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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)