SPATIAL STUDIES OF *SHOREA PARVIFOLIA* SPP. *PARVIFOLIA* (DIPTEROCARPACEAE) IN A LOWLAND AND HILL DIPTEROCARP FOREST

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LEE SL, NG KKS, NG CH, TNAH LH, LEE CT, TANI N & TSUMURA Y. 2016. Spatial studies of *Shorea parvifolia* spp. *parvifolia* (Dipterocarpaceae) in a lowland and hill dipterocarp forest. Variation in tree species floristic composition and local-scale distribution in tropical forests is thought to be associated with habitat. This study compared the spatial distribution pattern and spatial genetic structure of *Shorea parvifolia* spp. *parvifolia* in a lowland and a hill dipterocarp forest and postulated how the spatial structure of a tropical tree species may be influenced by habitat heterogeneity. The significant spatial aggregation of *S. parvifolia* spp. *parvifolia* in both the lowland and hill dipterocarp forests indicated that seed dispersal was limited. The higher degree of habitat heterogeneity (e.g. topography, habitat type and resource availability) in hill dipterocarp forests compared with lowland dipterocarp forests, as established by previous research, may have contributed to the higher level of aggregation of *S. parvifolia* spp. *parvifolia* in the hill dipterocarp forest in the present study. The significant spatial genetic structure observed in the lowland dipterocarp forest may be due to restricted pollen and seed dispersal. In contrast, the absence of significant spatial genetic structure in the hill dipterocarp forest may indicate extensive pollen flow, and consequently, energetic and generalist pollinators (e.g. social bees *Apis* spp. and *Trigona* spp.) may be involved in the pollination of dipterocarps in the hill dipterocarp forests of Peninsular Malaysia.

Keywords: Spatial genetic structure, spatial aggregation, habitat heterogeneity, red meranti, tropical tree species

INTRODUCTION

The spatial distribution pattern within plant populations is influenced by various ecological and evolutionary processes such as seed dispersal (Seidler & Plotkin 2006), intra- and inter-specific competition (Condit et al. 2000) and environmental heterogeneity (Plotkin et al. 2000), which take place during the life history of a plant. The seed shadow basically determines the spatial distribution pattern of cohorts (Plotkin et al. 2002). After seed dispersal, compensatory mortality due to intra- and interspecific competition and environmental heterogeneity affects spatial distribution patterns (Plotkin et al. 2002). The degree to which individuals are aggregated affects plant reproductive biology and also how plant species use resources or can be used as resources (Condit et al. 2000).

The spatial genetic structure within plant populations, in addition to the ecological and evolutionary processes that affect spatial distribution patterns, can also be influenced by limited pollen dispersal, local genetic drift, inbreeding and selection favouring the same or different genotypes (Heywood 1991, Vekemans & Hardy 2004, Dick et al. 2008, Hardy et al. 2006). Studies of spatial genetic structure in plant populations can reveal the operation of key evolutionary processes (Smouse & Peakall 1999). When spatial genetic structure develops, it may influence the patterns of local breeding and evolution (Epperson 1992). In addition, logging activities will increase production of seeds by selfing but if a tree species is genetically structured within a population, logging activities may reduce inbreeding by consanguineous mating (Lee 2000).

Information on spatial distribution pattern and spatial genetic structure has been reported extensively for temperate and tropical forest tree species (in Africa and South America) but

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is limited for tropical forest trees from South-East Asia (Dick et al. 2008). In our previous study of three dipterocarps with different habitat preferences within a hill dipterocarp forest in Sungai Lalang Forest Reserve (FR), i.e. *S. curtisii* (on the ridges), *S. leprosula* (in the valleys) and *S. macroptera* (on the ridges and in valleys), significant spatial aggregation was observed in small-diameter trees of all three species but significant random distribution was observed only in large-diameter trees of *S. macroptera* (Ng et al. 2006). This significant spatial aggregation was explained by limited seed dispersal. The study concluded that *S. macroptera* is a habitat generalist, while *S. curtisii* and *S. leprosula* are habitat-specific. The study also surmised that if seed dispersal is restricted but pollen flow is extensive, no spatial genetic structure but significant spatial aggregation will be observed for the small-diameter trees, regardless of whether the species is habitat-specific or a habitat generalist.

As an extension, it would be interesting to understand how spatial structure of tropical tree species can be influenced by different degrees of habitat heterogeneity. Hilly, uneven terrain, steep slopes, sheltered valleys, or high degrees of environmental heterogeneity are some of the common characteristics of hill dipterocarp forests (Niiyama et al. 1999). Besides the distinctive topography differences, studies have shown differences in the soil characteristics between both forest types (Zaidey et al. 2010). Soil resource availability is often correlated with local-scale variation in tree species distribution in tropical forests (John et al. 2007). Variation in tree species floristic composition is strongly associated with available phosphorus concentrations in Pasoh Forest soil (Wan Juliana 2001, Davies et al. 2003), suggesting that the outcome of competition for phosphorus might be an important determinant of this pattern.

