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REVIEW

Using intraspecific molecular and phenotypic variation to promote multi-functionality of reforestation during climate change – A review of tropical forest case studies in South-east Asia

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Abstract

The study of intraspecific genetic variation in plant traits for use in tropical forest restoration has broad potential for increasing our ability to achieve multi-functional objectives during this era of climate change. Developing seed-sourcing guidelines that optimize phenotypic characteristics best suited to a particular planting site as well as to future conditions imposed by environmental change could be useful for effective reforestation. Because evolution operates differently across tree species, this is an especially cumbersome task in tropical forests that contain thousands of species. Partially due to this high plant diversity, research and application of intraspecific variation in genetics, plant traits, and plant function in tropical forests wane far behind less diverse forest biomes. To examine the potential for improving reforestation efforts in tropical forests by considering intraspecific variation in plant traits and functions, we review the state of knowledge on intraspecific variation in South-east Asia as a case study. We focus on the dipterocarp family (*Dipterocarpaceae*), a highly diverse family of 16 genera with approximately 695 known species that often dominate lowland tropical rainforests of South-east Asia with many of these forests in a degraded state and in need of restoration. We found that there is research accumulating to understand genetic variation in approximately 10% of these 695 species. Intraspecific molecular variation exists at different spatial scales among species with 74% of species having moderate to high population differentiation (Fst > 0.10) and 92% of species with evidence of fine-scale genetic structure. Although this suggests a high potential for trait variation, few studies associated molecular with phenotypic variation. Seventeen tree species across 11 studies revealed intraspecific variation in traits or functions. Research indicates that intraspecific variation in growth may vary two-fold and drought tolerance four-fold among genotypes highlighting the possibility to pre-adapt trees to climate change during reforestation and to use intraspecific variation to promote the use of native species in commercial forestry. Our review presents opportunities and ideas for developing seed-sourcing guidelines to take advantage of intraspecific variation in traits and function by identifying how to locate this variation, which species would benefit, and how to test for trait variation. We also highlight an emerging area of research on local adaptation, common garden studies, and adaptive drought conditioning to improve reforestation during climate change.

Keywords: tropical forest restoration, climate pre-adaptation, assisted migration, local adaptation, fine-scale genetic structure, seed source guidelines, “climate-adjusted” provenancing

Introduction

The application of evolutionary-based research to tropical reforestation efforts has broad potential to increase our ability to achieve multi-functional objectives during this era of climate change. Specifically, intraspecific variation in plant traits such as wood density, specific leaf area (SLA), foliar nitrogen (N) content, leaf lifespan, photosynthetic and transpiration rates, leaf-level water-use efficiency, and carbon isotope discrimination are often related to key ecosystem functions such as growth rate, promotion of canopy arthropod diversity, carbon sequestration potential,

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drought tolerance, nutrient-use, and economic values such as timber and fruit production (Grady *et al*., 2013; Gregorio *et al*., 2017; Axelsson *et al*., 2022). Such trait-function relationships can be identified and incorporated into seed collection protocols for use in reforestation to match appropriate phenotypes to specific environmental conditions of the planting site to maximize growth, survivorship, and desired functionality. However, the functionality of different genotypes/phenotypes may be impacted by environmental changes such as global warming, drought, or deforestation. As such, site-matching should include both appropriate phenotypes for current and future environmental conditions. While much tropical research has focused on intraspecific variation in traits of commercially valuable species that are largely non-native to areas where they are grown, there is a growing need to assess how genetic variation in a broad range of native tree species can be utilized during reforestation for both commercial and conservation values (Thomas *et al*., 2014; Prober *et al*., 2015; Gregorio *et al*., 2017; Jalonen *et al*., 2018; Axelsson *et al*., 2020). Such research has a high potential to diversify the portfolio of tree species that can be used in both commercial forestry and ecosystem restoration during climate change. It is widely recognized that restoration of native ecosystems is fundamentally necessary for achieving multiple benefits such as rebuilding native flora and fauna while at the same time promoting the livelihoods of local people. Achieving multi-functional benefits as a goal of restoration is highlighted by The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) and the United Nations Declaration of the Decade of Restoration (FAO, 2020).

Improved seed-sourcing guidelines of native tropical tree species during reforestation is a crucial step toward meeting reforestation objectives and contributing to solving the global biodiversity and climate crises (Gregorio *et al*., 2017; Bosshard *et al*., 2021). Using inappropriate seed sources that do not achieve desired plant functions can increase the costs (Gregorio *et al*., 2017; Jalonen *et al*., 2018) and reduce the long-term benefits of reforestation (Gardiner *et al*., 2019; Andivia *et al*., 2021). Furthermore, as climate change is expected to make locally adapted populations maladapted to future climates (Alberto *et al*., 2013; Isaac-Renton *et al*., 2018), reforestation efforts may benefit by selecting genetic material adapted to future climatic conditions (Prober *et al*., 2015; Axelsson *et al*., 2020). In non-tropical ecosystems, much research has illustrated high-intraspecific variation in functional traits that corresponds to environmental variation (Grady *et al*., 2015; Zucchi *et al*., 2017; Pastorino and Marchelli, 2020); much less research on intraspecific trait variation has been conducted in the tropics (though see Vargas Cruz *et al*., 2019; Barton *et al*., 2020). As such, in contrast to the wide application of evolutionary-based themes in non-tropical systems such as assisted migration (Aitken and Whitlock, 2013; Grady *et al*., 2015), pre-adapting forests to climate change during reforestation (Axelsson *et al*., 2020), or using a “climate-adjusted” provenancing strategy when conducting restoration (Prober *et al*., 2015), few such efforts are being tested or used in tropical ecosystems. Unless the forests that are established through restoration today can maintain functionality in the climate of tomorrow, restoration efforts might be ineffective. Understanding the magnitude of intraspecific trait variation at multiple scales, and examining if that variation is related to climatic and/or biotic factors and/or is locally adapted, is an important first step toward identifying and applying the correct trait-function genotypes that promote functional resilience in trees undergoing climate change. A review of the research literature related to intraspecific trait variation in tropical forests of South-east Asia research will promote the development of germplasm/seed collection strategies for reforestation.

Review methodology

We conducted a rapid review on the available literature pertaining to spatial scales of intraspecific molecular and phenotypic variation, intraspecific variation in trait-to-function relationships, and local adaptation of the dipterocarps. Rapid reviews are the recommended review type in cases such as this when there are time constraints that need consideration (Grant and Booth, 2009). To find literature relevant to our objective, we built a search string consisting of two components (Appendix S1). The first component contained nine terms in relation to intraspecific variation, phenotypic variation, genetics, population differentiation, and local adaptation plus relevant synonyms. To delimit our search to dipterocarps we added a second component with synonyms to *Dipterocarpaceae* as well as each of the genera within the family. Using this search string, we compiled a database of articles extracted from Web-of-Science using the “all databases” and “Topic” features on May 25, 2023. We delimited our search to empirical articles published in peer-reviewed journals (but kept review articles for reference).

