

INTEGRATING GENETIC FACTORS INTO MANAGEMENT OF TROPICAL ASIAN PRODUCTION FOREST: A REVIEW OF CURRENT KNOWLEDGE

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Abstract

Maintaining the genetic viability of timber species is especially important to sustaining the productivity and quality of timber in tropical production forests because the diversity of tree species is high, their population densities are low, and pollen dispersal of many species is limited to short distances. Conservation the genetic diversity of timber species also enhances the conservation value of production forests and contributes to landscape connectivity. Tropical forests are commonly managed under selection logging regimes with minimum diameter cutting limits. These typically result in systematic removal of the largest and often the most fecund trees. Very little guidance is available to forest managers on the measures needed to maintain viable populations of timber species in production forests. We reviewed current knowledge regarding the impacts of logging on genetic processes in tropical Asian tree species to find foundations for developing practical guidelines for managing these impacts and to identify research needs. The review focuses on mixed dipterocarp forests, where the canopy layer is dominated by trees of the Dipterocarpaceae family, one of the most globally important timber family. We examined the impacts of practices including logging intensity, minimum diameter cutting limits and spatial patterns of tree removal with regards to biological parameters such as effective breeding units, size at reproductive maturity, fine-scale spatial genetic structure and the importance of general flowering in producing diverse seed. Research conducted to date shows that because of characteristics such as naturally low population densities, limited pollen dispersal and fine-scale spatial genetic structure, many tree species in mixed dipterocarp forests are sensitive to reductions in the density of reproductive conspecifics; in most cases tree extraction resulted in increased inbreeding. Although genetic research in these forests is still limited, enough knowledge exists to initiate the development of practical management guidelines e.g. on minimum population densities as a precondition for logging or documentation of sources of propagation material used in enrichment planting. Future research should focus on studying species characteristics which can indicate vulnerability to genetic erosion and the prevalence of these characteristics among species in mixed dipterocarp forests, to identify species or species groups which may require specific measures to maintain genetically viable populations in logged forests and in the larger landscape. Such characteristics may include large size at reproductive maturity or slow increase in fecundity with size, fine-scale spatial genetic structure, low population densities, limited pollen dispersal, or high juvenile mortality.

Keywords: genetic diversity; population size; selective logging; habitat fragmentation; forest management guidelines; Dipterocarpaceae

1. INTRODUCTION

The focus of biodiversity conservation in production forests is often the protection of rare and endangered species. To sustain productivity and quality of timber yields over time, forest management practices should also maintain genetically viable populations of timber species which are not subject to inbreeding, produce large numbers of progeny with good survival and retain evolutionary potential in the longer term. Consideration of population size is particularly important in tropical forests where diversity of tree species is high, population densities are low, and many species are insect-pollinated, which may limit pollen flow to relatively short distances (Dick et al., 2008). Natural forests in the humid and subhumid tropics are commonly managed under selection logging regimes (Putz et al., 2012), applying minimum diameter cutting limits which may result in removing trees before they reach their optimal regeneration size. This can result in smaller reproductive populations which are at risk of inbreeding. Increased inbreeding and loss of genetic diversity can have severe negative effects on populations, for instance, reducing growth, reproductive output, ability to resist pests and diseases and capacity to adapt to environmental variation (Ellstrand and Elam, 1993; Hughes et al., 2008).

Incorporating genetic conservation measures in the management of the approximately 400 million hectares of production forests in the tropics (Blaser et al., 2011) would enhance the conservation value of these forests and complement other strategies for genetic conservation, such as the establishment of genetic reserves and restoration of endangered tree species. International criteria and indicators for sustainable forest management already require that forest managers take measures to conserve genetic diversity (e.g. ITTO, 2005; FSC, 2010; PEFC, 2010), but little guidance is available on how to integrate genetic conservation in the management of production forests (see, however, Jennings et al., 2001; Sist et al., 2003a).

In tropical Asia, selective logging of natural mixed dipterocarp forests is an important economic activity. These forests are among the most species-rich in the world, with 150–250 tree species ha^{-1} (Manokaran and Kochummen, 1987; Cannon et al., 1998; Brearley et al., 2004) and correspondingly low densities of individual species. The canopy is dominated by dipterocarp species (Dipterocarpaceae; including the genera *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, *Shorea*, *Upuna* and *Vatica*). The proportion of dipterocarps species varies according to forest type and site but is, on average, 25–30% of all stems and 50–80% of stems in the emergent layer (Appanah, 1998). Population densities of dipterocarps in unlogged forest vary from less than one reproductive tree ha^{-1} up to 10–15 trees ha^{-1} depending on the gregariousness of the species and the forest type (Kitamura et al., 1994; Konuma et al., 2000; Lee, S.L. et al., 2006). Logging prescriptions in dipterocarp forests generally allow the cutting of all trees 100 of commercial species which exceed the minimum diameter cutting limits (Table 1). Extraction rates vary between 8 to 15 stems or 50 to 100 $\text{m}^3 \text{ha}^{-1}$ (Sist et al., 2003a). In some cases, maximum cutting limits or maximum volumes for timber extraction are defined to control logging (Table 1). Some guidelines also exist to control species composition of the residual stand; for example, in Peninsular Malaysia, a higher minimum diameter cutting limit is applied to dipterocarp species than to non-dipterocarps, with the goal of maintaining the proportion of dipterocarps in emergent canopy layers over time (Forestry Department of Peninsular Malaysia, 1997; Shaharuddin, 2011). The aim of the Selective Management System (SMS) of Malaysia is to ensure sufficient residual stock and advanced regeneration (Appanah, 1998) and enrichment planting is usually limited to cleared areas such as forest roads, logging tracks and timber collection areas (Forestry Department of Peninsular Malaysia, pers. comm.). In contrast, large-scale propagation and planting has

Table 1 Typical prescriptions in selective logging guidelines, with examples from Malaysia.