Shorea parvifolia (locally known as meranti sarang punai) is a widely distributed dipterocarp occurring in extreme south-east peninsular Thailand, throughout Peninsular Malaysia (except Perlis, extreme north-western Kedah and the Langkawi Islands), Sumatra, Borneo and intervening islands. It is one of the main sources of light red meranti timber (Desch 1941) and can be found in lowland as well as hill dipterocarp forests up to 800 m above sea level (asl) in Peninsular Malaysia (Symington 1943). *Shorea parvifolia* is a polymorphous species. In Peninsular Malaysia, at least three forms occur, i.e. Selangor, Pahang and Perak (Symington 1943). The Selangor form (leaves ovate, broad at the base and more or less smooth on the lower surface; stipules broad) is the typical type of *S. parvifolia* in Peninsular Malaysia and is recognised as subspecies *parvifolia* (Ashton 1982).

This study tried to understand how spatial structure of a tropical tree species can be influenced by habitat heterogeneity, by comparing the spatial distribution pattern and spatial genetic structure of *S. parvifolia* spp. *parvifolia* in lowland and hill dipterocarp forests. Based on the higher degree of habitat heterogeneity in hill dipterocarp forests, such as topography (Niiyama et al. 1999), habitat type (Wan Juliana et al. 2009) and resource availability (Wan Juliana 2001, Davies et al. 2003, Potts et al. 2004, John et al. 2007), it is postulated that *S. parvifolia* spp. *parvifolia* will display stronger spatial aggregation in hill dipterocarp forest than in lowland dipterocarp forest. Based on the limited seed and pollen dispersal of *S. parvifolia* spp. *parvifolia* we further postulate that there will be a significant level of spatial genetic structure in both the lowland and hill dipterocarp forests.

MATERIALS AND METHODS

Study plots and sample collection

A 50-ha research plot (2° 59' N, 102° 19' E) in Pasoh FR, Negeri Sembilan, and a 33-ha research plot (3° 05' N, 101° 52' E) in Sungai Lalang FR, Selangor, were chosen to represent the lowland dipterocarp forest and hill dipterocarp forest respectively. In Pasoh FR the soil group comprised of alluvial, granitic, shale and mix sandstone/shale (Wan Juliana et al. 2009, Adzmi et al. 2010), whereas acrisol and sandy clay soil was found in Sungai Lalang FR (J Vijayanathan, unpublished data). The enumeration of the Pasoh 50-ha plot in 1995 recorded 102 individuals of *S. parvifolia* spp. *parvifolia* with diameter at breast height (dbh) > 27 cm. However, during our sample collection in 2000, we recorded 33 of these individuals as dead and thus collected only 69 samples. For the Sungai Lalang plot, our sampling in 2001 collected 79 of the 95 individuals of *S. parvifolia* spp. *parvifolia* (dbh > 27 cm) recorded in a 2000 census (SL Lee & KKS Ng, unpublished data).

Within each plot, all individuals of *S. parvifolia* spp. *parvifolia* with dbh > 27 cm were mapped (Figure 1). Leaves and inner bark tissues were sampled from all mapped individuals. A total of 69 and 79 samples were collected from Pasoh and Sungai Lalang respectively.

Microsatellite analysis

Genomic DNA was extracted from leaves or inner bark tissues using a procedure adapted from Murray and Thompson (1980) with modification and further purified using High Pure PCR Template Preparation Kit (Roche). The samples were genotyped using six microsatellite loci (*Sle074a*, *Sle384*, *Sle111a*, *Sle118*, *Sle280* and *Sle294*) developed for *S. leprosula* (Lee et al. 2004).

Microsatellites amplifications were performed in 10 µL consisting of approximately 5 ng of template DNA, 50 mM KCl, 20 mM Tris-HCl (pH 8.0), 1.5 mM $MgCl_2$, 0.2 mM each of primer, 0.2 mM each of dNTP and 1 U of *Taq* DNA polymerase (Promega). The reaction mixture was subjected to amplification in a GeneAmp 9700 thermal cycler (Applied Biosystems), for an initial denaturing step at 94 °C for 4 min, followed by 35 cycles consisting of 1 min at 94 °C, 30 sec at 52–54 °C and 40 sec at 72 °C. A final cycle of 30 min at 72 °C was used to complete the extension of any remaining products before holding the samples at 4 °C until analysed.

Genotyping was subjected to 5% denaturing polyacrylamide gels electrophoresis (containing 6 M urea and run with 1× TBE buffer) of fluorescently-labelled PCR products on an ABI

