGS) including: sample size (N); F1, average pairwise kinship coefficient and its standard error (± stderr) among individuals in the shortest distance class (0–25 m); *DistF*, geographic distance (meters) up to which (F) significantly deviates from zero; bLd, slope of regression of the pairwise kinship coefficient (F) on ln(diJ), the natural logarithm of the geographic distance between pairs of individuals, and its standard error (±stderr); ω multi-class test criterion for null hypothesis $r = 0$.$^{***}p < 0.001$ and Sp (±stderr, standard error); intensity of FSGS, following Vekemans and Hardy (2004): $Sp = -\text{bLd}/(1 - \text{F1})$.

Species	*N*	*F*1 (±stder)	DistF (m)	bLd (±stderr)	ω		Sp (±stderr)
Dipterocarpus crinitus	23	0.083 ± 0.058	200	−0.024 ± 0.009	41.398	NS	
Diptericarpus globulus	289	0.069 ± 0.014	75	−0.006 ± 0.001	86.257	***	0.007 ± 0.001
Dryobalanops aromatica	375	0.067 ± 0.006	200	−0.009 ± 0.001	113.361	***	0.010 ± 0.002
Dryobalanops lanceolata	26	0.066 ± 0.023	50	−0.015 ± 0.005	39.980	NS	
Shorea amplexicaulis	27	0.021 ± 0.037	50	−0.001 ± 0.005	24.253	NS	
Shorea acuta	144	0.094 ± 0.007	200	−0.013 ± 0.002	69.781	***	0.015 ± 0.002
Shorea beccariana	115	0.083 ± 0.019	300	−0.017 ± 0.004	107.571	***	0.019 ± 0.004
Shorea curtisii	50	0.075 ± 0.010	250	−0.024 ± 0.004	85.768	***	0.026 ± 0.005
Shorea ovata	36	0.179 ± 0.012	200	−0.043 ± 0.004	86.263	***	0.052 ± 0.005
Shorea parviflora	42	−0.001 ± 0.039	25	−0.010 ± 0.004	4.445	NS	
Dipterocarpus grandiflorus	192	0.020 ± 0.006	100	−0.002 ± 0.001	51.239	***	0.002 ± 0.001
Parashorea tomentella	214	0.051 ± 0.023	300	−0.012 ± 0.003	110.798	***	0.013 ± 0.003
Shorea accuminatissima	90	0.000 ± 0.033	100	−0.015 ± 0.007	89.999	***	0.015 ± 0.007
Shorea argentifolia	77	0.142 ± 0.050	100	−0.026 ± 0.011	72.128	***	0.030 ± 0.013
Shorea gibbosa	97	0.053 ± 0.027	50	−0.007 ± 0.003	63.261	***	0.007 ± 0.003
Shorea smithiana	339	0.067 ± 0.016	300	−0.012 ± 0.002	111.058	***	0.012 ± 0.002
Shorea xanthophylla	170	0.052 ± 0.011	100	−0.006 ± 0.001	123.797	***	0.007 ± 0.002
Vateriposis seychellarum	116	0.187 ± 0.022	1200	−0.033 ± 0.004	94.256	***	0.041 ± 0.005
Vateria indica	240	0.122 ± 0.013	1200	−0.027 ± 0.004	84.517	***	0.031 ± 0.005

the center of the cluster ρ. $2\sigma^2$ can be estimated from the Ripley's K function with the function pcp() of the *R* package "splancs". Finally, we calculated the mean clump radius ($\sigma\sqrt{\pi \div 2}$). All details can be found in the Supplementary information (Figs. S1–S4; Table S2).

2.4. Statistical test of different species traits as indirect indicators of FSGS in dipterocarp populations

We used generalized least square models (GLS) to explore the relative importance of five species traits likely to be important in shaping both the intensity (*Sp*) and scale (*DistF*) of FSGS. The GLS model treated the two responses, intensity (*Sp*) and scale (*DistF*) of FSGS as two correlated measures of spatial metrics modelled simultaneously, with the interaction between these metrics quantified with a correlation coefficient (which can be positive or negative). Both responses were centered (by subtracting their mean) and standardized (by dividing by their standard deviation) prior to fitting the GLS (Pinheiro and Bates, 2000). The uncertainty surrounding estimates of *Sp* and *DistF* varies among species and so the contribution of each species to the model was weighted by the inverse of the standard errors of *Sp*. Using these GLS's, we

assessed the relationships between the traits (flower-size, inverse wing-loading, population density, mean clump radius and wood density; Table 2) and both metrics of FSGS. Models were fitted with each of these traits as a main effect and the correlation between measures of FSGS (i.e. *Sp-statistic* and *DistF*) as the response variable. None of the interactions of traits are significant (except the interaction IWL and mean clump radius) and since we aim here to develop indirect operational indicators, we only presented models fitted with only one trait as main effect. An information theoretic approach based upon Akaike's information criterion (AIC) was applied to identify the best predictors of FSGS. All analyses were performed with *R* 3.1.1 (R Development Core Team, 2008) using the packages 'nlme' (*R* package version 3.1–117; Pinheiro et al., 2015) and 'MuMIn' (*R* package version 1.10.15; Multi-model inference; Barton, 2015). This analysis was conducted on all 19 species including those with and without significant FSGS.