Using this search, we found 275 articles. We then reviewed titles and abstracts to determine if studies were pertinent to our main research objectives. Inclusion at this stage was based on if there was a genetic focus of relevant taxa (i.e., dipterocarps) and if studies were written in English. Studies with a purely phylogenetic focus or technical papers with a focus on developing molecular- or forensic tools (i.e., verify the origin of timber products) were not considered. Review papers addressing dipterocarps with a genetic focus were kept as reference but not included in the final list of papers. This generated 97 studies that were accessible online (Appendix S2).

USING MOLECULAR DATA TO LOCATE INTRASPECIFIC TRAIT VARIATION

Understanding the spatial and ecological drivers underlying intraspecific variation in tropical trees is daunted by the high species diversity in tropical forests, making the development of seed-sourcing guidelines challenging. One of the most commonly used measures of genetic structure is the fixation index Fst, which measures genetic differentiation among populations across large spatial scales. Fst essentially measures the level of genetic differentiation between two or more populations and ranges from 0 (i.e., no genetic differentiation) to 1 (complete genetic differentiation). For many tree species, high Fst (e.g., high population differentiation) across broad spatial scales is related to high environmental variation that reflects natural selection to different environmental factors (Carvalho *et al*., 2019). For species with high levels of Fst, we would expect high intraspecific variation in plant traits/functions as genetic variation generally correlates with phenotypic variation. For such species, intraspecific variation in traits could be examined among populations using greenhouse and common garden experiments to identify desirable plant characteristics for use in reforestation. In addition, tree species with high Fst would be potential candidates to screen for evidence of local adaptation. Where local adaptation exists, strategies such as assisted migration (Aitken and Whitlock, 2013) may be useful to apply in a reforestation context. Seed-sourcing recommendations could be developed accounting for which populations are best suited to current and future environmental conditions.

In tropical forests, we expect many species to also exhibit low within population genetic differentiation where neighboring individuals are highly genetically related. Such related groups of individuals can be genetically distinct from nearby groups of other individuals (e.g., at distances less than 1 km; Tito de Morais *et al*., 2015) where there are limits to gene flow among them. This genetic aggregation and isolation is referred to as fine-scale genetic structure (FSGS). High FSGS is thought to be found where there are strong barriers to gene flow such as where trees are pollinated by wingless insects that cannot travel long distances or from limited seed or pollen dispersal (Harata *et al*., 2012; Tito de Morais *et al*., 2015; Lee *et al*., 2016). Limited gene flow can lead to closely genetic-related neighboring individuals with a high occurrence of inbreeding and subsequent high potential for reduced fitness and low ability to adapt to changing environments. FSGS may be common in highly diverse forests where a high diversity of tree species inherently creates obstacles to gene flow. For example, in a forest with 100 or more species per hectare, the probability is low of a tree being in close proximity to a conspecific tree neighbor that would promote pollination. For species with high levels of FSGS, we would expect intraspecific variation in traits at relatively short distances (e.g., trees separated by 50 m–1200 m; Harata *et al*., 2012; Tito de Morais *et al*., 2015). Greenhouse and common garden experiments could be used to screen species with FSGS for desirable phenotypes for use in reforestation.

Anthropogenic factors such as deforestation that cause population fragmentation are also known to influence the genetic structure of species (Pandey and Geburek, 2010; Ismail *et al*., 2014; Dai *et al*., 2018). Both Fst and FSGS and disturbance-related genetic impacts are likely to vary among species such that seed-sourcing guidelines would vary widely depending on the species being used in reforestation. The interaction of deforestation with naturally occurring intraspecific trait variation could be incorporated into the development of a strategic plan for seed sourcing during reforestation (Thomas *et al*., 2014).

LOCAL ADAPTATION AND PRE-ADAPTING FORESTS TO FUTURE CLIMATES

In tropical forests, species selection to climatic conditions may be weak where homogenous atmospheric temperatures and consistently high precipitation do not result in natural selection pressures great enough to result in adaptation (Pimm and Sugden, 1994). In such forests, water may not be a limiting resource, and selection to it may be absent considering that soil saturation is often present at both high (i.e., 300 cm per year) or very high (600 cm per year) levels of precipitation. While intraspecific variation that is related to variation in climatic conditions has been rarely studied in wet tropical forests (though see Barton *et al*., 2020), there is evidence emerging highlighting the evolutionary consequences of drought in a seasonal tropical rainforests (Ng *et al*., 2021). Furthermore, the amount and seasonality of rainfall varies across altitudinal gradients, and plant species distribution patterns are correlated with rainfall even in wet tropical forests (Engelbrecht *et al*., 2005). Species turnover across environmental gradients and differences among species in distribution ranges suggest that evolution influences the interspecific variation of plant species in different ways. There is evidence of variation among species in response to drought (Bartlett *et al*., 2016; Axelsson *et al*., 2021) suggesting that drought tolerance is an important factor that could be under selection in tropical forests (Axelsson *et al*., 2020; Ng *et al*., 2021). Knowledge regarding functional genetic variation across geographical gradients is commonly used in non-tropical systems to enhance restoration success, e.g., via assisted migration (Grady *et al*., 2015; Zucchi *et al*., 2017) or low-intensity breeding (Pastorino and Marchelli, 2020). We acknowledge that other factors such as nutrient limitation, inter- and intraspecific competition among trees (Grady *et al*., 2017), insect and pathogen impacts on trees (Grady *et al*., 2015), among others, could also have evolutionary impacts such as have been found in non-tropical systems and that these factors may interact in complex ways with adaptation to climate. Improved understanding of the extent and evolutionary causes of functional and adaptive intraspecific variation of native tree species in tropical forests could potentially be used to direct seed collection campaigns to support reforestation during global warming and other environmental changes.

A REVIEW OF SOUTH-EAST ASIAN DIPTEROCARPS

Here we review the current knowledge about intraspecific molecular and phenotypic variation in tree species in the dipterocarp family (*Dipterocarpaceae*), a highly diverse family of 16 genera and about 695 known species typically dominating lowland tropical rainforests of South-east Asia. We were explicitly interested in assessing the extent of, and knowledge about, intraspecific variation in traits and function across different spatial scales in order to examine the potential to incorporate such variation into commercial forestry using native species and conservation-based reforestation efforts where adapting to future environmental conditions is important. We specifically reviewed the literature where Fst and FSGS values were reported as these measures can be used to distinguish among species variation in the scale of population differentiation. That is, as high Fst is often correlated to high trait variation among populations and high FSGS values would suggest low intraspecific variation at very small scales (e.g., trees less than 1 km apart), and high intraspecific variation at intermediate scales (e.g., trees greater than 1 km apart; Tito de Morais *et al*., 2015). We also reviewed research that evaluated intraspecific variation in plant traits, and research that correlated such variation to environmental variables such as drought, nutrient limitation, and atmospheric temperature. Finally, we reviewed the literature for studies on local adaptation within dipterocarp tree species. Compiling this knowledge is the first step to examine the application of intraspecific variation in plant traits and function to native species commercial forestry and conservation-based reforestation efforts during climate change in dipterocarp-dominated forests of South-east Asia. Through this review, we specifically aimed to address the following questions of relevance for seed-sourcing guidelines and reforestation success in the face of climate change.

a. How does intraspecific molecular variation of dipterocarp species vary among different spatial scales and what are the potential drivers of this variation? Can we use such molecular data to catalyze efforts to understand phenotypic variation and apply it to reforestation?
b. What amount of phenotypic variation in plant characteristics and function have been found that could be incorporated into reforestation to achieve multi-function objectives?
c. What is the evidence that such genetic/phenotypic variation is locally adapted or associated with variation in response to a changing climate?