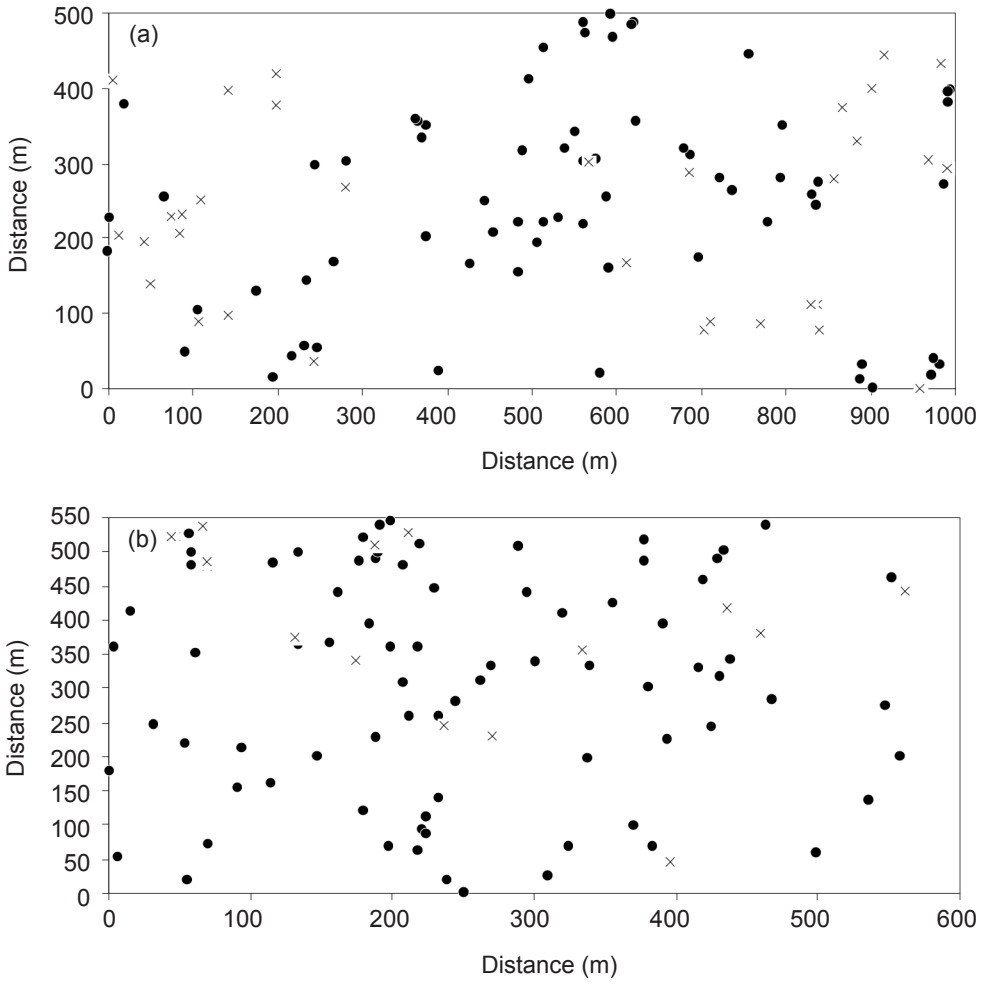

Figure 1 The spatial distribution of *Shorea parvifolia* spp. *parvifolia* with diameter at breast height ≥ 27 cm within (a) a 50-ha lowland dipterocarp forest plot in Pasoh Forest Reserve and (b) a 33-ha hill dipterocarp forest plot in Sungai Lalang Forest Reserve; trees from which samples were collected for spatial genetic analysis are marked with •, while × markers denote dead trees

Prism 377 automated DNA sequencer (Applied Biosystems). Allele sizes were assigned against the internal size standard and individuals were genotyped using GeneScan Analysis 3.1 and Genotyper 2.1 software (Applied Biosystems).

Data analysis

Spatial distribution pattern analysis was conducted using Ripley's K-function (Ripley 1976) based on the program of Haase (1995). Ripley's K-function was calculated separately for 0 to 240 m in 30 m increments. A null distribution was generated using the Monte Carlo method and 19 randomly generated sets of spatial points. Deviation from complete spatial randomness was established by comparing the envelope surrounding the null distribution of K to the observed distribution.

Spatial autocorrelation analysis (Sokal & Oden 1978) was carried out to determine the spatial genetic structure. Moran's I coefficient (Moran 1950) was selected over the more recent kinship coefficient (Loiselle et al. 1995) considering Moran's I coefficient's usefulness for investigating spatial genetic structure due to gene flow. Moran's method is also less influenced by ploidy level and selfing rate (Hardy & Vekemans 1999, 2001). Moran's I coefficients were calculated only for alleles with a frequency greater than 5% on eight continuous distance classes, each of 30 m, from 0–30 m to 210–240 m, using the Spatial Genetic Software (SGS) program (Degen et al. 2001). For statistical reasons, these number and dimension of spatial distance classes were assigned so that each included at least 30 pairs of data points. An indication of the trends in spatial scale of genetic substructuring was obtained using correlograms (Sokal & Oden 1978). Average Moran's I coefficients were calculated for all alleles as a summary statistic. A permutation procedure using a Monte Carlo simulation was applied to test significant deviations from random distributions of each calculated measure (Manly 1997). Each permutation consisted of a random redistribution of multilocus genotypes over the spatial coordinates of the sample points. For each of the spatial distance classes, observed values were compared with the distribution obtained after 1000 permutations. Then a 95% confidence interval for the parameter was constructed as an interval (Streiff et al. 1998).