3. Results

3.1. Genetic diversity and inbreeding

Adult populations: Average allelic richness ranged from 4.31 in *Shorea curtisii* to 15.17 in *Dipterocarpus globulus* (Table 3). Across all species gene diversity (*He*) varied from 0.440 (±0.086) in *S. accuminatissima* to 0.843 (±0.055) in *D. globulus*. Within the genus *Shorea,* overall sites, *He* ranged from 0.440 (±0.086) in *S. accuminatissima* to 0.819 in *S. curtisii*. Fourteen of the 19 species exhibited significant inbreeding coefficients (F_{IS}) in adult populations (Table 3). F_{IS} varied from −0.011 in *Shorea parvifolia* to 0.318 in *S. gibbosa*. Inbreeding coefficients of *Dipterocarpus crinitus*, *Dryobalanops lanceolata*, *S. curtisii* and *Shorea ovata* were not significantly different from zero. The selfing rate (s) for each species with a $F_{IS} > 0.15$ varied from 27% of selfing events for *S. accuminatissima* ($s = 0.27$) to 51% in *Va. seychellarum* ($s = 0.51$).

Seedling populations: Gene diversity ranged from 0.479 (±0.067) in *S. accuminatissima* to 0.772 (±0.051) in *Va. seychellarum* (Table 3). In the genus *Shorea*, *He* varied from 0.479 (±0.067) in *S. accuminatissima* to 0.702 (±0.048) in *S. argentifolia*. Six species displayed inbreeding coefficients (F_{IS}) significantly greater in seedlings than within adult populations at the same site (Table 3). F_{IS} ranged from 0.067 in *V. indica* to 0.397 in *Va. seychellarum*. *Shorea gibbosa* seedlings exhibited an equivalent level of inbreeding as the adult populations (0.315). Inbreeding coefficient of *S. argentifolia* was not significantly different to zero.

3.2. Spatial distribution patterns

Thirteen species displayed highly aggregated spatial patterns (Figs. S1–S4; Table S2) as indicated by Ripley-*K* values significantly greater than expected under a random spatial pattern at all scales. *Shorea parvifolia* presented a complete random pattern at small scales (<100 m), and then displayed an aggregated spatial pattern at larger scales. By contrast, four species (*S. ovata*, *S. curtisii*, *D. crinitus* and *Dr. lanceolata*) were aggregated at small scales, but were randomly distributed at larger scales. *Shorea amplexicaulis* was randomly distributed at all scales. The mean clump radius ranged from 18.5 m (*D. crinitus*) to 248.5 m (*S. parvifolia*) (Table S2).

3.3. Fine scale genetic structure

Significant FSGS was detected in 15 of the 19 species (Table 4). *Dipterocarpus crinitus*, *Dr. lanceolata*, *S. amplexicaulis* and *S. parvifolia* showed no significant FSGS (Figs. S1–S3).

Intensity of FSGS: For all 15 species with significant FSGS we calculated the *Sp-statistic* as a measure of the intensity of FSGS. *Sp-statistic* ranged from $Sp = 0.002$ (±0.001) in *D. grandiflorus* to $Sp = 0.052$ (±0.005) in *S. ovata* (Table 4). In *Shorea*, values of the *Sp-statistic* ranged from 0.007 for *S. gibbosa* (±0.003) and *S. xanthophylla* (±0.002) to 0.052 in *S. ovata* (±0.005).

Scale of FSGS: The furthest distance class with a significant kinship coefficient between pairs (*DistF*) varied widely among the species. Over all species, *DistF* ranged from 50 m in *S. gibbosa* to 1200 m in *V. indica* and *Va. seychellarum*. In *Shorea*, *DistF* ranged from 50 m in *S. gibbosa* to 300 m for *S. smithiana* and *Shorea beccariana*. The mean kinship coefficient at the shortest distance class of 0–25 m (*F*) ranged from 0.000 (±0.033) in *S. accuminatissima* to 0.1872 (±0.0219) in *Va. seychellarum*. Within the genus *Shorea*, (*F*) ranged from 0.000 (±0.033) for *S. accuminatissima* to 0.1787 (0.0116) in *S. ovata* (Table 4).