Based on the state of knowledge of intraspecific variation in plant traits, we then highlight opportunities for developing seed-sourcing guidelines to (1) enhance forest functionality and achievement of multi-functional objectives during reforestation, and (2) enhance plant fitness under changing climatic conditions.

Material and methods

DIPTEROCARP FORESTS

Mixed-dipterocarp forests are a dominant forest ecosystem throughout South-east Asia. These forests are subjected to considerable degradation, and restoration is urgently required (Kettle, 2009). In addition to being a dominant component of overall plant community composition in South-east Asia, dipterocarps are emergent species, occupying the highest places in the forest canopy with some species reaching over 80 m in height. As such, they have a key role in carbon sinks and are thus very important from a climate change perspective. Dipterocarps also promote a wide array of other diverse taxa such as insects (Sakai *et al*., 1999; Axelsson *et al*., 2022), birds (Engstrom *et al*., 2020), and mammals (Charles, 1996; Chapman *et al*., 2018). Furthermore, tropical forests of South-east Asia have been managed by local communities for thousands of years (Barker *et al*., 2017) and many tree species are culturally significant to local communities (Barker *et al*., 2017; Axelsson *et al*., 2021). Due to their foundational role in these dipterocarp-dominated forests (Axelsson *et al*., 2022), a range of species within this family are commonly included in reforestation efforts in the region (Kettle, 2009; Gustafsson *et al*., 2016; Axelsson *et al*., 2020). Many dipterocarp species are categorized as near threatened or endangered as a result of exploitation and massive population reduction (Guan and Yen, 2000; BGCI, 2021) highlighting an evident need to strengthen research related to genetic conservation of dipterocarps. Being a highly diverse family of 16 genera with approximately 695 known species, the dipterocarp family has species with varying mating systems that, in turn, generate large differences among species in genetic structure (Tito de Morais *et al*., 2015). This in combination with reports of both variations in Fst and FSGS suggests that dipterocarps are a likely candidate taxonomic group for evaluating the potential of intraspecific trait-matching to current and future conditions during reforestation.

Results

In total, we found 97 studies that covered 67 species and 2 subspecies (Fig. 1). These 67 species represent roughly 10% of the known species in the dipterocarp family (i.e., 67/695). The most commonly studied species were *Shorea leprosula*, *Shorea parvifolia*, and *Shorea curtisii* that occurred in 22, 15, and 11 studies, respectively. Most species were, however, represented in very few studies, i.e., 75% of the species or subspecies were only represented in one or two studies (Fig. 1). A large majority of the studies were molecular studies focusing on the genetic variation among populations (i.e., population differentiation, Fst) or genetic variation within populations (i.e., fine-scale genetic structure, FSGS) and spatial genetic structure in natural- or semi-natural populations (i.e., effects of forest management, degradation, etc.). In a subset of such studies, molecular data were used to link species variation in spatial genetic structure and gene flow with life history traits, breeding system, and pollination syndromes (Harata *et al*., 2012; Tani *et al*., 2012; Tito de Morais *et al*., 2015). Studies were also found that linked spatial genetic structure to landscape features such as elevation and topography (Lee *et al*., 2013; Lee *et al*., 2016; Smith *et al*., 2018). Molecular genetic information has also been used to enhance *ex situ* (Lee *et al*., 2000; Li *et al*., 2002; Kusuma *et al*., 2019) and *in situ* conservation (Ng *et al*., 2019). We found a small number of nine studies addressing phenotypic variation or genetic variation in plant functioning but few that linked molecular to phenotypic data. The phenotypic traits and functions addressed included variation in seed size and germination (Naito *et al*., 2005; Lee *et al*., 2006; Lee *et al*., 2013; Takeuchi and Diway, 2021), seedling performance and growth rate (Lee *et al*., 2006; Ismail *et al*., 2014; Nutt *et al*., 2016; Axelsson *et al*., 2020; Ng *et al*., 2021; O'Brien and Escudero, 2022). Only two studies included research on intraspecific variation in response to climatic factors (Axelsson *et al*., 2020; Ng *et al*., 2021), three studies examined intraspecific variation in response to soil nutrients, forest type, or insect herbivory (Indriani *et al*., 2019; Li *et al*., 2021; Ng *et al*., 2022), and one common garden study examined local adaptation to abiotic and biotic conditions (O'Brien and Escudero, 2022).

POPULATION DIFFERENTIATION (FST) AND FINE-SCALE GENETIC STRUCTURE (FSGS)

A large majority of the studies included in this review used molecular tools to assess intraspecific genetic variation in species of dipterocarps. These studies reveal that intraspecific genetic variation ranges from small to large and that the extent of population differentiation (Fst) varies widely among species. Mean population differentiation estimates (Fst) range from 0 (no significant differentiation) to 0.519 and differ across species and vary across different spatial scales (Table 1). Although these molecular-based studies never included a phenotypic component, the majority of the 34 species that presented population structure data generally showed moderate to high population structure (Table 1). For example, of the 34 species included, 25 species (74%) had at least one study where moderate to high population differentiation was reported (Fst, Gst, or Rst above 0.10) while for 6 species (18%), at least one study confirmed a low level of genetic differentiation (Fst, Gst, or Rst between 0.05 and 0.099). In sum, 74% of species had at least one study showing moderate to high levels of population differentiation. Moderate to high genetic differentiation among populations suggests the potential to identify populations with desirable traits/functions as well as to explore the potential for local adaptation.