RESULTS AND DISCUSSION

Spatial distribution pattern

The spatial distribution pattern studies on a majority of tropical tree species showed significant spatial aggregation at various diameter-classes (Hubbell 1979, Itoh et al. 1997, Condit et al. 2000, Plotkin & Seidler 2006). Similarly, in this study, significant spatial aggregation was observed for *S. parvifolia* spp. *parvifolia* in both the lowland and hill dipterocarp forest plots (Figure 2) and the degree of aggregation was much higher in the hill (> 240 m) than in the lowland dipterocarp forest (~ 90 m). At the lowland dipterocarp forest, above ca. 90 m, the complete spatial random distribution observed was possibly due to mortality. Our results concur with that of previous studies that found significant spatial aggregation for many tropical tree species at various diameter-classes (e.g. Hubbell 1979, Itoh et al. 1997, Condit et al. 2000, Plotkin & Seidler 2006). The possible mechanisms of clumping have been discussed from the aspect of seed dispersal (Seidler & Plotkin 2006, Smith et al. 2015), gap recruitment (Itoh et al. 1997, Plotkin et al. 2000), distance-dependent mortality (Itoh et al. 1997), density-dependent recruitment (Okuda et al.1997), topography (Plotkin et al. 2000), pest effect (Wills & Condit 1999, Harms et al. 2000), herbivores and plant diseases (Condit et al. 2000) and species density (Condit et al. 2000, Flugge et al. 2012). The significant spatial aggregation found in both the lowland and hill dipterocarp forest plots indicates that seed dispersal for *S. parvifolia* spp. *parvifolia* is limited. Seed dispersal for this species has been found to seldom exceed 30 m from the mother tree based on an 'inverse wing loading' test (Harata et al. 2012). Although *S. parvifolia* spp. *parvifolia* produces winged seeds, seed dispersal is due mainly to gravity (Chan 1980) and gyration (Harata et al. 2012).

In Peninsular Malaysia, lowland dipterocarp forests consist mainly exploitable forests, which are well-drained primary forests of the plains, undulating land and foothills up to about 300 m asl. On the other hand, hill dipterocarp forests can be found inland at altitudes ranging between 300 and 800 m asl (Symington 1943). The higher degree of habitat heterogeneity in hill dipterocarp forests compared with that in lowland dipterocarp forests may be one of the factors that contributed to a level of aggregation

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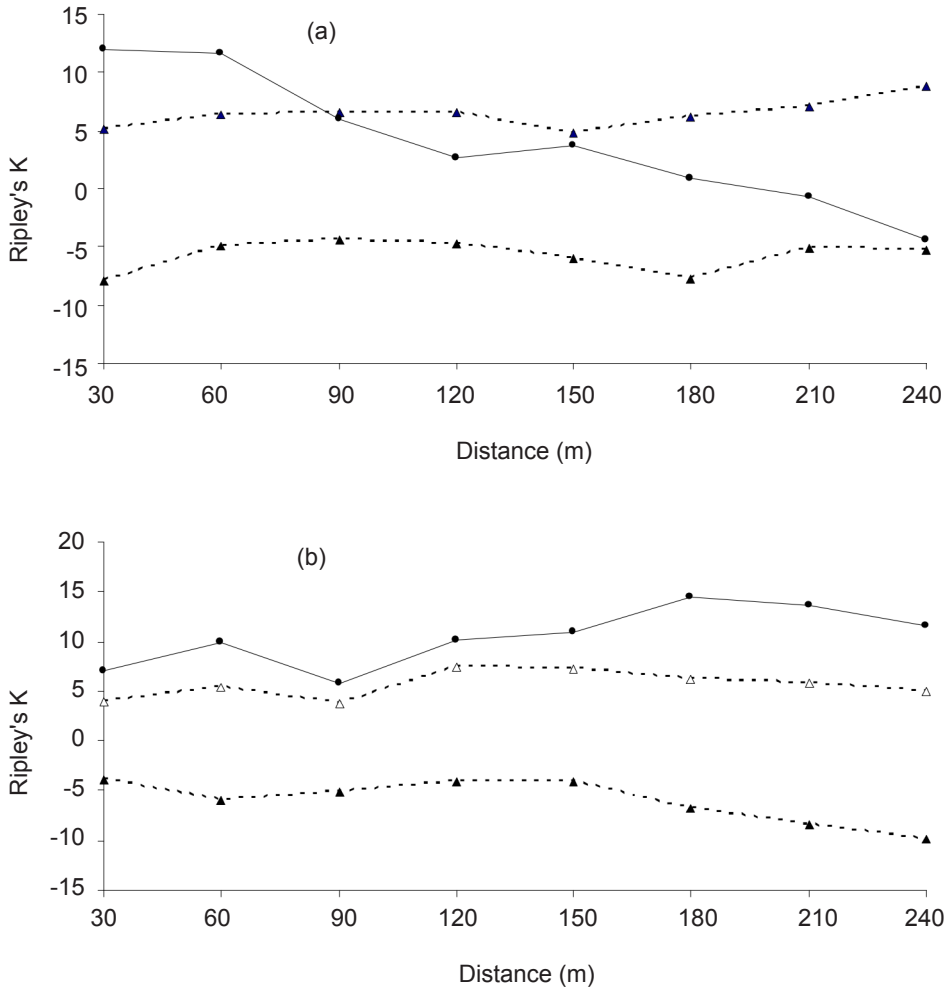