Prescription	Example
Pre-felling inventory	All tree species ≥ 5 cm dbh or ≥ 15 cm of height by dbh class, species and volume or stems ha^{-1} , inventoried 1-2 years before logging, to assess harvestable volume and regeneration (Peninsular Malaysia)
Minimum diameter cutting limit	65 cm and 55 cm dbh for dipterocarps and non-dipterocarps, respectively (Peninsular Malaysia)
Maximum diameter cutting limit ^a	120 cm dbh (Sabah, Malaysia)
Target length of cutting cycle	30 years (Peninsular Malaysia)
Maximum extraction limit ^a	85 $\text{m}^3 \text{ha}^{-1}$ (including trees damaged during logging, typically estimated at 30%; Peninsular Malaysia)
Species protected from harvesting	Fruit tree species: <i>Mangifera</i> spp., <i>Durio</i> spp., <i>Lansium</i> spp., <i>Nephelium</i> spp.; bee nesting trees: <i>Koompassia excelsa</i> (Becc.) Taub. (Fabaceae); valuable threatened timber and non-timber spp.: <i>Intsia</i> spp., <i>Aquilaria malaccensis</i> Lam. (Thymelaeaceae) (Sabah, Malaysia)
Residual trees	At least 32 trees ha^{-1} exceeding 30 cm dbh. Preferred species are defined in a Reference Species list. (Peninsular Malaysia)
Mother trees	At least 4 healthy trees ha^{-1} exceeding 30 cm dbh, at an approximately even spacing. Preferred species are defined in a Reference Species list (Peninsular Malaysia)
Post-felling inventory	2-5 years after logging, using systematic line plots to determine residual stocking and appropriate silvicultural treatments (Peninsular Malaysia)

^a Not a common prescription

Sources: The Government of the State of Sabah (1968); Thang (1988); Forestry Department of Peninsular Malaysia (1997); Shaharuddin (2011); Forestry Department, Peninsular Malaysia (pers. comm.)

been carried out in Indonesia as part of the Selective Cutting and Planting System TPTI (Weinland, 1998) which has involved clearing the understory and the destruction of advanced regeneration.

Dipterocarps have many unique characteristics which suggest that their genetic response to disturbance differs from other species. Most of the dipterocarps flower and produce seeds at irregular intervals, typically at synchronized general flowering events occurring every few years (also known as mast fruiting; Ashton, 1982; Cannon et al., 2007). They are monoecious and pollinated by insects, many of which are small, which limits pollen flow (Chan and Appanah, 1980; Momose et al., 1998), yet they have relatively high outcrossing rates (Lee, S.L. et al., 2000a; Tsumura, 2011). Self-incompatibility mechanisms are generally weak (Bawa, 1998) and inbreeding depression is considerable (section 2.3). Seed dispersal occurs mainly via gravity over short distances, typically 20–50 m (Chan, 1980). As a result of limited pollen or seed dispersal or both, many dipterocarp species demonstrate a fine-scale spatial genetic structure (FSGS) in which nearby individuals are genetically related (section 2.2). Seeds of dipterocarps are recalcitrant, so the species lack a soil seed bank (Ashton, 1982). Seedlings are generally shade-tolerant and can persist in the understory for several years, although increased light is required for satisfactory establishment and growth (Ashton, 1998). Most dipterocarp species have a reverse J-shaped diameter distribution where most individuals belong to the smallest diameter classes; the density of saplings and pole-sized trees is, however, generally low (Appanah and Weinland, 1993; Appanah, 1998).

Despite the commercial importance and specific biology of dipterocarps, few studies exist on the genetic impacts of disturbance on these species, and most studies are on the impacts of logging (e.g. Murawski et al., 1994; Lee S.L., 2000; Ng et al., 2009). Currently, most knowledge about the genetic impacts of habitat degradation and fragmentation in tropical tree species comes from studies in the Neotropics (reviewed in Lowe et al., 2005). Frequent long-distance pollination has been observed in many neotropical tree species (Ward et al., 2005), indicating that they may be relatively tolerant to reduction in population densities as a result of logging (Degen et al., 2006; Silva et al., 2008). Specific long-distance pollinators are less common in tropical Asia than in the Neotropics (Momose et al., 1998). Because of their typically limited pollen dispersal, dipterocarp species may be more vulnerable to disturbances that reduce the density of reproductive individuals than neotropical species. Other characteristics common among dipterocarps, namely lack of a soil seed bank, slow attainment of reproductive maturity and risk of damage by logging operations to juvenile tree cohorts, were also linked to increased vulnerability of reproduction to logging (Jennings et al. 2001). In addition, the impacts of logging on tree density tend to be higher in Asian dipterocarp forests than in Latin American or African tropical forests because the number of trees removed per ha is higher (Sist et al., 2003b).

In this paper we review current knowledge about the impacts of logging on the genetic diversity, reproduction and mating systems of tree species in tropical Asia. We focus on the impacts at individual and population levels (the latter is similar to the typical scale of concession areas in mixed dipterocarp forests, 100–200 ha; Forestry Department of Peninsular Malaysia, pers. comm) but include insights from the few existing studies of the impacts of anthropogenic habitat fragmentation on tropical Asian tree species. We focus on dipterocarp species because of their commercial importance and the fact that most of information available is on this family. However, we recognize that the number of commercially harvested species in tropical forests is increasing as more forest area enters the second cycle of selective logging (Putz et al. 2012), and knowledge about the genetic diversity and vulnerability of other tropical Asian species is urgently needed (Wickneswari, 2011). Where studies on the genetic response of tropical Asian tree species to logging regimes are particularly limited, we include research results from other tropical regions to explore what factors, generally, may affect such responses. Research gaps are then discussed with respect to identifying thresholds that may be specific to species or groups of species and developing practical recommendations. Genetic diversity is just one factor affecting the successful establishment and development of seedlings; others include light and soil conditions, seed dispersal and predation, herbivory, disturbance regimes and adverse weather. Reviewing ecological aspects of regeneration is outside the scope of this review, but a combination of conservation approaches based on ecological and genetic factors would best ensure regeneration success in the short term and population viability in the long term.