Our case studies with two species (*Shorea macrophylla* and *Dipterocarpus alatus*) in which pairwise Fst values have been reported across a multitude of populations show that species vary in how spatial scale influences genetic differentiation. In *S. macrophylla* genetic differentiation follows a linear fit and Fst increases mainly across large spatial scales. In *D. alatus*, genetic differentiation follows a logarithmic fit and Fst increases quickly across relatively small spatial scales (Fig. 2). The Fst to spatial distance relationship also has a better fit in *S. macrophylla* (R^2 = 0.66) than in *D. alatus* (R^2 = 0.52) suggesting that *D. alatus* may have a larger proportion of variation explained by environmental factors other than distance (Fig. 2). Such information can be used to guide the scope of seed sourcing to increase the likelihood of

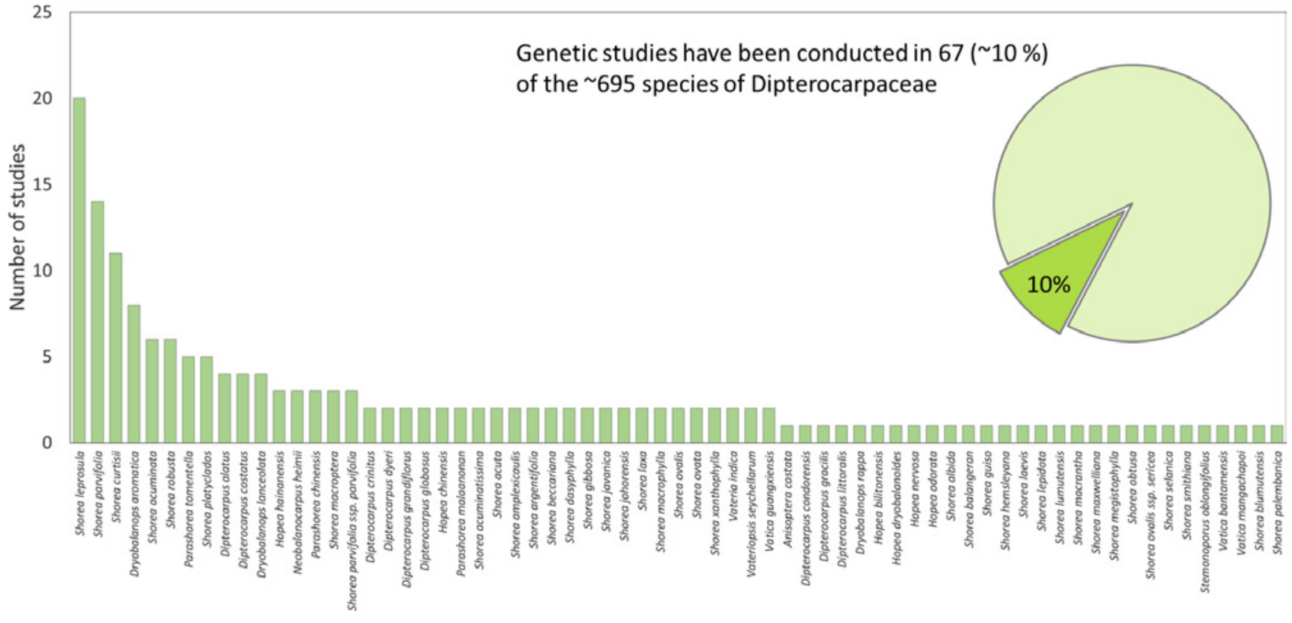


Fig. 1. Genetic aspects have been studied in 67 species of dipterocarps which represents roughly 10% of the ~695 known species in the family. A few species are well studied as represented in the literature whereas a majority of the species have only been included in one or two studies.

finding phenotypic variation that can be tested in common gardens to infer local adaptation to environmental conditions.

In addition to moderate to high overall population structure among dipterocarp species (74% of species with a moderate to high level of population differentiation), we also found that 92% of species studied had at least one case where fine-scale genetic (FSGS) structure was present (Table 2). Only 2 out of 26 species investigated across a total of 13 studies did not have FSGS. The distance at which genetically related individuals were aggregated varied among species (Table 2) and multiple studies on the same species generally followed the same trends for evidence, strength, and distance of FSGS (Table 2). Intraspecific variation in phenotypic traits for any of these species was not reported. Table 2 illustrates that for 92% of dipterocarp species, collecting seeds from different mother trees spaced at 1200 m would ensure genetic differentiation for 92% of dipterocarps. Using this seed-sourcing guideline could be useful for developing studies to examine phenotypic variation and future applications of using this phenotypic variation in reforestation efforts. In addition, such a protocol could be established for screening for phenotypic variation where seeds from different mother trees at least 1200 m apart could be grown in greenhouse or common garden environments (Axelsson *et al*., 2020).

Genetic isolation appears to be driven by low gene flow in trees pollinated by less mobile insects such as wingless thrips or small beetles compared to larger pollinators such as giant honeybees (Apis dorsata; Harata *et al*., 2012; Tito de Morais *et al*., 2015). Tree species with smaller flowers tend to be pollinated by smaller insects that only disperse short distances and both flower size and pollinator size have been correlated to FSGS. In addition, seed dispersal by wind is common for dipterocarps but dipterocarps have heavy seeds that do not disperse far, are actively fed on by a variety of herbivores, have long periods between flowering events (some species up to 20 years), and are quickly decomposed and unviable if germination is not immediate; taken together, seed dispersal is limited and limits gene flow (Harata *et al*., 2012; Tito de Morais *et al*., 2015).

A range of studies also highlight how landscape features such as landscape connectivity (Pandey and Geburek, 2010; Ismail *et al*., 2014), and logging and forest degradation may impact intraspecific genetic variation, inbreeding and gene flow within and among populations (Obayashi *et al*., 2002; Wickneswari *et al*., 2004; Ng *et al*., 2009; Ang *et al*., 2016; Widiyatno *et al*., 2016; Widiyatno *et al*., 2017) and that such effects can vary in extent depending on mating system (Ng *et al*., 2009). Widiyatno *et al*. (2016) found that the genetic diversity of logged tropical forests gradually decreases depending on logging rotation times, especially with respect to sensitive genetic parameters such as the numbers of rare alleles, and that enrichment planting can be used to increase the genetic variation of logged forests. Molecular genetic information has also been used to identify genetically unique populations that may be particularly interesting for conservation (Lee *et al*., 2000; Li *et al*., 2002; Kusuma *et al*., 2019; Ng *et al*., 2019). Incorporating genetically unique populations into reforestation as well as avoiding populations with high inbreeding such as those found in highly degraded forests will promote genetic diversity in reforestation efforts.

PHENOTYPIC VARIATION/GENETIC VARIATION IN PLANT FUNCTIONING

A limited number of 11 studies addressed intraspecific variation in traits and functions within a total of 17 species of dipterocarps (Table 3). These studies show that seeds from different mother trees can vary in size, germination rate, and seedling survival (Ismail *et al*., 2014; Nutt *et al*., 2016; Tito de Morais *et al*., 2020; Takeuchi and Diway, 2021). For example, Tito de Morais *et al*. (2020) found that low genetic diversity increased the probability of seedling mortality over 30 months in three out of four species. Nutt *et al*. (2016) found that seedling survival, but not growth, of seedlings from different mother trees of *Parashorea tomentella* over 18 months increased with greater heterozygosity. Furthermore, Ismail *et al*. (2014) found that the growth of selfed progeny was approximately 75% of the growth of outbred progeny in *Vateria indica*. Axelsson *et al*. (2020) studied seedling performance in a nursery experiment and found that basic characteristics such as growth and susceptibility to herbivory commonly varied among half-sib families originating from different mother trees. Variation was shown to be quite substantial, i.e., in some cases growth varied two-fold among families (Fig. 3). Also, in two species, seedling performance was influenced by water availability which indicated intraspecific variation in drought tolerance (Axelsson *et al*., 2020). Ng *et al*. (2021) exposed seedlings to drought and were able to detect the upregulation of genes associated with drought tolerance. The same “drought tolerance” genes were also shown to be associated with landscape-level variation in precipitation (Ng *et al*., 2021) providing molecular evidence for the evolutionary relevance of drought in some dipterocarp species despite a general lack of an annual dry season in these systems. Identifying and deploying drought-tolerant genotypes could be useful during reforestation as tropical forests in South-east Asia are confronting longer and more severe droughts as well as record-high temperatures.