Figure 2 The spatial distribution pattern analysis using Ripley's K-function of *Shorea parvifolia* spp. *parvifolia* in a (a) lowland and (b) hill dipterocarp forest plot; continuous lines represent the sample statistic and dashed lines represent 95% confidence limits

of *S. parvifolia* spp. *parvifolia* in the present study that was higher in the hill dipterocarp forest than in the lowland dipterocarp forest. Species distributions are strongly aggregated with respect to variation in topography, soil water and soil nutrient status (Clark et al. 1998, Palmiotto et al. 2004, Potts et al. 2004).

Spatial genetic structure

Moran's I correlograms revealed significant spatial genetic structure in a distance class of size between 0–90 m for *S. parvifolia* spp. *parvifolia* in the lowland dipterocarp forest, but no significant spatial genetic structure in the hill dipterocarp forest (Figure 3).

The majority of spatial genetic structure studies on temperate forest tree species have shown weak spatial genetic structure consistent with long-distance seed and pollen dispersal (e.g. Chung et al. 2000, Epperson & Chung 2001, Parker et al. 2001, Chung et al. 2011). For tropical forest trees, Hamrick et al. (1993) showed that spatial genetic structure was present in small and intermediate diameter classes of three tropical tree species in Panama. Similarly, a study on two dipterocarps with contrasting breeding systems and different ploidy levels, i.e. *Shorea leprosula* (predominantly outcrossing, diploid) and *S. ovalis* spp. *sericea* (apomictic, tetraploid) within a lowland dipterocarp forest found that the magnitude of spatial genetic structure decreased from smaller- to larger-diameter size classes (Ng et al. 2004). This finding was attributed to the limited seed dispersal and apomictic mode of reproduction of *S. ovalis* spp. *sericea,* and limited seed and pollen dispersal of *S. leprosula* (Ng et al. 2004). In addition, several studies have

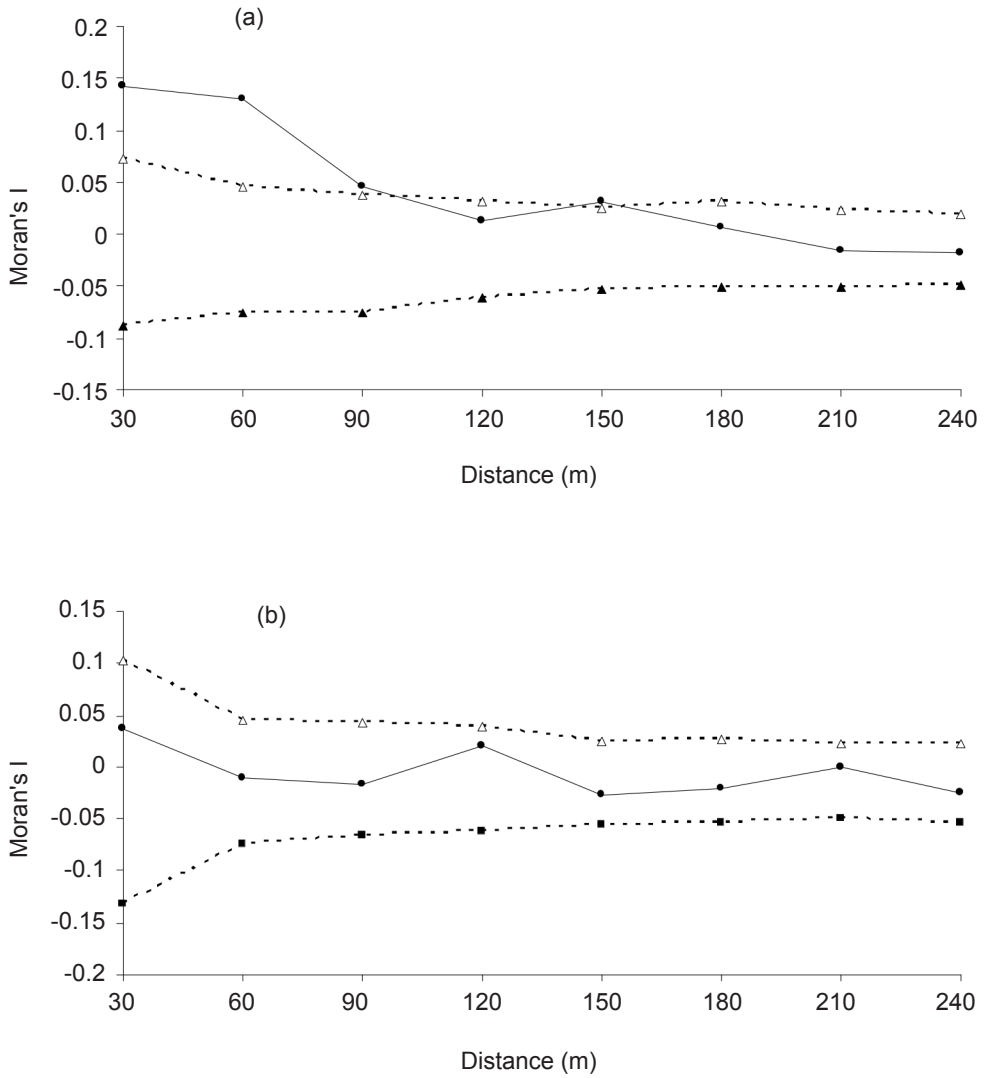

Figure 3 Correlograms of average Moran's I coefficient of *Shorea parvifolia* spp. *parvifolia* in a (a) lowland and (b) hill dipterocarp forest plot; continuous lines represent the sample statistic and dashed lines represent 95% confidence limits