3.4. Factors influencing scale and the intensity of FSGS patterns

Based upon model selection using the information theoretic approach (AIC), wood density offers the most reliable predictor of significant FSGS (AIC = 29.76; *p*-value = 0.0001; intensity increases with wood density; Table 5), followed by flower size (AIC = 66. 24; *p*-value = 0.0001; scale declined with decreasing flower size). Mean clump radius is the third predictor of FSGS patterns (AIC = 83.71; *p*-value = 0.0041; intensity and scale declined with increased mean clump radius), followed by IWL (AIC = 87.90; *p*-value = 0.0007; scale declined with increased inverse wing loading). The relationship between tree density and FSGS was not significant (Table 5).

Wood density has a significant positive impact on the intensity of FSGS but no significant influence on the scale of FSGS (Table 6). Flower size was negatively related to the scale of FSGS but the results are not significant for the intensity. There is a significant but weak negative effect of mean clump radius on both FSGS scale and intensity. There is a negative relationship between clump size and FSGS patterns (scale and intensity of FSGS). IWL has significant negative impact on the scale but no significant relation to the intensity of FSGS (Table 6).

4. Discussion

Our multi-site, multi-species comparison provides indirect operational indicators based upon traits likely to be important in shaping FSGS in dipterocarps. Only four of the 19 species showed no significant FSGS. Our examination of scale (*DistF*) and intensity (*Sp*) of FSGS indicates that wood density and flower size are useful predictors of strong FSGS. Genetic diversity was high among adult trees across all 19 species. The majority of species studied had low or non-significant F_{IS} values suggesting that they exhibited outcrossing. Five species, however, had high inbreeding coefficients (>0.15) in the adult populations, which indicated mixed-mating systems, with either self-fertilization or bi-parental inbreeding. Evaluation of mating system and FSGS within different species are important factors for evaluating how logging may impact genetic diversity of tree populations in the future. Below we critically interpret our results and suggest

Table 5
Summary of generalized least squared models. Models; degrees of freedoms for residuals (df (residuals); Akaike Information Criterion (AIC); *p*-values, $^{***}p < 0.001$, NS = Non-significant.

Models	df (residuals)	AIC	*p*-value	
Wood density	22(18)	29.76	0.0001	***
Tree density	26(22)	58.55	0.0869	NS
Flower sizes	30(24)	66.24	0.0001	***
Mean clump radius	28(24)	83.71	0.0041	**
IWL	30(26)	87.90	0.0007	***

Table 6
Summary table for generalized least square model results, Species traits; Akaike Information Criterion (AIC); Estimates; Standard Errors (SE); *t*-value; *p*-values for estimates.

Dependent correlated variable "value"	Species traits	AIC		Estimate	SE	*t*-value	*p*-value
Sp/DistF	Wood density	29.767	Intercept (DistF)	−0.328001	0.418045	−0.784608	0.4429
			Sp	−1.538227	0.592037	−2.598193	0.0182
			DistF: Wood density	0.270217	0.823021	0.328323	0.7465
			Sp: Wood density	4.271375	0.823021	5.189874	0.0001
	Tree density	58.555	Intercept (DistF)	−0.233913	0.098629	−2.371644	0.0269
			Sp	0.615380	0.127362	4.831716	0.0001
			DistF: Tree density	0.049187	0.062408	0.788164	0.4390
			Sp: Tree density	−0.117848	0.062408	−1.888357	0.0722
	Flower size	66.249	Intercept (DistF)	1.087470	0.215195	5.053408	0.0000
			Sp	−0.668794	0.224083	−2.984575	0.0064
			DistF: Flower size M	−1.077809	0.395189	−2.727321	0.0117
			Sp: Flower size M	−0.481255	0.395189	−1.217782	0.2351
			DistF: Flower size S	−1.298130	0.237407	−5.467937	0.0000
			Sp: Flower size S	−0.101446	0.237407	−0.427310	0.6730
	Mean Clump Radius (MCR)	83.719	Intercept (DistF)	0.400585	0.225857	1.773621	0.0888
			Sp	0.332229	0.360389	0.921861	0.3658
			DistF: MCR	−0.005547	0.002379	−2.330911	0.0285
			Sp: MCR	−0.005303	0.002379	−2.228427	0.0355
	Inverse Wing Loading (IWL)	87.900	Intercept (DistF)	0.529627	0.190765	2.776334	0.0101
			Sp	−0.316693	0.180699	−1.752605	0.0915
			DistF: IWL	−0.019540	0.006042	−3.233758	0.0033
			Sp: IWL	0.003626	0.006042	0.600175	0.5536

operational guidelines for the mitigation of FSGS into forest management practices.