2. ADVANCING LOGGING PRACTICES IN SOUTHEAST ASIAN PRODUCTION FORESTS TO ACCOUNT FOR GENETIC FACTORS

2.1 Maintaining effective breeding units: tree extraction and diameter cutting limits

Both experimental studies and theoretical studies involving modeling have shown relationships between the density of flowering conspecifics, outcrossing rates and genetic relatedness among progeny (Lowe et al., 2005). Of the nine studies which we found on tropical Asian species, the effects of logging or

naturally lower density of flowering trees as compared to other populations resulted in increased inbreeding in seven cases (Murawski et al., 1994; Liengsiri et al., 1998; Lee, S.L., 2000; Obayashi et al., 2002; Naito et al., 2005, 2008b; Fukue et al., 2007) (Table 2). In one study the difference in outcrossing rate between unlogged and logged populations was negligible, possibly because the density of flowering trees remained high even after logging (Kitamura et al., 1994), and in one study a moderate decrease in the proportion of flowering trees between years did not affect the proportion of outcrossed progeny among seedlings but increased inbreeding resulting from mating between relatives (Kenta et al., 2004). In addition to these nine studies on mating systems, we found one study where the impact of habitat degradation on reproductive output was analyzed. The proportion of fruits of *Shorea siamensis* developing to maturity was significantly lower on a heavily disturbed site that had been subject to widespread tree extraction than on an undisturbed site, while no difference was found between moderately disturbed and undisturbed sites (Ghazhoul et al., 1998).

We found six studies where the impacts of anthropogenic habitat fragmentation on mating systems of Asian tree species were analyzed, and in four of these, negative impacts on inbreeding (Lee S.L. et al., 2002; Ismail et al., 2012; Bodare et al., 2013) or kinship among juveniles (Finger et al., 2012) were observed (all except Ismail, 2013; Takeuchi et al., 2013). Pollen was dispersed mainly over short distances of up to 50-150 m and probably only within forest fragments (cf. Kramer et al., 2008), with the exception of *Dysoxylum malabaricum*, which maintained extensive pollen flow across the landscape (Ismail et al., 2012; Bodare et al., 2013). Pollen dispersal distances were shorter in the fragmented than the continuous populations (Ismail et al., 2012; Takeuchi et al., 2013). Selection against inbred seedlings in some species (Ismail, 2013) and self-compatibility in others (Finger et al., 2012) may provide some resistance against genetic erosion in fragmented habitats. Over time, however, the former may result in reduced regeneration whereas the latter may impair fitness of future tree generations, although such impacts are little understood. Shorter pollen dispersal distances in fragmented populations suggest that the combined effects of habitat fragmentation and reduced population densities (e.g. as a result of selective logging) on mating systems may be severe. Synergistic effects of different types of disturbances on forest biodiversity have hardly been studied (Bawa and Seidler, 1998). We found no documented evidence of stimulation of pollen flow as a result of logging, habitat fragmentation or reproductive isolation in tropical Asian tree species, contrary to what was observed in forest fragments elsewhere (Lowe et al., 2005; Kramer et al., 2008). When density of flowering trees in the population decreases, average pollen flow distance can increase because short distance mating events become less frequent, but probability of long distance mating events is not necessarily higher (cf. Tani et al., 2012).

The threshold of reproductive tree density at which negative effects on reproductive success increase disproportionately depends, for instance, on the number and relative fecundity of flowering trees, flowering synchrony (Lee, S.L., 2000), pollination patterns and site-specific factors such as temperature, wind and solar radiation, which affect pollination (Sedgley and Griffin, 1989; Liow et al., 2001). There is evidence from community-level studies that dipterocarp trees exceeding 30 cm dbh commonly flower (Appanah and Rasol, 1993; Nguyen-Thé and Sist, 1998; Numata et al., 2011). This size corresponds to a minimum diameter requirement for parent trees in Malaysian logging guidelines (Table 1). Fecundity is related to crown size and geometry, which vary widely among dipterocarps from subcanopy to emergent species (Osunkoya et al., 2007). Very little is known about the relation between tree size and fecundity in specific species. Medium-sized *Shorea acuminata* trees flowered less frequently than large (>70 cm dbh) trees and instead concentrated their reproductive investment in general flowering events. Flower production and total dry mass of fruit increased monotonically with tree size up to 90 cm dbh. However,

Table 2 Impact of disturbance on outcrossing rates of tropical Asian tree species^a. Form of disturbance is logging except for *Pterocarpus macrocarpus* for which it included deforestation, soil erosion, fuel wood harvesting and cattle grazing. The other species all belong to the family of Dipterocarpaceae.

Species	Forest type (Country)	Outcrossing (%)		Reference
		Undisturbed	Disturbed	
<i>Dryobalanops aromatica</i> Gaertn. f.	lowland dipterocarp forest (Brunei)	77	68-72	Kitamura et al. (1994)
<i>Dryobalanops aromatica</i>	lowland dipterocarp forest (Malaysia)	92	77	Lee, S.L. (2000)
<i>Pterocarpus macrocarpus</i> Kurz (Fabaceae)	Mixed deciduous, hill evergreen and dry dipterocarp forests (Thailand)	95-96	72-90	Liengsiri et al. (1998)
<i>Shorea curtisii</i> Dyer ex King	Hill dipterocarp forest (Malaysia)	96	52	Obayashi et al. (2002)
<i>Shorea megistophylla</i> (Thw.) Ashton	(Sri Lanka)	87	71	Murawski et al. (1994)

^a The studies cited in the text include those examining the impact of natural variation in population density on 590 habitat fragmentation outcrossing rates.

seed set did not correlate with tree size (Naito et al., 2008a). A high variation in male fecundity was observed in *Shorea curtisii*, with small trees (<50cm dbh) contributing less than large trees to the analysed seed pool (Tani et al., 2012). If trees in large diameter classes are on average more fecund than trees in small or intermediate diameter classes, minimum diameter cutting limits that promote the systematic removal of large trees may negatively affect reproduction (Mack, 1997; Tani et al., 2012).