investigated factors affecting differences in spatial genetic structure among species. Kettle et al. (2011) in a study comparing adult trees of three different dipterocarp species in Sepilok FR reported that species with the shortest seed dispersal or least mobile pollinators did not have the strongest spatial genetic structure. Harata et al. (2012) in their study on 10 coexisting dipterocarps in Lambir Hill National Park, Sarawak revealed that spatial genetic structure was stronger at the smaller spatial scale (≤ 100 m) than at larger spatial scales (> 100 m) for each species. They also suggested that seed dispersal distance was important at the smaller spatial scale whereas at the larger spatial scale, pollinators and spatial distribution of adult trees were important determinants of spatial genetic structure.

The major causes of spatial genetic structure within populations have been reported to be due to restricted pollen and seed dispersal (Wright 1943, Latta et al. 1998). The significant spatial genetic structure of *S. parvifolia* spp. *parvifolia* in the lowland dipterocarp forest and not in the hill dipterocarp forest in the present study, may have been due to restricted pollen and seed dispersal in the former. Chan (1981) reported that dispersal of dipterocarp seeds in Pasoh FR was found to be less than 20 m from the mother tree, due to impedance by the density of the canopy in that lowland forest. At the hill dipterocarp forest plot in our study, seeds could potentially be dispersed farther from the mother trees. Wind-aided dispersal of up to 80 m has been recorded for *S. curtisii* on slopes and ridges (Burgess

1975). Restricted pollen dispersal in the lowland dipterocarp forest plot in the present study could be due to the pollination system in this forest reserve. A previous pollination ecology study in this lowland dipterocarp forest showed that the low energetic thrips (Thysanoptera), *Thrips* and *Megalurothrips,* are the main pollinators for *S. parvifolia* spp. *parvifolia* (Chan & Appanah 1980, Appanah & Chan 1981). The significant spatial genetic structure of *S. parvifolia* spp. *parvifolia* in the lowland dipterocarp forest may have been due to restricted pollen and seed dispersal.

In contrast, the absence of significant spatial genetic structure of *S. parvifolia* spp. *parvifolia* in hill dipterocarp forest may infer extensive pollen flow, which is typically associated with energetic pollinators. While dipterocarp pollinators have not been documented for Sungai Lalang FR, thrips have been reported as the major pollinators at other dipterocarp forests in the Peninsular Malaysia, i.e. the lowland forest Pasoh FR (Appanah & Chan 1981) as stated earlier, and Semangkok FR, a hill dipterocarp forest (Kondo et al. 2016). Small beetles (Momose et al. 1998, Sakai et al. 1999) and social bees (Momose et al. 1998) have been reported as the main pollinators in Lambir Hill National Park, a mixed dipterocarp forest in Sarawak, East Malaysia. Ashton et al. (1988) suggested that the quick response of pollinators to the intense flowering of the general flowering in dipterocarps can determine the dominant pollinators. Pollinators with short generation times and high fecundity such as thrips may be able to quickly increase populations in response to massive floral resources available during general flowering periods (Kondo et al. 2016), while energetic pollinators such as the social bees *Apis* and *Trigona* (Momose et al. 1998) and carpenter bees *Xylocopa* spp. (Appanah 1990), may migrate to areas during mass flowering periods. This demonstrated that different pollinators might be involved in the pollination of dipterocarps in different forest types, depending on their responses to flowering cues. Based on the inferred extensive pollen flow from this study, we postulate that energetic and generalist pollinators such as social bees (*Apis* spp. and *Trigona* spp.) may be involved in the pollination of dipterocarps in the hill dipterocarp forests of Peninsular Malaysia. Further research on pollination systems in dipterocarps during future mass flowering events could offer greater insights into the reproductive biology of dipterocarps in the hill dipterocarp forests of Peninsular Malaysia.

In conclusion, the contrasting spatial structures of *S. parvifolia* spp. *parvifolia* in lowland and hill dipterocarp forests revealed that besides life history traits and demographic past history, the spatial distribution is necessarily a product of environmental influences, i.e. habitat heterogeneity. In addition, knowledge of spatial genetic structure provides a valuable tool for inferring these causal factors and the underlying genetic processes such as differential selective pressures within each forest type and gene flow. Consequently, information about dispersal, pollinator behaviour, habitat and other genetic and ecological processes operating within the populations represents key features for conservation managers to better manage this forest resource.