Although local adaptation to biotic conditions has seldom been reported, we did find that common garden studies are becoming increasingly used to evaluate local adaptation and population variation in important plant traits. In Sabah, Malaysia, half-sib families from six mother trees of six dipterocarp species from either riparian or upland ecotones were grown in replicated common gardens and compared (O’Brien and Escudero, 2022). While genotypes from riparian and upland ecotones did not appear to be locally adapted to abiotic conditions, when they were exposed to varying levels of tree competition there was variation in growth rates among genotypes from riparian compared to upland ecotones. Such genetic by environmental (G × E) interaction was found for all six species (*Shorea leprosula, Shorea johorensis, Shoea parvifolia, Parashorea malaanonan, Hopea nervosa, Dryobalanops lanceolata*). This suggests that competition has differently impacted the riparian and upland genotypes and may indicate natural selection to the biotic environment; however, given the data provided, it was not possible to tease apart the genetics by multiple interacting environmental factors.

In another common garden experiment, nine populations of *Shorea leprosula* were grown in a common garden in Peninsular Malaysia (Ng *et al*., 2022). Intraspecific variation in herbivory by a scale insect and growth rate were detected with the fastest growing populations being those that were most resistant to the scale insect. Local adaptation to environmental factors was not evaluated and molecular data was not included. However, a few studies did link molecular data with landscape features in attempts to address how selection to different environments may affect genetic variation (Indriani *et al*., 2019; Li *et al*., 2021). For example, Indriani *et al*. (2019) explored to what extent populations of *Shorea balangeran* occurring on wet peat forest and dry heath forest differed genetically but found no evidence of genetic clustering of populations according to forest type. However, the study by Li *et al*. (2021) provides some evidence of the existence of adaptive genetic variation in *Parashorea chinensis* related to soil nutrient availability.

Discussion

The aim of this article was to review what we currently know about intraspecific variation in traits and functioning of dipterocarp species, a family of trees dominating mixed dipterocarp forests of South-east Asia and in high need for conservation and restoration (Kettle, 2009), and its potential for application to reforestation. We found a wide range of studies presenting values of both low and high population variation (Fst, Gst, Rst) among tree species (Table 1) with a majority of species with moderate to high levels

Table 1. Population differentiation values (Fst, Rst, and Gst) reported for dipterocarp tree species in studies conducted across different spatial scales.

Species	Populations (n)	Life stage	Fst min	Fst	Fst max	Gst	Spatial scale (km)	Authors and year
Dipterocarpus alatus	7	adults	—	—	0.135	—	30	Chokthaweepanich *et al*. (2022)
Dipterocarpus alatus	5	Unspecified	0.317	0.274	0.492	—	150	Vu *et al*. (2019)
Dipterocarpus alatus	10	Adults	—	0.266	0.492	—	350	Tam *et al*. (2014)
Dipterocarpus alatus	5	Adults	—	0.274	0.492	—	150	Vu *et al*. (2019)
Dipterocarpus condorensis	8	adults	0.024	0.122	0.138	—	200	Nguyen *et al*. (2022)
Dipterocarpus costatus	3	Unspecified	0.053	0.347	0.403	—	150	Vu *et al*. (2019)
Dipterocarpus costatus	4	mature trees	0.315	0.405	0.481	—	209	Duc *et al*. (2016)
Dipterocarpus costatus	3	Adults	—	0.347	0.403	—	150	Vu *et al*. (2019)
Dipterocarpus dyeri	6	adults	—	0.132	0.192	0.135	300	Nguyen *et al*. (2020)
Dipterocarpus dyeri	2	Adults	—	0.123	0.123	—	50	Tam *et al*. (2019)
Dipterocarpus dyeri	2	Juveniles	—	0.188	0.188	—	50	Tam *et al*. (2019)
Dipterocarpus gracilis	4	Seedlings	—	0.251	0.251	—	2	Romadini *et al*. (2021)
Dipterocarpus littoralis	2	Adults	0.05	0.05	0.05	—	1	Dwiyanti *et al*. (2014)
Dipterocarpus littoralis	2	Saplings	0.036	0.036	0.036	—	1	Dwiyanti *et al*. (2014)
Dryobalanops aromatica	10	Unspecified	—	—	—	0.036	400	Lee *et al*. (2000)
Dryobalanops aromatica	5	Seedlings	—	—	—	0.067	450	Lim *et al*. (2002)
Dryobalanops aromatica	3	Adults	—	—	—	0.126	150	Ritonga *et al*. (2018)
Hopea bilitonensis	2	Unspecified	—	—	—	0.116*	3	Lee *et al*. (2013)
Hopea chinensis	4	Adults	—	—	—	0.0735	400	Tang *et al*. (2015)
Hopea hainanensis	7	unsepcified	−0.046	—	0.295	—	100	Chen *et al*. (2022)
Hopea hainanensis	10	Adults	0.001	0.23	0.271	0.229	250	Wang *et al*. (2020)
Hopea odorata	3	Adults	0.17	0.251	0.31	0.193	1000	Nguyen *et al*. (2014)
Neobalanocarpus heimii	32	Adults	—	0.127	0.127	0.39	700	Tnah *et al*. (2013)
Parashorea chinensis	15	Unspecified	—	0.32	0.3202	—	1.2	Li *et al*. (2022)
Parashorea tomentella	3	Adults	—	0.078	0.078	—	6	Kettle *et al*. (2011)
Shorea acuminata	3	unspecified	−0.003	—	0.093	—	200	Ishiyama *et al*. (2008)

Continued

Table 1. Continued.