Reduced density of large trees and intensity of flowering probably contributed to lower abundance of bees and different species composition of bee communities in logged and other disturbed forests as compared to primary forests in Malaysia and Singapore (Liow et al., 2001; Samejima et al., 2004). Even if population sizes of pollinators were maintained following disturbance, pollination processes may be disrupted through changes in pollinator foraging behaviour, such as reduced movement between trees (Ghazoul et al., 1998). Such changes may also affect tree species which are mainly pollinated by long-distance pollinators: pollen dispersal distances were reduced by half and the proportion of short distance mating events almost doubled in forest fragments where the density of mature *Dysoxylum malabricum* (Meliaceae) trees was low, as compared to fragments with a high density of mature trees (Ismail et al., 2012). Impacts of reduced tree population sizes on inbreeding may be exacerbated by subsequent changes in pollination patterns, but little is known about these interactions.

As a rule of thumb, it has been proposed that tree populations should be able to recover to at least 50 reproductive trees after logging (Jennings et al., 2001). In general, a random sample of 50 individuals can be expected to contain at least one copy of all common alleles in a population at >95% certainty (Brown and Hardner, 2000). Based on an observation that neotropical trees pollinated by small diverse insects received 95% of their pollen from within an area of 40–60 ha (Stacy et al., 1996), Jennings et al. (2001) proposed that on average at least one tree ha⁻¹ per species should be retained during logging to achieve a population size of at least 50 trees. Sist et al. (2003a) adapted this logic to recommend that dipterocarp species which occur at average densities lower than one reproductive tree ≥ 50 cm dbh) ha⁻¹

should not be harvested. They also proposed a minimum diameter cutting limit of 60 cm dbh for dipterocarp species which have a reverse J-shaped diameter distribution to ensure that reproductive trees are maintained in sufficient numbers. However, because population densities vary widely depending on species and site, they may be more easily managed through guidelines on minimum population densities as a precondition for logging than through minimum cutting diameters.

One approach to approximating the population size is the breeding unit, which can be estimated as the circular area around a female tree within which 99% of potential mates are expected to occur, based on paternity analysis (Nason et al., 1998). Breeding units have been estimated for two tropical Asian tree species which are predominantly outcrossing but otherwise have differing life-history traits. In a primary forest the breeding unit of *Neobalanocarpus heimii*, a widespread and semi-gregarious species, was estimated to include 62 trees, corresponding to an area of 68 ha and population density of 0.7 reproductive trees ha⁻¹ (Konuma et al. 2000). The breeding unit size for *Shorea lumutensis*, a rare but locally abundant species, was estimated to be 52 trees (12 ha with 4.3 trees ha⁻¹) (Lee, S.L. et al., 2006). Studies are ongoing on *Shorea leprosula*, *S. parvifolia* and *S. curtisii*, with preliminary results revealing breeding units varying from 90 to over 200 trees over areas of approximately 70 ha (Lee, S.L. et al., unpublished).

Requirements are already in place in many countries for retaining a prescribed number of residual and reproductive trees (Appanah, 1998; Shaharuddin, 2011). However, such prescriptions are probably not sufficient to maintain viable populations through high outcrossing rates because residual or reproductive trees retained in adjacent areas in species-rich tropical forests may be of different species. Residual trees may also include trees that are not reproductively mature. Guidelines on average minimum densities for reproductive trees as a precondition for logging, evaluated over areas of 50–100 ha, could complement the current guidelines on the total number of residual or reproductive trees by adding the dimension of effective breeding unit, and help reduce the risk of inbreeding after logging (Jennings et al., 2001; Sist et al., 2003a; Tsumura, 2011). The information available on breeding unit sizes for dipterocarp species suggests that retaining at least one reproductive tree ha⁻¹ per species would contribute to maintaining viable populations of timber trees throughout multiple cutting cycles. However, higher minimum densities are probably needed for some species (Konuma et al., 2000; Lee, S.L. et al., unpublished). Such guidelines could be readily implemented, as information about tree density per species is already collected as a standard procedure in many cases, through mandatory pre-felling inventories of harvestable trees by species or species codes (Table 1).

However, the accuracy of species identification by field staff affects the implementation and effectiveness of such forest management practices (Lacerda and Nimmo, 2010). The pre-felling inventory associated with the Malaysian Selective Management System was insufficient to accurately estimate species diversity (α -diversity) in lowland dipterocarp forests at small spatial scales of 1–4 ha, but could be used to extrapolate species diversity accurately enough at scales of approximately 100 ha (Potts et al., 2005). Tree identification to species level is considered accurate for the main commercial tree species but less accurate for lesser-known, non-commercial species or closely related species (Forestry Department of Peninsular Malaysia, pers. comm.), which suggests that species-specific guidelines could effectively be applied at least for the main timber species on the basis of the pre-felling inventories. Including forest botanists in the field teams conducting pre-felling inventories is increasingly important as more and more species are harvested (Putz et al. 2012) but there is shortage of adequately trained staff for species identification.

More research is needed on breeding units and the impacts of tree extraction on inbreeding for a larger number of species with differing life-history traits, across sites, under different logging regimes and over multiple years to provide a foundation for managing the negative effects of logging on mating systems. Information on the size at which trees reach maturity and high fecundity would help in assessing whether the current guidelines for the sizes of residual trees (Table 1) are sufficient to restore a reproductive and fecund population over the cutting cycle at given diameter growth rates. There are no empirical results yet to indicate whether higher minimum diameter cutting limits, or the retention of some trees larger than the current minimum diameter limits, would increase reproductive output and genetic diversity in progeny. Effects of environmental conditions, including disturbance and light regime, on maturity and fecundity are little understood and require further research on a variety of species. More research is also needed on the impacts of current forest management practices on pollination patterns, including (i) the impacts of logging and habitat fragmentation on pollinator behaviour and, consequently, reproductive output in tropical Asian tree species, and (ii) the impact of current practices intended to favour populations of pollinators and seed dispersers, such as protection from logging of fruit tree species and bee nesting trees (Table 1).