4.1. Genetic diversity and inbreeding

Genetic diversity varies among the 19 species (He = 0.440 for *S. accuminatissima* to 0.843 for *D. globulus*; Table 3) but is comparable with other dipterocarp species (Lim et al., 2002; Obayashi et al., 2002; Kenta et al., 2004; Takeuchi et al., 2004; Ng et al., 2004, 2006). Within the genus *Shorea,* across all sites, our estimates of genetic diversity (*He* = 0.673–0.843) were similar to published estimates for other *Shorea* species (*He* = 0.680–0.800) (Obayashi et al., 2002; Takeuchi et al., 2004; Ng et al., 2004, 2006). Relatively high polymorphism is consistent with predominantly outcrossing long-lived tree species (Hamrick and Godt, 1996). Indeed, four species (*D. crinitus*, *Dr. lanceolata*, *S. curtisii*, *S. ovata*) show no significant inbreeding in adult populations, (Table 3), which is also consistent with high outcrossing rates. Alternatively, it is possible that progeny are produced through selfing or inbreeding but strong selective forces lead to early abortion of inbred seed and or differential mortality of inbred seedlings (Naito et al., 2005, 2008). Eight of the nine species for which we had seedling data showed significant F_{IS} at seedling stages. Only *S. argentifolia* showed no significant homozygous excess in the adults and seedlings (see Table 3). The significant and high *Fis* values in seedlings and adults of these eight species are consistent with a mixed mating system. These results indicate that selection against inbred progeny is relatively weak for species such as *S. gibbosa* and *S. amplexicaulis* where self-fertilization is a frequent occurrence. This would explain the high frequency of homozygotes in adult trees of these species. For species that are predominately selfing, deleterious recessive alleles are likely to have already been purged from these populations (Charlesworth and Charlesworth, 1987). In contrast, predominately outbreeding species are likely to be much more vulnerable to effects of inbreeding depression, as deleterious recessives have not been purged.

4.2. Indirect indicators of FSGS patterns across dipterocarp species

4.2.1. Is flower size a useful indicator of intensity of FSGS across dipterocarps?

Our expectation was that dipterocarps would exhibit significant FSGS due to limited seed and pollen dispersal. Empirical studies demonstrated that species with large flowers depend on larger pollinators which might enhance pollen dispersal distances and weaken FSGS (Kettle et al., 2011b). Flower size does indeed have a strong negative impact on the scale of FSGS across our species (Fig. 3; Table 6). The four species that lacked FSGS, *D. crinitus*, *Dr. lanceolata*, *S. amplexicaulis* and *S. parvifolia*, support the idea that large flower size as a surrogate of long distance pollen dispersal prevents the establishment of FSGS. *Dipterocarpus crinitus* and *Dr. lanceolata* have large flowers (8–20 mm for calyx tube diameters) that are known to attract large pollinators (Sakai et al., 1999; Ashton, 2003). These species also had non-significant inbreeding coefficients, which is indicative of extensive outcrossing rates. *Dryobalanops lanceolata* is pollinated by small to large bees, including *Apis* species (Momose et al., 1998), which are known to promote long distance gene flow due to their foraging behavior (Momose et al., 1998). *Shorea amplexicaulis* has similarly large flowers, although it is thought to be pollinated by beetles (Chrysomelidae and Curculionidae, size range: 2 mm to 2 cm) which are presumed to transfer pollen over large distances (Bawa, 1990; Fukue et al., 2007; Tani et al., 2009; Masuda et al., 2013). *Shorea parvifolia* has small flowers (2 mm calyx tube diameter) and is predominately pollinated by beetles (Sakai et al., 1999). Thus, in this case flower size alone might not be entirely indicative of short pollen dispersal distances as small beetles are thought to be more mobile than thrips which are the pollinators of most small flowered dipterocarps (weaker flyers with poor energetics). This difference in pollinator mobility may partly explain the lack of FSGS in *S. parvifolia.* Across tropical tree species in general, FSGS is attributed to limited pollen dispersal distance and pollinator size (Vekemans and Hardy, 2004; Hardy et al., 2006; Dick et al., 2008). Our results for dipterocarps are consistent with this view (see also Kettle et al., 2011a; Harata et al., 2012), although, we acknowledge that flower size is one factor among many that contribute to FSGS (Kettle et al., 2011a).