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REFERENCES

Adzmi Y, Suhaimi WC, Amir Husni MS, Mohd Ghazali H, Amir SK & Baillie I. 2010. Heterogeneity of soil morphology and hydrology on the 50-ha long term ecological research plot at Pasoh, West Malaysia. *Journal of Tropical Forest Science* 22: 21–35.

Appanah S & Chan HT. 1981. Thrips: the pollinators of some dipterocarps. *Malayan Forester* 44: 234–252.

Ashton PS. 1982. Dipterocarpaceae. *Flora Malesiana* 9: 237–552.

Ashton PS, Givnish TJ & Appanah S. 1988. Staggered flowering in the Dipterocarpaceae: new insight into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132: 44–66.

Berg EE & Hamrick JL. 1995. Fine-scale genetic structure of a turkey oak forest. *Evolution* 49: 110–120.

Boshier DH, Chase MR & Bawa K. 1995. Population genetics of *Cordia alliodora* (Boraginaceae), a neotropical tree. III. Gene flow, neighborhood and population substructure. *American Journal of Botany* 82: 484–490.

Chan HT. 1980. Reproductive biology of some Malaysian dipterocarps. II. Fruiting biology and seedling studies. *Malayan Forester* 43: 438–451.

Chan HT & Appanah S. 1980. Reprodutive biology of some Malaysian dipterocarp. I. Flowering biology. *Malayan Forester* 43: 132–143.

Chung MG, Chung MY, Oh GS & Epperson BK. 2000. Spatial genetic structure in a *Neolitsea sericea* population (Lauraceae). *Heredity* 85: 490–497.

Chung MY, Nason JD & Chung MG. 2011. Significant demographic and fine-scale genetic structure in expanding and senescing populations of the terrestrial orchid *Cymbidium goeringii* (Orchidaceae). *American Journal of Botany* 98: 2027–2039.

Clark DB, Clark DA & Read JM. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology* 86: 101–112.

Condit R, Ashton PS, Baker P et al. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.

Davies SJ, Nur Supardi MN, LaFrankie JV & Ashton PS. 2003. The trees of Pasoh Forest: stand structure and floristic composition of the 50-hectare forest research plot. Pp 35–50 in Okuda T *et al.* (eds). *Pasoh: Ecology and Natural History of a Southeast Asian Lowland Tropical Rain Forest*. Springer, Berlin.

Desch HE. 1941. *Manual of Malayan Timbers*. Malayan Forest Record No. 15. Caxton Press Ltd, Kuala Lumpur.

Degen B, Petit R & Kremer A. 2001. SGS–Spatial genetic software: a computer program for analysis of spatial genetic and phenotypic structures of individuals and populations. *Journal of Heredity* 92: 447–449.

Dick CW, Hardy OJ, Jones FA & Petit RJ. 2008. Spatial scales of pollen and seed-mediated gene flow in tropical rain forest trees. *Tropical Plant Biology* 1: 20–33.

Epperson BK. 1992. Spatial structure of genetic variation within populations of forest trees. *New Forest* 6: 257–278.

Epperson BK & Chung MG. 2001. Spatial genetic structure of allozyme polymorphisms within populations of *Pinus strobus* (Pinaceae). *American Journal of Botany* 88: 1006–1010.

Flugge AT, Olhede SC & Murrell DJ. 2012. The memory of spatial patterns: changes in local abundance and aggregation in a tropical forest. *Ecology* 93: 1540–1549.

Haase P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *Journal of Vegetation Science* 6: 575–582.

Hardy OJ & Vekemans X. 1999. Isolation by distance in a continuous population: reconciliation between spatial autocorrelation analysis and population genetics models. *Heredity* 83: 145–154.

Hardy OJ & Vekemans X. 2001. Patterns of allozymic variation in diploid and tetraploid *Centaurea jacea* at different spatial scales. *Evolution* 55: 943–954.

Hardy OJ, Maggia L, Bandou E et al. 2006. Fine-scale genetic structure and gene dispersal inferences in 10 Neotropical tree species. *Molecular Ecology* 15: 559–571.

Hamrick JL, Murawski DA & Nason JD. 1993. Influence of seed dispersal mechanisms on the genetic struture of tropical tree populations. *Vegetatio* 107/108: 281–297.

Harata T, Nanami S, Yamakura T et al. 2012. Fine-scale spatial genetic structure of ten dipterocarp tree species in a Bornean rain forest. *Biotropica* 44: 586–594.

Heywood JS. 1991. Spatial analysis of genetic variation in plant populations. *Annual Review of Ecology and Systematics* 22: 335–355.

Hubbell SP. 1979. Tree dispersion, abundance and diversity in a dry tropical forest. *Science* 203: 1299–1309.

Itoh A, Yamakura T, Ogino K, Lee HS & Ashton PS. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. *Plant Ecology* 132: 121–136.

John R, Dalling JW, Harms KE et al. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences* 104: 864–869.

Kettle CJ, Hollingsworth PM, Burslem DFRP, Maycock CR, Khoo, E & Ghazoul J. 2011. Determinants of fine-scale spatial genetic structure in three co-occurring rain forest canopy trees in Borneo. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 47–56.