2.2 Considering fine-scale spatial genetic structure in tree extraction

Inbreeding may occur more frequently when reproductive trees are clumped than when they are randomly distributed (Stacy et al., 1996; Lee, S.L., 2000; Harata et al., 2011). This is especially true for species with weak pollen or seed dispersal and for which neighbouring trees are, therefore, commonly related (fine scale spatial genetic structure, FSGS) (Takeuchi et al., 2004; Ng et al., 2004; Harata et al., 2011). Such species may be particularly vulnerable to increased inbreeding or loss of genetic diversity as a result of disruption in pollination patterns, changes in population sizes or habitat fragmentation, which increase the proportion of mating events at short distances (Kettle et al., 2011a, 2012; Ismail et al., 2012). Both experimental and simulation studies indicate that for species with a significant FSGS, removing and retaining trees in clumps, rather than individually, may further reinforce FSGS and its negative effects on mating systems and genetic diversity (Ng et al., 2004, 2009; see also Lee, S.L., 2000). Being able to predict the occurrence of FSGS based on species traits, without the need for genetic studies, would help forest managers adjust logging practices by species or species groups so as to minimize inbreeding.

Clumped distribution may reflect low survival of seedlings under shade and dependency on gap formation for regeneration (Kettle et al., 2011a), or narrow habitat niche of the species (Ng et al., 2006; see also Kettle et al., 2012) which may be revealed through small clump radius and long distance between the clumps (Harata et al., 2011). Clumped distribution of reproductive trees is common among species in lowland dipterocarp forest (Okuda et al., 1997). Small sizes of flowers and of pollinators can indicate weak pollen dispersal (Harata et al., 2011, Kettle et al., 2011a, 2011b). Effective pollen dispersal (Konuma et al., 2000; Ng et al., 2006; Kettle et al., 2011a) and population densities which allow for overlapping seed dispersal of unrelated trees (Hamrick et al., 1993; Vekemans and Hardy 2004; Ng et al., 2006; Pandey and Geburek, 2011) may counteract factors contributing to FSGS. In addition, FSGS may be less pronounced among emergent canopy trees which can disperse pollen and seed further than small trees (Takeuchi et al., 2004).

Because of the complexity of the factors shaping FSGS, more comparative studies on its relationship with species traits and trait combinations are needed before FSGS can be better predicted at a species level (Kettle et al., 2011a). Nevertheless, the studies conducted so far suggest that FSGS is

common among dipterocarps in lowland forests (Takeuchi et al., 2004; Ng et al., 2004, 2006; Harata et al., 2011; Kettle et al., 2011a). Given the risk of inbreeding in species with pronounced FSGS, harvesting trees individually rather than in clumps should be considered when species have known or potentially significant FSGS. Isolation of trees from conspecifics should, however, be avoided in species with limited pollen flow as it is also associated with increased selfing (section 2.1; Nagamitsu et al., 2001). Retaining relatively high densities of conspecifics (Hamrick et al., 1993; Vekemans and Hardy, 2004) or enabling longer generation time (i.e. longer cutting cycles or retention of large trees) (Loveless and Hamrick, 1984) could help reduce the negative implications of pronounced FSGS.

2.3 Promoting reproduction and the vigour and survival of progeny

Large seedling populations were suggested to serve as an indicator of low risk of genetic erosion in species with a reverse J-shaped diameter distribution by Jennings et al. (2001). They associated directly the size and genetic diversity of tree cohorts, proposing that since the juvenile cohorts are the largest, they would also be genetically the most diverse. However, species with weak incompatibility mechanisms may compensate for the reduction in reproductive conspecifics by increased mating between close relatives or selfing, and, therefore, produce abundant but genetically inferior seed (Murawski and Hamrick, 1992; Aldrich et al., 1998). The value of seedling abundance as an indicator of genetic health would thus depend on the level of inbreeding depression and the developmental phase at which it is expressed.

Because dipterocarps generally have considerable inbreeding depression, at least part of which occurs at an early stage (Konuma et al., 2000; Lee, S.L., 2000; Lee S.L., et al., 2000b; Naito et al., 2005), it is possible that changes in inbreeding may be reflected in the size of the seedling pool. Survival of seeds and seedlings of *Shorea* spp. is known to be low in sporadic flowering years and much higher during general flowering (Chan, 1980; Sakai, 2002; Tokumoto et al., 2009), when the larger parental pool results in more effective outcrossing and gene recombination and seed is assumed to be genetically more diverse (Chan, 1980; Tani et al., 2012). Intense flowering stimulates pollinator activity, which further contributes to cross-pollination (Sakai, 2002), even if densities of flowering trees for particular species were relatively low (Tani et al., 2009). Male mating success was higher during general flowering than sporadic flowering of *Shorea curtisii* (Tani et al., 2012), *S. leprosula* and *S. parvifolia*, although the density of flowering trees of *S. parvifolia* was actually lower than during a sporadic flowering (Tani et al., 2009). It has been recommended that collection of seed of dipterocarps for planting should rely on general flowering events (Chan, 1980). Satiation of fruit and seed predators may also contribute to better survival of regeneration during general flowering than sporadic flowering (Curran et al., 1999). According to a study in Indonesian Borneo, logging, coupled with climatic effects such as El Niño, contributed to reducing the amount of viable seed and seedling establishment, resulting in widespread recruitment failure among dipterocarp genera. Seedling production in logged forests remained low compared to that in unlogged forest even several years after logging and after general flowering events (Curran et al., 1999).