Species	Populations (n)	Life stage	Fst min	Fst	Fst max	Gst	Spatial scale (km)	Authors and year
Shorea albida	11	Adults	0.0003	0.04	0.1374	—	50	Ogasahara *et al.* (2023)
Shorea balangeran	2	unspecified	—	—	—	0.03	30	Indriani *et al.* (2019)
Shorea curtisii	3	unspecified	−0.01	—	0.083	—	200	Ishiyama *et al.* (2008)
Shorea curtisii	2	adults and saplings	—	0.519	0.519	—	1400	Kamiya *et al.* (2012)
Shorea curtisii	6	adults and saplings	—	0.033	0.033	—	500	Kamiya *et al.* (2012)
Shorea curtisii	2	adults and saplings	—	0.035	0.035	—	125	Kamiya *et al.* (2012)
Shorea guiso	4	Adults	—	0.05	0.107	—	700	Tinio *et al.* (2014)
Shorea javanica	6	Adults	—	0	0	—	600	Rachmat *et al.* (2012a)
Shorea javanica	6	Adults	−0.064	0.076	0.158	—	500	Rachmat *et al.* (2012b)
Shorea laevis	7	Adults	—	—	—	0.736	1000	Zulfahmi *et al.* (2015)
Shorea leprosula	7	adults and saplings	—	0.25	0.471	—	1900	Cao *et al.* (2006)
Shorea leprosula	2	adults and saplings	—	0.404	0.404	—	1500	Cao *et al.* (2009)
Shorea leprosula	8	Adults and seedlings	—	—	—	0.117	900	Lee *et al.* (2000)
Shorea leprosula	7	Adults and seedlings	—	—	—	0.085	600	Lee *et al.* (2000)
Shorea leprosula	10	Seeds	0.00012	—	0.023	—	1	Lee *et al.* (2000)
Shorea lumutensis	10	>1 cm dbh	—	—	—	0.058[*]	300	Lee *et al.* (2006)
Shorea macrophylla	13	Adults	—	0.093	0.166	—	1000	Utomo *et al.* (2018)
Shorea obtusa	5	Adults	—	0.03	0.056	—	500	Senakun *et al.* (2011)
Shorea parvifolia	6	adults and saplings	—	0.31	0.717	—	1900	Cao *et al.* (2006)
Shorea parvifolia	2	adults and saplings	—	0.336	0.336	—	1500	Cao *et al.* (2009)
Shorea parvifolia	18	Adults	—	0.15	0.1555	—	2000	Ohtani *et al.* (2021)
Shorea parvifolia	7	Adults	—	—	—	0.582	2000	Zulfahmi *et al.* (2015)
Shorea platyclados	3	Unspecified	0.01	—	0.11	—	250	Muhammad *et al.* (2016)
Shorea platyclados	27	Unspecified	—	0.060	0.060	—	900	Ng *et al.* (2019)
Shorea robusta	15	Adults	—	0.043	0.047	—	500	Pandey and Geburek (2010)
Shorea selanica	3	Adults	0.394	0.702	0.907	—	300	Rachmat *et al.* (2012a, b)
Stemonoporus oblongifolius	4	adult and subadult	—	—	—	0.163	10	Murawski and Bawa (1994)
Vateria indica	2	Adults	—	0.071	0.071	—	2.3	Ismail *et al.* (2014)
Vateria indica	2	Wildings	—	0.098	0.0979	—	2.3	Ismail *et al.* (2014)
Vateriopsis seychellarum	7	Adults	—	0.2	0.27	—	20	Finger *et al.* (2012)
Vateriopsis seychellarum	7	juveniles	—	0.38	0.66	—	20	Finger *et al.* (2012)
Vatica guangxiensis	3	Unspecified	—	—	—	0.3764	900	Li *et al.* (2002)
Vatica mangachapoi	11	DBH ≥ 1.5 cm	0.156	—	0.257	—	200	Dai *et al.* (2018)

[*] Rst.

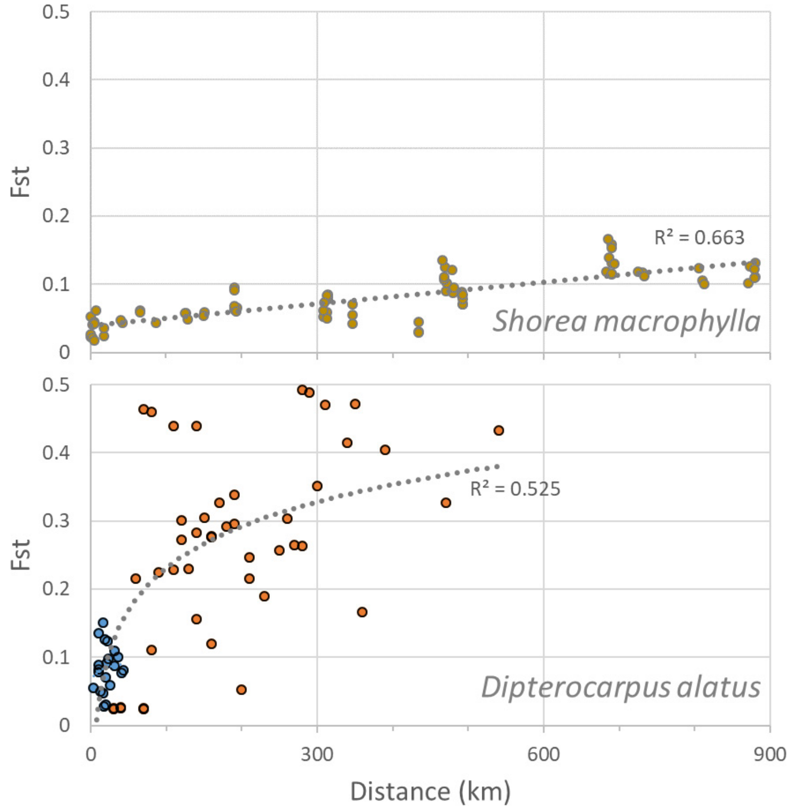


Fig 2. Illustration of how genetic differentiation (Fst) is influenced by spatial scale differently for two dipterocarp tree species. The blue data points are from Chokthaweepanich *et al*. (2022), red from Tam *et al*. (2014) and yellow from Utomo *et al*. (2018). In *S. macrophylla*, genetic differentiation follows a linear fit and Fst increases mainly across large spatial scales. In *D. alatus,* genetic differentiation follows a logarithmic fit and Fst can increase quickly across relatively small spatial scales.

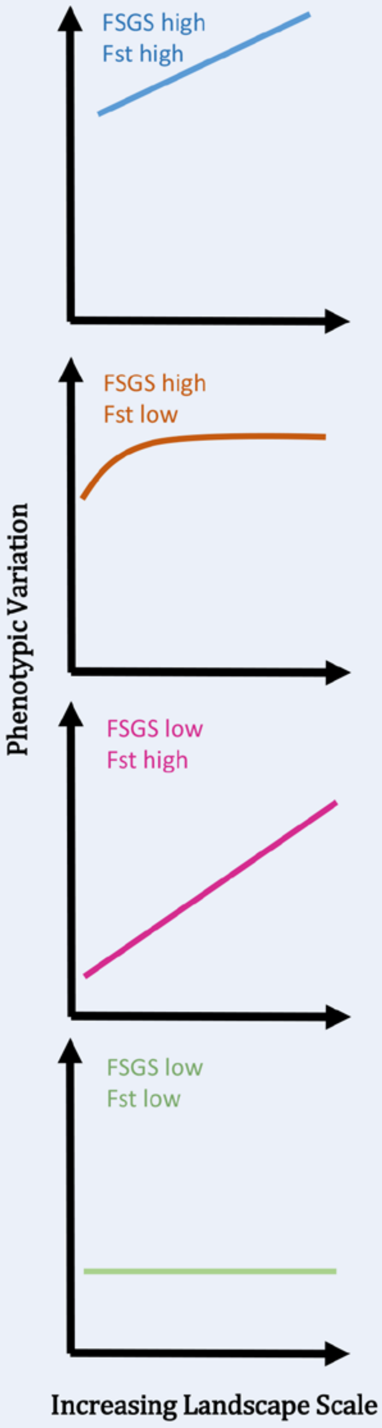
of Fst (74%). A high degree of population differentiation makes such species obvious candidates for screening traits and functions appropriate for site-matching to current and future environmental conditions. Although only a few studies estimated FSGS, there was broad congruence across these studies in the occurrence of FSGS (92% of study species revealed FSGS). A few studies explained high levels of FSGS by differences in gene flow as influenced by species variation in mating systems and pollination syndromes (Takeuchi *et al*., 2004; Harata *et al*., 2012; Tani *et al*., 2012; Tito de Morais *et al*., 2015). The spatial scale of aggregation of genetically related individuals for species with FSGS differed among species between 50 and 1200 m (Tito de Morais *et al*., 2015). This means that intraspecific variation in traits would be expected for some species at very close distances between trees (i.e., 50 m), and for other species at slightly larger scales (i.e., 1200 m between trees). Using seed-sourcing strategies for enhanced functional diversity could potentially benefit from considering the genetic structure of the species. This is so because spatially determined population differentiation is likely to predict how seed sourcing across different spatial scales may impact the level of genetic and phenotypic variation covered (Box 1).