4.2.2. Is inverse wing loading a useful indicator of FSGS across dipterocarps?

Seed dispersal in the dipterocarps is limited compared to many tropical trees with long distance zoochoric dispersal (Suzuki and Ashton, 1996; Seidler and Plotkin, 2006). In ten neotropical tree species Hardy et al. (2006) found higher FSGS in species with seed dispersal limited to gyration and gravity than species whose seeds were dispersed by birds or bats. Inverse wing loading (IWL)

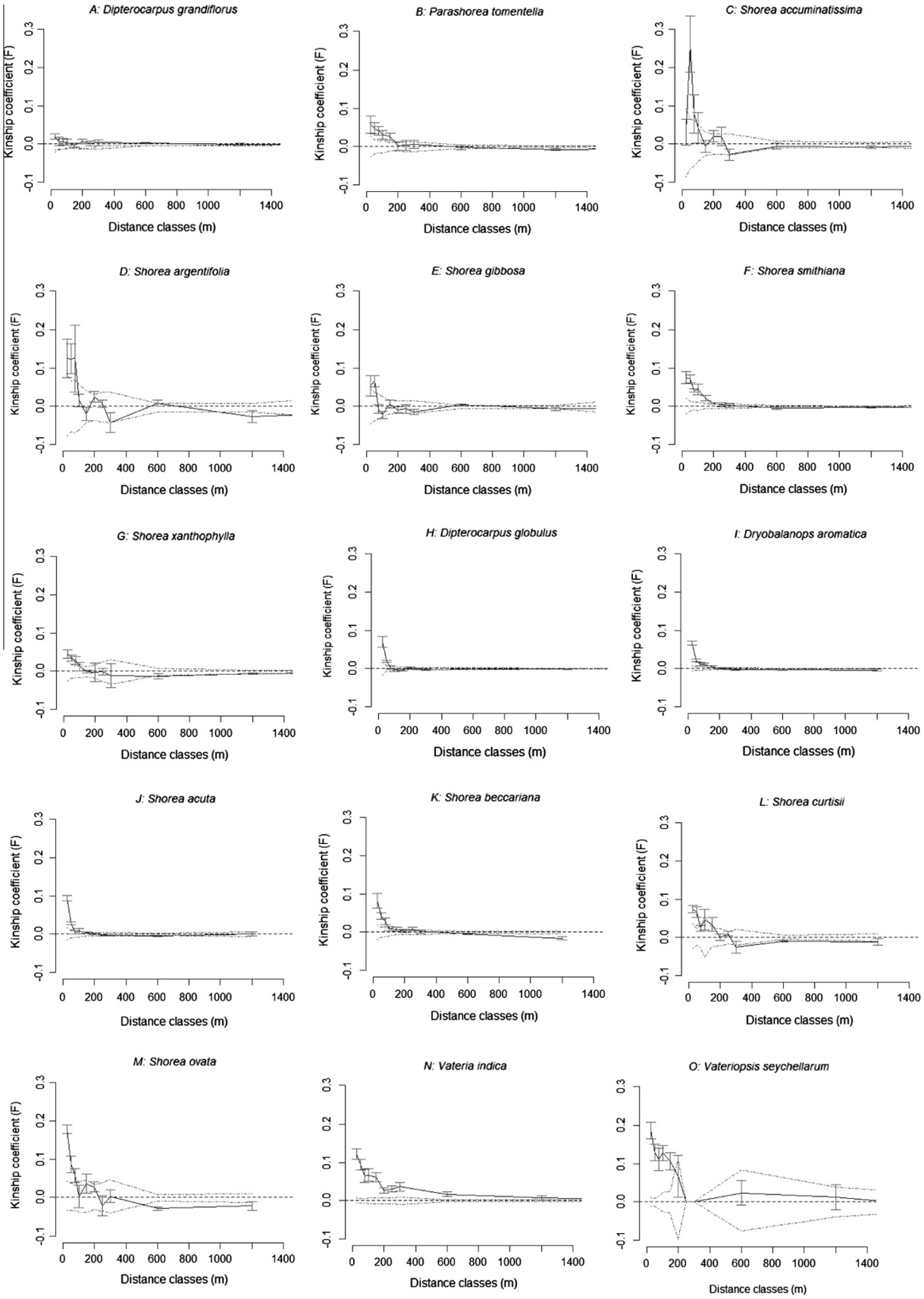

Fig. 2. Fine scale genetic structure of dipterocarps species. Dotted lines represent the 95% confidence intervals for the average Kinship coefficients F (Loiselle et al., 1995). Figures are sorted by alphabetical order within sites. A-G: Sepilok Forest Reserve, H-M: Lambir Hills National Park, N: India, O: Seychelles.