Population-level studies combining both genetic and ecological measurements and comparing logged and unlogged populations can reveal relationships between the genetic diversity of seedling pools and that of their parental gene pools (Aldrich et al., 1998). Simulation methods could also be applied to study these questions, as was recently done for a neotropical tree, *Dicorynia guianensis* (Fabaceae), with results showing that juvenile mortality (dbh 1–10 cm) was the main factor affecting genetic diversity, genetic distance between tree generations and the number of genotypes over time (Wernsdörfer et al., 2011). Selfing rate had the greatest impact on observed heterozygosity and fixation index. *Dicorynia*

guianensis reaches reproductive maturity at approximately 25 cm dbh, high fecundity at 46 cm dbh and is typically felled at 60 cm dbh. The simulations assumed effective cross-pollination with a fixed number of 15 pollen donors per mother tree (Wernsdörfer et al., 2011). Similar studies should be conducted on species which can be assumed to be more vulnerable to genetic erosion e.g. because of shade intolerance, slower size-related increases in fecundity, limited gene flow that restricts the number of pollen donors, or weak self-incompatibility mechanisms. Evaluating the relative importance of juvenile mortality vs. mating system in determining genetic diversity in progeny also requires further improvements in the description of genetic processes in simulation models. For example, minimum cutting diameters and population density were fixed parameters in the model of Wernsdörfer et al. (2011), while in another simulation study they were found to be the most important variables affecting genetic parameters in four neotropical tree species (Degen et al., 2006). It remains unclear how changes in genetic parameters estimated on the basis of presumably neutral DNA markers relate to changes in adaptive traits (Wernsdörfer et al., 2011).

While experimental evidence for the relationship between the number and genetic diversity of progeny remains scant, monitoring and protecting regeneration certainly contributes to sustainable forestry. Seedling mortality is expected to increase with climate change, and large, diverse seedling populations are likely to favour adaptation by tree populations under conditions of changing climate (Guariguata et al., 2008; Sgrò et al., 2011). For shade-tolerant species such as most dipterocarps, density of young trees, seedlings and saplings should be evaluated prior to logging, and if low, logging should be suspended (Seng et al., 2004). Although such guidelines already exist in many countries (Shaharuddin, 2011), their implementation also needs to be ascertained. Negative impacts of logging on general flowering could possibly be alleviated e.g. by postponing logging until seedling establishment if general flowering occurred in the area, or restricting logging to the periods after flowering events which have resulted in high seedling recruitment, as was recommended under the Malayan Uniform System (MUS, Wyatt-Smith, 1963; Jennings et al., 2001). However, since general flowering events are unpredictable, established seedlings are easily destroyed during logging and negative impacts of logging on regeneration seem to persist for years (Curran et al., 1999), these impacts may be best managed by reducing logging intensity rather than timing.

If enrichment planting is conducted after logging, the propagation material should originate from a high number of non-related parent trees growing in conditions that are ecologically similar to those on the target site, to ensure sufficient genetic diversity for adaptation to the site conditions under changing climate and prevention of inbreeding in future generations (Bozzano et al., 2014). The origin of propagation material should be systematically documented, as is already required in some management guidelines in tropical Asian countries (e.g. The Government of the State of Sabah, 1968). Guidelines for seed zones and transfer of propagation material should be developed to conserve genetic integrity and facilitate the adaptation of introduced seedlings. To our knowledge there are currently no such guidelines for tropical Asian forest tree species which would be consistently applied (but see the Cambodia Tree Seed Project, 2003). Their development can be informed by recent phylogenetic studies which show distinct evolutionary lineages in different parts of insular Southeast Asia [e.g. *Shorea curtisii*, Kamiya et al., 2012; *S. parvifolia*, Iwanaga et al., 2012; *Intsia* spp. (Fabaceae), C. Jolivet, unpubl.] and within the Malay Peninsula (*Neobalanocarpus heimii*, Tnah et al., 2013). Propagation material should be tested before being moved across such evolutionary units. However, ensuring the genetic diversity of propagation material is more important for the successful establishment of resilient populations with evolutionary potential than sticking to strictly local germplasm sources that may be degraded and affected

by inbreeding or genetic drift (Broadhurst et al., 2008). Because reduction in population densities seems to commonly result in increased inbreeding among dipterocarp species (section 2.1), the quality of their populations as seed sources may be particularly sensitive to habitat degradation and fragmentation. Kettle (2010) and Kettle et al. (2010) stressed the importance of developing strategies and institutional capacities to collect seed and propagate large amounts of seedlings after general flowering events to ensure the availability of quality germplasm of dipterocarps.

2.4 Maintaining genetic diversity for fitness and evolutionary potential

Directional changes in the genetic composition of selectively logged populations are theoretically possible (Cornelius et al., 2005; Finkeldey and Hattermer, 2007) and were demonstrated through simulation studies (Degen et al., 2006). However, the effects of selection pressure on quantitative traits like growth, timber quality or tolerance to various stressors are difficult to establish in a natural environment because such traits are controlled by multiple loci and their expression is affected by environmental conditions (Finkeldey and Hattermer, 2007). Consequently, there are few scientifically rigorous studies on dysgenic selection through logging (but see Ziehe and Hattermer, 2002; Cornelius et al., 2005). Here we use overall genetic diversity and its distribution among generations as a proxy for adaptive capacity and population viability.

We found a total of 16 published cases (16 species or populations in a total of 7 studies) where impacts of logging on genetic diversity were examined for tropical Asian tree species. Genetic diversity was significantly reduced in five of the cases. In two of these, the same tree populations were compared before and immediately after logging (Wickneswari et al. 1997; 2004). In the other three cases the affected stands had been logged 40–50 years earlier and the impacts on genetic diversity were still evident decades later when logged stands were compared to adjacent unlogged stands, with the assumption that genetic diversity of the two stands was similar prior to logging (Lee, C.T. et al., 2002a; Wickneswari et al. 2004; Ng et al., 2009). Alleles lost through logging were mainly rare but included some common ones (Ng et al., 2009). Differences in genetic diversity between logged and unlogged populations were negligible in 11 other study species or populations (Lee, C.T. et al., 2002a, 2002b; Obayashi et al., 2002; Wickneswari et al., 1997, 2004; Zheng et al., 2005; Ng et al., 2009).