The frequent evidence of variation in genetic structure (Fst or FSGS) found in our review was rarely linked to differing phenotypes or plant function. Significant research gaps in research on intraspecific variation in traits and function limit our ability to effectively incorporate genetic variation into reforestation strategies despite the great opportunities that such research has elucidated in non-tropical systems. However, these research gaps highlight the need for future research toward developing better intraspecific site-matching guidelines. Below, we discuss how a better understanding of intraspecific variation in plant traits and functions can improve achieving multi-functional restoration objectives, and we discuss experimental design strategies to screen likely candidate species (i.e., species with high Fst and high FSGS) to identify intraspecific variation in traits and functions. Second, there is an incomplete understanding of local adaptation in dipterocarps and only few studies considering how to conduct reforestation to match appropriate phenotypes to specific environmental conditions of either current or future conditions imposed by environmental change. Following, we discuss the potential for incorporating molecular and phenotypic data to pre-adapt forests to future environmental conditions.

GENETIC VARIATION IN PHENOTYPES AND PLANT FUNCTION TO IMPROVE MULTI-FUNCTIONALITY

Only a few studies using a limited number of 17 species confirm intraspecific variation in plant traits and functions such as growth (Ismail *et al*., 2014; Axelsson *et al*., 2020) and drought tolerance (Axelsson *et al*., 2020) in these dipterocarp forests. While these traits/functions are important, there are a wide array of other plant traits and functions that could be selected to improve reforestation effectiveness and to achieve multiple objectives or forest multi-functionality. Understanding intraspecific variation in growth rates and other traits is extremely important for achieving timber and carbon sequestration objectives (Jayawickrama, 2001) and as a starting point for developing native tree breeding programs. The majority of tropical forest restoration efforts continue to rely on exotic non-native tree species due to their rapid growth rates under a variety of environmental conditions. For example, forest landscape restoration (FLR) programs, large-scale projects across thousands of hectares such as those implemented in China (Xu, 2011) and South Korea (Temperton *et al*., 2014), focus almost exclusively on the use of exotic tree species to increase tree cover in deforested landscapes. However, the selection of these non-native timber

Box 1. A framework for identifying how phenotypic variation in seed sourcing can be maximised based on knowledge about the underlying genetic structure of tree species assuming that genetic variation is linked to phenotypic variation. In species with fine-scale genetic structure (FSGS), where patches of trees can be highly inbreed because of limited pollen transfer and seed dispersal, phenotypic variation are predicted to increase quick from seed sourcing across even quite small spatial scales. In species with high population structure (Fst), were most genetic variation is occurring across populations, maximising phenotypic variation is most effectively achieved by seed sourcing across populations.



For Species A, genetic variation will increase rapidly from seed sourcing across quite small spatial scales (e.g. within a population) and continues to increase with increasing spatial scale (across populations). Focusing seed sourcing from multiple trees within as well as across populations will obtain maximal phenotypic and functional diversity.

For species B, with high FSGS and low Fst, genetic diversity will increase rapidly from seed sourcing across small spatial scales (within population) but does not increase much from seed sourcing on large spatial scales (across populations). For such a species, phenotypic and functional diversity are most effectively enhanced by collecting from as many trees as possible within a single population.

For species C, with low FSGS and High Fst, genetic diversity increase slowly from seed sourcing across small spatial scales (within populations) but will increase from seed sourcing across larger scales (across populations). For such a species, maximal phenotypic and functional diversity will be captured by incorporating as many populations as possible (e.g. collecting seeds from across a broad geographic area).

For species D, with low FSGS and low Fst there is very little increase genetic variation from seed sourcing across either small scales (within populations) or large scales (across populations). In such species most phenotypic and functional diversity is captured even within a very local population.

Table 2. Dipterocarp tree species variation in patterns of fine-scale genetic structure (FSGS) as indicated by F1 (mean pairwise kinship coefficient among geographically close individuals); Sp (index of the strength of fine-scale genetic structure); and Spatial Scale in meters (distance beyond which kinship relatedness is non-significant). Multiple values correspond to statistics reported for different studies. Where individual studies included more than two values, we report the highest value. We report studies that found non-significant F1 (*ns*). Only a Spatial Scale is reported where F1 or another indicator of FSGS was statistically significant. In several cases, neither F1 nor Sp were reported but other statistical procedures were used to evaluate FSGS – in such cases, only a Spatial Scale is reported. The region where the study was conducted is indicated by Bo = Borneo; PM = Peninsular Malaysia; and SI = South India.