provides a useful proxy of dispersal potential in gyration or gravity dispersed seeds (Augspurger and Hogan, 1983; Suzuki and Ashton, 1996; Osada et al., 2001; Smith et al., 2015). We predicted that IWL would correlate negatively with both scale and intensity of FSGS (Hardy et al., 2006; Dick et al., 2008; Kettle et al., 2011a; Harata et al., 2012). This prediction was supported by the finding that spatial scale of FSGS (*DistF*) increased as IWL declined. In contrast we observed no significant relationship between IWL and intensity of FSGS (*Sp*, Fig. 3; Table 6). One explanation for this could be that there was low variation in seed dispersal among our study species, which would undermine the power of the test. Interestingly, intensity of FSGS in *V. indica* and *Va. seychellarum* (two species with completely wingless fruits) was particularly high (Fig. 2, Table 4), which may be related to the extremely limited seed dispersal in these two species (Finger et al., 2012 and Ismail et al., 2014 respectively). In addition to the wingless fruit, these two species are sampled in fragmented landscapes which are expected to increase the intensity of FSGS in future generations (Finger et al., 2012). Although earlier previous studies have indicated that seed dispersal distance may be less important than regeneration strategy in driving the intensity of FSGS for some dipterocarps (Kettle et al., 2011a), this conclusion was based upon very few species. The inclusion of more species in this new analysis provides additional evidence that generalizations based upon seed dispersal potential alone can be misleading in dipterocarps. Therefore we conclude that IWL is likely to be a relatively poor indicator of intensity of FSGS, although very small flowered and thrip pollinated dipterocarps and wingless dipterocarp species are likely to have strong FSGS.

4.2.3. Is wood density a useful indicator of FSGS across dipterocarp species?

Wood density is a useful proxy for the regeneration strategy of many tree species as high wood density reflects both slow growth and low mortality, and may be attributed to increased investment in structural tissue, shade and drought tolerance, and resistance to pests and pathogens (Swaine and Whitmore, 1988; Poorter and Bongers, 2006; Van Gelder et al., 2006; Poorter et al., 2010). Low wood density is associated with fast growth in high light conditions, and high mortality under shade (Verburg and van Eijk-Bos, 2003). The accumulation of high wood density species in the seedling bank over multiple reproductive events should increasing genetic diversity. This pattern of recruitment would result in weaker FSGS in the adult population. In contrast, light-demanding, lower wood density species have higher mortality at seedling stage. This can result in the accumulation of clusters of progeny from relatively few reproductive events which are thought to lead to high FSGS in adult trees (Jones and Hubbell, 2006). Studies on pioneer neotropical trees with limited dispersal showed that colonization processes such as founder events have equivalent effect on raising FSGS in tree population as limited gene flow (Wade and Mccauley, 1988; Davies et al., 2010; Silvestrini et al., 2015). Kettle et al. (2011a) observed high FSGS patterns in the dipterocarp *P. tomentella* despite is large flowers (4.2 mm calyx tube width) and high IWL. This anomaly was interpreted as an outcome of the association of recruitment to canopy gap creation resulting in clusters of progeny from few reproductive events in this species. The results presented in our study across multiple species suggest that increasing wood density is a positive indicator of FSGS in dipterocarps and therefore contradicts the interpretation based on *P. tomentella*. (Fig. 3, Table 6, c.f. Kettle et al., 2011a). There are a number of possible explanations why high wood density species might have a greater intensity of FSGS. Over time lower mortality rates in high wood density species could lead to an aggregation of higher number of half-sib progeny (from the same mother) beneath long-lived mother trees than in low wood density species, assuming limited dispersal in dipterocarps. Another important and poorly resolved factor is the frequency of fruiting across different dipterocarp species. Our data does not enable us to empirically test these ideas, but future studies which relate patterns of FSGS with spatial patterns of recruitment and frequency of flowering will be important in advancing our understanding of what drives FSGS in dipterocarps.

4.2.4. Are population density and mean clump radius useful indicators of FSGS across dipterocarp species?

Population density and FSGS are assumed to be negatively correlated in tropical trees because an increasing number of potential pollen donors in high density populations reduces the likelihood of mating between related individuals (Hamrick et al., 1993; Vekemans and Hardy, 2004; Hardy et al., 2006; Dick et al., 2008). Contrary to this expectation, tree density was not a significant species factor influencing FSGS patterns among species (Table 5). Very limited seed dispersal is a plausible explanation for this relationship and consistent with the conclusions of Harata et al. (2012). Coincident with this pattern, clump size had a significant negative influence on both scale and intensity of FSGS (Fig. 3; Table 6), which we interpret as covariance between the spatial scales of FSGS and stem density within populations.