We also found seven studies where the impacts of anthropogenic habitat fragmentation on genetic diversity of tropical Asian tree species were studied (Lee, S.L. et al., 2002; Nageswara Rao et al., 2007; Dai et al., 2012; Finger et al., 2012; Ismail et al., 2012; Bodare et al., 2013; Ismail, 2013). In six of these, negative impacts on genetic diversity were observed (all except Bodare et al., 2013). Interestingly, genetic differentiation was higher among juveniles than among adults (Finger et al., 2012; Ismail et al., 2012) even when allelic richness among cohorts was not affected by habitat fragmentation (Ismail et al., 2012). The juvenile cohorts of *Vateriopsis seychellarum* contained only half of the rare alleles found in adult trees, indicating a severe genetic bottleneck (Finger et al., 2012).

Factors that appeared to reduce species' vulnerability to the impacts of logging or habitat fragmentation included:

- relatively high population densities after logging—*Scaphium macropodum*, when compared to affected stands of the same species (Lee, C.T. et al., 2002a; Wickneswari et al., 2004) and *Quercus tiaooshanica* (Fagaceae) (Zheng et al. 2005)
- long-distance pollen flow—*Dryobalanops aromatica* (Wickneswari et al., 2004) and *Dysoxylum malabaricum* (Ismail et al., 2012)

- mode of reproduction—apomixis in *Shorea ovalis* ssp. *sericea* (Ng et al., 2009) and self compatibility in *Vateriopsis seychellarum* (Finger et al., 2012)
- low logging pressure—low-quality timber species *Parkia speciosa* (Fabaceae) (Lee, C.T. et al., 2002b).

It should be noted that in several of the studies on the impacts of logging, only adult trees which pre-dated the harvest were sampled, and that may partly explain the lack of impacts on genetic diversity. As the results from fragmentation studies demonstrate, genetic parameters may differ notably between juvenile and adult trees in populations affected by human activity (Finger et al., 2012, Ismail et al., 2012, Vranckx et al., 2012). Human impacts associated with habitat fragmentation may have been more intense and longer lasting than logging impacts, where studies were often conducted in stands that had been logged only once. There may also be a considerable lag in time between logging and the effects on recruitment, especially for species which do not reproduce annually.

In neotropical trees, both negative and negligible impacts of logging on genetic diversity were observed in experimental and simulation studies (reviewed in Lowe et al., 2005). Logging tended to increase genetic distance between age classes (Lacerda et al., 2008; Sebenn et al., 2008) even when significant impacts on genetic diversity (mean and effective number of alleles) were not found (Degen et al., 2006). This pattern is similar to that described as resulting from habitat fragmentation on tropical Asian tree species (Finger et al., 2012; Ismail et al., 2012). Factors associated with tolerance to logging included reaching reproductive maturity at a moderate size (cf. Lacerda et al., 2008), high population density (Degen et al., 2006; cf. Lacerda et al., 2008; Sebenn et al., 2008), extensive pollen and seed dispersal (Degen et al., 2006; Silva et al. 2008, cf. Sebenn et al., 2008), low juvenile mortality (Wernsdörfer et al., 2011) and presence of overlapping generations (e.g. as in slow-growing and shade tolerant species), which allowed reproductive trees to contribute their genes to seedling populations over several reproductive events (Degen et al., 2006). Most of these are atypical among dipterocarps. It should be noted that risk of mating among related individuals may be higher if generations overlap (Jennings et al., 2001), especially for species with a pronounced FSGS.

Simulation studies showed that increasing minimum diameter cutting limits or extending cutting cycles consistently reduced the loss of genetic diversity or genetic distances between tree generations for neotropical (Degen et al., 2006; Sebenn et al., 2008; Wernsdörfer et al., 2011) and tropical Asian tree species (Ng et al., 2009). Because fecundity of dipterocarp species may increase with size long after they reach reproductive maturity (Naito et al., 2008a; Tani et al., 2012), minimum diameter cutting limits that exceed size at reproductive maturity could help avoid loss of and directional changes in population genetic diversity. Simulation methods can be helpful in studying long-term impacts of logging practices on genetic diversity and its distribution, but to our knowledge, dynamic forest growth models which include genetic parameters have not yet been applied to tropical Asian tree species.

In conclusion, research results on tropical Asian tree species suggest that genetic diversity found in harvested trees may often be, but is not consistently represented in non-harvested trees, either residual reproductive trees or younger tree cohorts. Even if rare alleles are present in seedling populations, they may easily be lost through seedling mortality (Lacerda et al., 2008). Current knowledge of the genetic response of Asian and other tropical species to disturbance suggests that characteristics typical to dipterocarps, e.g. restricted pollen dispersal, considerable inbreeding depression and fine-scale spatial genetic structure make many dipterocarps vulnerable to genetic erosion as a result of reproductive isolation and habitat fragmentation (see also section 2.1). This is supported by the evidence against the assumption that over time, gene flow from surrounding unlogged forests would compensate for the

reduction in diversity on logged areas (Lee, C.T. et al., 2002a; Wickneswari et al. 2004; Ng et al., 2009). These findings underline the need for incorporating genetic conservation measures in harvesting guidelines. Comparative studies, for instance by studying responses of several tree species within the same forest (Wickneswari et al., 1997; Lowe et al., 2005) and the impact of the same logging regimes across sites and landscape contexts (Bawa and Seidler, 1998), would be particularly useful for understanding how species characteristics (e.g. population densities, growth rate, shade tolerance, size at the onset of reproductive maturity, pollen and seed dispersal patterns), logging regime and environmental factors influence the genetic response of a species. Results also suggest that negative genetic impacts of anthropogenic habitat fragmentation may differ from and enhance the negative impacts of logging (see also section 2.1). Carefully designed studies are needed to distinguish these impacts and assess their combined effects on the fitness and adaptive capacity of tree populations in the heavily fragmented forested landscapes of tropical Asia, in order to inform management strategies at the level of forest management units. Molecular methods using presumably neutral DNA markers should be complemented with provenance and progeny trials to assess impacts on seedling performance. Simulation studies could help understand the complex interactions of disturbance impacts over tree generations.