Kondo T, Otani T, Lee SL & Tani N. 2016. Pollination system of *Shorea curtisii*, a dominant species in hill dipterocarp forests. *Journal of Tropical Forest Science* 28: 318–323.

Latta RG, Linhart YB, Fleck D & Elliot M. 1998. Direct and indirect estimates of seed versus pollen movement within a population of ponderosa pine. *Evolution* 52: 61–67.

Lee SL. 2000. Mating system parameters of *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae) in three different forest types and a seed orchard. *Heredity* 85: 338–345.

Lee SL, Tani T, Ng KKS & Tsumura Y. 2004. Isolation and characterization of 20 microsatellite loci for an important tropical tree *Shorea leprosula* (Dipterocarpaceae) and their applicability to *S. parvifolia*. *Molecular Ecology Notes* 4: 222–225.

Manly BFJ. 1997. *Randomization, Bootstraps, and Monte Carlo Methods in Biology*. Chapman & Hall, London.

Momose K, Yumoto T, Nagamitsu T et al. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85: 1477–1501.

Moran PAP. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37: 17–23.

Murray M & Thompson WF. 1980. Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* 8: 4321–4325.

Ng KKS, Lee SL & Koh CL. 2004. Spatial studies and genetic diversity of two dipterocarps with contrasting breeding system and different ploidy levels. *Molecular Ecology* 13: 657–670.

Ng KKS, Lee SL, Saw LG, Plotkin JB & Koh CL. 2006. Spatial structure and genetic diversity of three tropical tree species with different habitat preferences. *Tree Genetics and Genomes* 3: 121–131.

Niiyama K, Abd Rahman K, Iida S, Kimura K, Azizi R & Appanah S. 1999. Spatial patterns of common tree species relating to topography, canopy gaps and understorey vegetation in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science* 11: 731–745.

Okuda T, Kachi N, Yap SK & Manokaran N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rain forest—implications for regeneration and maintenance of species diversity. *Plant Ecology* 131: 155–177.

Palmiotto PA, Davies SJ, Vogt KA, Ashton MS, Vogt DJ & Ashton PS. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology* 92: 609–623.

Parker KC, Hamrick JL, Parker AL & Nason JD. 2001. Fine-scale genetic structure in *Pinus clausa* (Pinaceae) populations: effects of disturbance history. *Heredity* 87: 99–113.

Plotkin JB, Potts M, Leslie N, Manokaran N, LaFrankie J. & Ashton PS. 2000. Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology* 207: 81–99.

Plotkin JB, Chave J & Ashton PS. 2002. Cluster analysis of spatial pattern in Malaysian tree species. *American Naturalist* 160: 629–644.

Potts MD, Davies SJ, Bossert WH, Tan S & Nur Supardi MN. 2004. Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia* 139: 446–474.

Ripley BD. 1976. The second-order analysis of stationary processes. *Journal of Applied Probability* 13: 255–266.

Sakai S, Momose K, Yumoto T, Kato M & Inoue T. 1999. Beetle pollination of *Shorea parvifolia* (section *Mutica*, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia. *American Journal of Botany* 86: 62–69.

Seidler TG & Plotkin JB. 2006. Seed dispersal and spatial pattern in tropical trees. *PLOS Biology* 4: e344.

Smith JR, Bagchi R, Ellens J et al. 2015. Predicting dispersal of auto-gyrating fruit in tropical trees: a case study from the Dipterocarpaceae. *Ecology and Evolution* 5: 1794–1801.

Smouse P & Peakall R. 1999. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity* 82*:* 561–573.

Sokal RR & Oden NL. 1978. Spatial autocorrelation in biology: I. Methodology. *Biological Journal of Linnean Society* 10: 199–228.

Streiff R, Labbe T, Bacilieri R, Steinkellner H, Glossl J & Kremer A. 1998. Within-population genetic structure in *Quercus robur* L. & *Quercus petraea* (Matt.) Liebl. assessed with isozymes and microsatellites. *Molecular Ecology* 7: 317–328.

Symington CF. 1943. *Foresters' Manual of Dipterocarps*. Malayan Forest Record No. 16. University Malaya Press, Kuala Lumpur.

Vekemans V & Hardy OJ. 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology* 13: 921–935.

Wan Juliana WA, Burslem DFRP & Swaine MD. 2009. Nutrient limitation of seedling growth on contrasting soils from Pasoh Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science* 21: 316–327.

Wan Juliana WA. 2001. Habitat specialization of tree species in a tropical rain forest. PhD thesis, University of Aberdeen.

Wills C & Condit R. 1999. Similar non-random processes maintain diversity in two tropical rainforests. *Proceedings of the Royal Society of London* 266: 1445–1452.

Wright S. 1943. Isolation by distance. *Genetics* 28: 114–138.

Zaidey AK, Arifin A, Zahari I et al. 2010. Characterizing soil properties of lowland and hill dipterocarp forests at Peninsular Malaysia. *International Journal of Soil Science* 5: 112–130.

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