4.3. Importance of mating systems when considering indicators of FSGS across dipterocarps

This multi-species and multi-site comparison supports the view that several factors shape FSGS in tropical trees (Vekemans and Hardy, 2004; Dick et al., 2008; Kettle et al., 2011a; Harata et al., 2012). In dipterocarps, wood density (which is a proxy for life history strategy) is correlated to FSGS. Seed dispersal, mating system, and growth strategy are important traits which are likely to influence the vulnerability of genetic diversity in dipterocarp species to fragmentation, deforestation and forest management strategies. The variability of mating systems across dipterocarp species suggests that consideration of individual species mating system is essential for the management of genetic resource in logged forests. For example, dipterocarp species which are predominately outcrossing are likely to be more vulnerable to inbreeding due to logging than species that are predominately selfing (Murawski et al., 1994; Lee, 2000; Ward et al., 2005; Breed et al., 2013).

4.4. Recommendations for integration of FSGS into management and restoration of dipterocarp forests

Multiple factors contribute to shaping local patterns of genetic diversity in tropical trees. Simple operational guidelines for forest managers need to be developed if they are to take genetic factors into account. To this end, we identify traits that would enable forest managers to integrate an understanding of patterns of FSGS to help minimize inbreeding and erosion of genetic diversity (Ashton and Kettle, 2012; Jalonen et al., 2014). Trees can be vulnerable to inbreeding and loss of genetic diversity in logged and fragmented forests where trees become increasingly isolated, or where genetic factors may undermine natural forest regeneration (Ismail et al., 2014).

Logging: Although the importance of retaining reproductive trees in logged forest as a means of conserving genetic diversity has been previously acknowledged (Jennings et al., 2001; Sist et al., 2003a,b; Jalonen et al., 2014), our results indicate that this alone may not be sufficient. Our results highlight that the spatial arrangement of these trees will influence future patterns of mating and potentially the extent of inbreeding due to differential FSGS. However, patterns of FSGS are not easily detected. Our results suggest that heavy hard wood dipterocarp species are likely to have