Some loss of rare alleles after logging is inevitable, and preventing any loss is not a reasonable goal of genetic conservation practices in production forests. However, the implications of ongoing loss of rare alleles on population viability over time remain unknown. Retaining some large trees that exceed the cutting limits may be important to maintain the genetic diversity of timber tree populations in managed forests as a buffer against environmental changes (Degen et al., 2006; Sebenn et al., 2008; Ng et al., 2009; Wernsdörfer et al., 2011). For example, forestry guidelines in Sabah, Malaysia, already require that trees exceeding 120 cm dbh should be retained in logging as they are valued as seed trees (The Government of the State of Sabah, 1968). Guidelines should also ensure that recruitment of trees to the largest size classes is possible. Retention of very large trees is also useful for reasons beyond genetics. They often have structural defects which reduce their commercial value—but not their value as seed trees if the form defects are not genetically controlled. Felling large trees can be risky and especially damaging to the residual stand. Large trees are important for carbon storage and as microhabitats for maintaining biodiversity, including populations of pollinators (Lindenmayer et al., 2012).

Proposed guidelines from previous studies and respective conclusions and research needs from this study are summarized in Table 3.

3 CONCLUSIONS

Research shows that dipterocarps, the most important timber tree family in Asia, are sensitive to reductions in population densities, which commonly result in increased inbreeding. Genetic diversity is less frequently affected by logging, at least by single logging events, but loss of genetic diversity has been observed in some species and it may persist for decades after the impact. Moreover, disturbances can result in increased genetic differentiation between tree cohorts or populations even when genetic diversity is not affected, indicating vulnerability to genetic erosion over time. Effects of logging on the reproductive output and the vigour of progeny of the affected tree species have hardly been explored in tropical Asia but the few existing studies suggest such effects warrant attention. Contrary to what is often assumed, gene flow from surrounding unlogged forests is not likely to compensate for the reduction in

population sizes and genetic diversity on logged areas for species with limited gene flow. This emphasizes the need to incorporate genetic conservation measures in logging guidelines. Although experimental research on the genetic impacts of logging and other forms of disturbance is still limited, practical genetic conservation measures can already be identified, building on the knowledge of species' characteristics and probable responses. More guidelines with a species-specific focus need to be developed which consider variation e.g. in natural population densities, mating systems and pollen and seed dispersal patterns. This requires more research on the reproductive biology and ecology of a wider group of tree species representing different life-history traits. Simulation models should be developed for tropical Asian tree species to study genetic implications of forest management practices over tree generations. Lastly, the combined impacts of logging with other forms of disturbance such as anthropogenic habitat fragmentation and climate change should be studied to better understand and manage the threats to genetic diversity of trees and to associated species such as pollinators and seed dispersers. Both threats and opportunities are conceivable: while incorporating genetic conservation measures in the management of tropical production forests is important for sustaining quality timber yields, it can also contribute to landscape connectivity and genetic conservation across species distribution ranges, given the vast extent of these forests.

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Table 3 Strategies for maintaining genetic diversity of timber species in managed forests, from literature.

Strategy	Species group of specific concern	Source	Main conclusions or research needs for mixed dipterocarp forests from this study
Discover size at reproductive maturity	Slow-growing species which reproduce only when large	Jennings et al. (2001)	Current cutting limits seem sufficient to allow many species reach maturity, but research is needed on the relationship between tree size and fecundity and its impacts on reproduction (section 2.1)
Ensure sufficient juveniles to replace each harvested tree or that the population recuperates to at least 50 reproductive trees before next logging. For species with low-energy pollinators, retain in average at least one tree per species ha ⁻¹ .	Any species	Jennings et al. (2001)	Number of reproductive trees after logging should not be lower than effective breeding unit to avoid inbreeding. Research on breeding unit size is needed on a variety of species, sites and between years to account for spatial and temporal variation (2.1)
Retain at least one reproductive tree per species ha ⁻¹	Dipterocarp species	Sist et al. (2003b)	May be easy to implement at least for the main commercial species. Higher minimum densities may be needed for some species (2.1)
Harvest maximum 8 trees ha ⁻¹	Dipterocarp species	Sist et al. (2003b)	Not reviewed (purpose to reduce logging damage); see the above point
Do not log unless there are more than 500 reproductively mature individuals in the population	Regionally rare or endemic species	Jennings et al. (2001)	Not reviewed
Define species-specific minimum diameter cutting limits depending on structure, density and diameter at reproductive maturity	Dipterocarp species; any species	Sist et al. (2003b) 2004; Lee, C.T. et al. (2002)	Research needed to identify species characteristics which indicate vulnerability to logging (e.g. mating system, pollination patterns, large size at maturity or high fecundity) and their relation with types and intensity of disturbances (2.1,2.4)
Do not harvest trees exceeding 100 cm dbh	Dipterocarp species	Sist et al. (2003b)	Maintaining some large trees can be

Strategy	Species group of specific concern	Source	Main conclusions or research needs for mixed dipterocarp forests from this study
Protect species which perform important ecological functions (e.g. by providing habitats to pollinators)	Any species	Jennings et al. (2001); Sist et al. (2003b)	useful for maintaining reproductive output, genetic diversity, and adaptive capacity (2.4) More research needed on the impact of disturbance on pollination processes and subsequent reproduction of tree species (2.1)
Remove species individually rather than in clumps	Species with a pronounced spatial genetic structure (FSGS)	Ng et al. (2009)	Recommended where species ecology or biology indicate potentially significant FSGS (2.2)
Open canopy prior to logging to promote regeneration, or restrict felling to periods following mast fruiting events; Time logging after general flowering events	Light demanding or other species for which commercial-sized stems form a large proportion of the total population; Species with general flowering pattern	Jennings et al. (2001); Tani et al. (2012)	Evidence exists of more effective mixed mating and better seed viability after general vs. sporadic flowering. Options to promote gene recombination and seedling establishment e.g. through reduced logging intensities should be assessed. (2.3)
Minimize the size and connectivity of gaps	Dipterocarp species	Sist et al. (2003b)	Not reviewed (purpose to limit colonization by pioneer and weedy species that can suppress regeneration of target species). Maintaining connectivity is important also at landscape scale, but for species with limited gene flow it is unlikely to rapidly restore genetic diversity of logged forest (2.4)

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