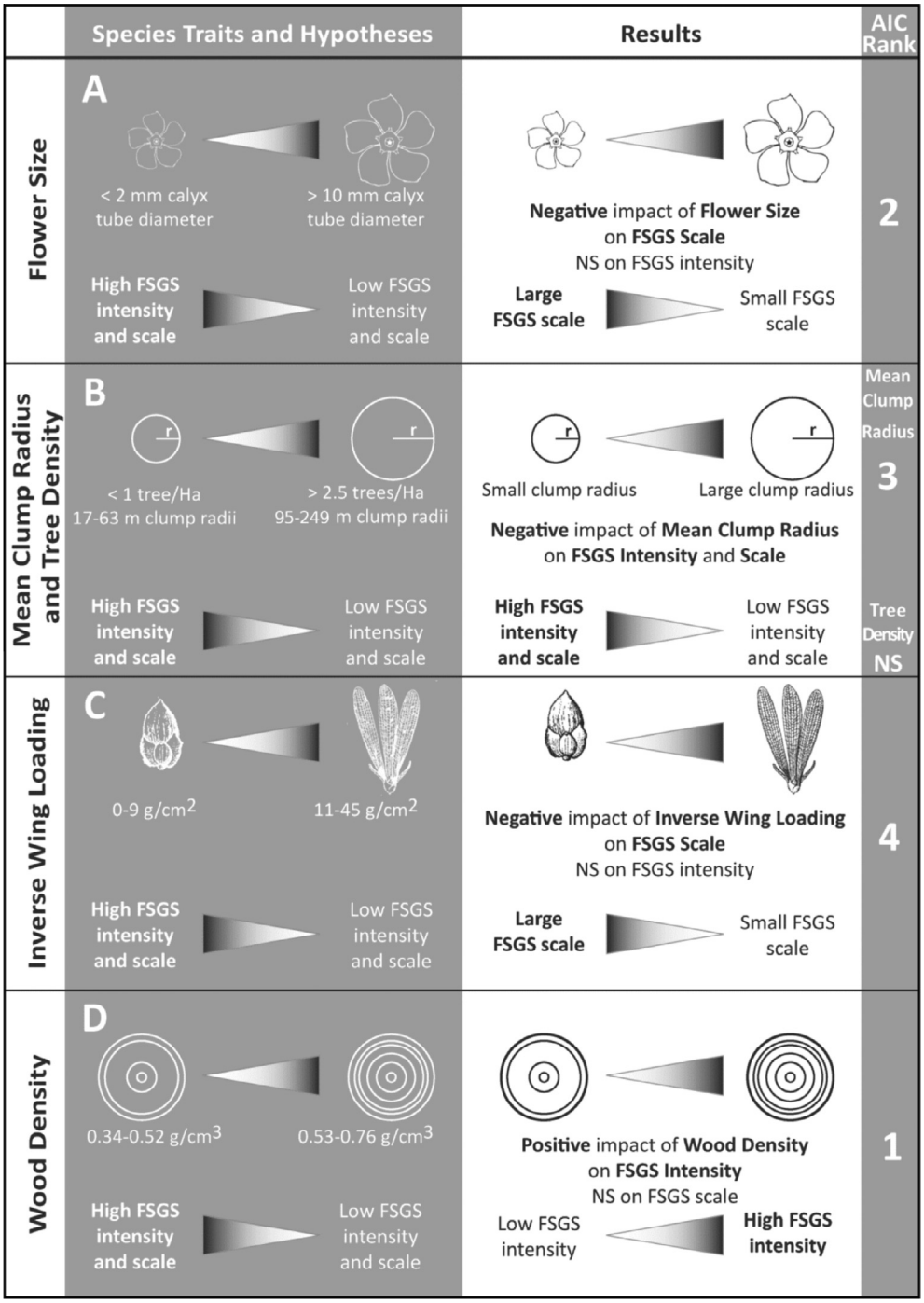

Fig. 3. Schematic summary of our results of generalized least square models linking species traits and Fine-Scale Genetic Structure patterns. NS = Non-significant.

high FSGS, thus the spatial arrangement of reproductive adults of these species should be given specific attention to avoid deleterious genetic processes associated with FSGS such as inbreeding. This recommendation is consistent with previous work highlighting the greatest threats to heavy hardwood dipterocarps (Ashton, 2004). One of our primary recommendations for logging operations is relevant to planning which reproductive adult trees are retained as seed trees. Our results highlight that species differ in patterns of FSGS and that high wood density small flowered dipterocarps are likely to be especially vulnerable. To help mitigate the effects of FSGS it will thus be important to consider both the number and spatial distribution of seed trees. Maintaining additional reproductively mature trees which include individuals >300 m apart within a logging compartment should help to mitigate the effects of intense FSGS in vulnerable species such as *Shorea ovata*. This minimum distance is based upon the average maximum distance (across all study species) at which individuals have significant kinship. This should help to reduce the likelihood of mating between relatives, especially for heavy hardwood species. In this regard to the current RIL guidelines (RIL Operation Guide Book, 2009) we emphasis that having detailed species level inventories is fundamental to developing management plans which avoid erosion of genetic resources within species.

Our results emphasize the importance of mating system, as a key trait in maintaining genetic diversity in dipterocarp species, which is important to sustainable management. We urge future

studies of FSGS in dipterocarps to include genotypes of early life stages. This provides a relatively low cost but efficient means of determining mating system. Genotyping a relatively small sample of adult and juvenile trees (<100) at neutral markers and calculating inbreeding coefficients would provide this information. We recommend this as a priority for vulnerable hardwood species. One major constraint in current management is that species are rarely considered as the unit of management in lowland dipterocarp forests. Because species are likely to be differentially vulnerable to management operations, for the reasons given above we highlight the urgent need for increased capacity in forest botanists who can provide species level inventories prior to logging.

Restoration: The spatial scale over which FSGS typically occurs in dipterocarps has relevance for seed collections for ecological restoration or enrichment planting. To maximize the genetic variation among trees used for restoration, we recommend ensuring a minimum distance of 300 m among neighbouring conspecific seed tree sources to avoid sampling seeds form related individuals and avoid planting related trees too closely. Equally when planting out seedlings it would be prudent to ensure that there are genetically diverse mixes of seedlings from different mother trees to avoid artificially creating clumps of highly related individuals. This will certainly be the result of sampling seeds from very few individuals.

5. Conclusions

In this study, the majority of our study species (15 species of 19) displayed significant FSGS. Species with significant FSGS are vulnerable to inbreeding and decreasing genetic diversity. To overcome potential negative effect of FSGS in logged forests we highlight the need for species level guidelines on spatial distribution of seed trees. Our results suggest that wood density and flower size offer useful indicators of FSGS in dipterocarps species. Asian tropical forests have received comparatively little attention in regards to the genetic consequences of logging and fragmentation, but we argue that dipterocarp trees are likely to be particularly vulnerable to these processes. With species exhibiting important variation in intensity and scale of FSGS which likely underpins differential vulnerability, there is an urge to implement forestry and conservation with species specific genetic guidelines. Our study presents a test case of indirect indicators for patterns of FSGS, which may help refine prescriptions for management that would reduce inbreeding and erosion of genetic diversity for the most vulnerable species in this globally important group of tropical rainforest trees.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.07.023.

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