Species	F1 (FSGS)	Sp (FSGS)	Spatial scale (m)	Region	References
Dipterocarpus crinitus	ns; ns	—	—	Bo	Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Dipterocarpus globosus	0.069	0.007; 0.044	75	Bo	Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Dipterocarpus grandiflorus	0.020; 0.029	0.002; 0.002	20, 100	Bo	Kettle *et al*. (2011); Tito de Morais *et al*. (2015)
Dryobalanops aromatica	0.067	0.010; 0.032	200	Bo	Tito de Morais *et al*. (2015); Harata *et al*. (2012)
Dryobalanops lanceolata	ns	0.035	—	Bo	Tito de Morais *et al*. (2015); Harata *et al*. (2012)
Hopea bilitonensis	—	—	30	PM	Lee *et al*. (2013)
Hopea dryobalanoides	—	—	300	PM	Takeuchi *et al*. (2004)
Parashorea tomentella	0.051; 0.083; 0.094	0.013; 0.013; 0.025	25, 140, 300	Bo	Kettle *et al*. (2011); Tito de Morais *et al*. (2015); Smith *et al*. (2018)
Shorea acuminatissima	0.001	0.015	200	Bo	Tito de Morais *et al*. (2015)
Shorea acuta	0.094	0.015; 0.051	200	Bo	Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Shorea amplexicaulis	ns; ns	—	—	Bo	Tito de Morais *et al*. (2015)
Shorea argentifolia	0.142	0.03	—	Bo	Tito de Morais *et al*. (2015)
Shorea beccariana	0.083	0.019; 0.041	300	Bo	Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Shorea curtisii	0.075	0.026; 0.033	250, 250	Bo	Ng *et al*. (2006); Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Shorea gibbosa	0.053	0.007	50	Bo	Tito de Morais *et al*. (2015)
Shorea laxa	—	—	1250	Bo	Takeuchi and Diway (2021)
Shorea leprosula	0.058	0.015	25, 35, 250, 250	Bo, PM	Lee *et al*. (2001); Ng *et al*. (2004, 2006); Smith *et al*. (2018)
Shorea lumutensis	—	—	100	PM	Lee *et al*. (2006)
Shorea macroptera	—	—	250	PM	Ng *et al*. (2006)
Shorea ovalis	—	—	35	PM	Ng *et al*. (2004)
Shorea ovata	0.179	0.052; 0.102	200	Bo	Harata *et al*. (2012); Tito de Morais *et al*. (2015)
Shorea parvifolia	0.072; ns	0.009; 0.010	25, 240, 300	Bo, PM	Takeuchi *et al*. (2004); Harata *et al*. (2012); Tito de Morais *et al*. (2015); Lee *et al*. (2016); Smith *et al*. (2018)
Shorea smithiana	0.067	0.012	300	Bo	Tito de Morais *et al*. (2015)
Shorea xanthophylla	0.046; 0.052	0.007; 0.007	100, 120	Bo	Kettle *et al*. (2011); Tito de Morais *et al*. (2015)
Vateria indica	0.122	0.028; 0.031	640, 1200	SI	Ismail *et al*. (2014); Tito de Morais *et al*. (2015)
Vateriopsis seychellarum	0.187	0.041	1200	Bo	Tito de Morais *et al*. (2015)

species has benefited tremendously from genetic testing for genetic improvement; i.e., the performance of commonly used species such as eucalypts, acacias, and teak, has been greatly improved by sourcing seeds from genotypes and populations with fast-growth characteristics followed by breeding programs using these sources. The high genetic/molecular variation found in many of the species reviewed here suggests that there is great potential for native species to compete with exotic timber using genetic and phenotypic

Table 3. Evidence of functional variation in plant performance and traits related to genetic variation in the dipterocarps.

Type of study	Species	Level of genetic variation	Life stage	Response	Main findings	References
Functional	*Shorea leprosula* *Shorea parvifolia* *Parashorea malaanonan* *Shorea johorensis* *Dryobalanops lanceolata* *Hopea nervosa*	Topography of seed-origin	Seedlings	Growth and survival	Within species, topographic seed-origin determined the response of seedling growth and survival.	O'Brien and Escudero (2022)
Molecular + Function	*Vateria indica*	Selfed vs. Outbred	Seedlings	Growth	Growth of selfed projeny ~75% of outbred	Ismail *et al*. (2014)
Molecular + Function	*Hopea bilitonensis*	"seed batches" from two different populations	Seeds	Germination	Germination after 15 days varied ~62–88% among "seed batches."	Lee *et al*. (2013)
Molecular + Function	*Shorea lumutensis*	Half-sib families	Seeds to seedlings	Germination and growth	Variation among mother trees in seed size and germination. Not necessarily translating to performance in the field.	Lee *et al*. (2006)
Molecular + Function	*Neobalanocarpus heimii*	Selfed vs. Outbred half-sib families	Seeds	Seed mass and germination	Significant effect of mother tree and selfing on seed mass + germination was influenced by seed mass and mother tree.	Naito *et al*. (2005)
Molecular + Function	*Shorea leprosula*		Seedlings	Upregulation	Drought causes upregulation of "drought tolerance" genes.	Ng *et al*. (2021)
Molecular + Function	*Parashorea tomentella*	Heterozygosity	Seed to seedlings	Gemination, growth rate, and survival	Seedling survival over 18 months increased with heterozygosity.	Nutt *et al*. (2016)
Molecular + Function	*Shoreo laxa*	perental relatadness	Seed	Seed size	Seed size was decreased with increasing pairwise relatedness of seed parents.	Takeuchi and Diway (2021)
Molecular + Function	*Shorea acuminatissima* *Shorea argentifolia* *Shorea gibbosa* *Parashorea tomentella*		Seedlings	Seedling performance	In three of four species, lower genetic diversity increased the probability of mortality over 30 months.	Tito de Morais *et al*. (2020)
Functional	*Dryobalanops keithii* *Dryobalanops lanceolata* *Shorea leprosula* *Shorea parvifolia* *Parashorea smythiesii*	Half-sib families	Seedlings	Growth and drought tolerance	Genetic variation in basic traits such as growth and susceptibility to herbivory. Two out of five species show genetic variation in drought tolerance.	Axelsson *et al*. (2020)
Molecular + Function	*Parashorea chinensis*	Genetic diversity	Overstory trees	Plant community composition	Genetic diversity of *P. chinensis* promotes the genetic diversity of one understory-abundant species.	Li *et al*. (2022)

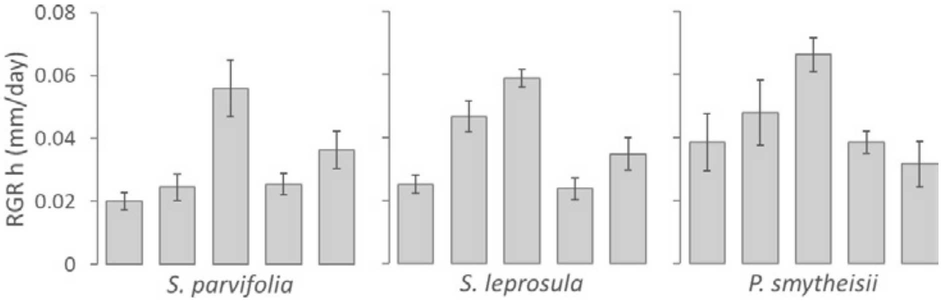


Fig. 3. Variation in height growth among five half-sib families of seedlings of different dipterocarp tree species growing in controlled settings in a nursery in the town of Luasong in Sabah, Malaysia on the island of Borneo. The graphs are reproduced from data in Axelsson *et al*. (2020).

testing. Incorporating a wide array of genetic variation into tree planting programs could promote the use of more native tree species in these programs to thereby enhance multi-functionality. Native species could compete not only on the timber market, but they are also more likely than exotic species to support desired functions such as supporting native food webs and the immense diversity found in the tree canopy and rhizosphere of tropical forests (Charles, 1996; Sakai *et al*., 1999; Chapman *et al*., 2018; Engstrom *et al*., 2020; Axelsson *et al*., 2022). With the new era defined as the Insect Apocalypse and the 6th Mass Extinction, we suggest that a reforestation framework that supports a large amount of diversity should be prioritized and that developing knowledge of genetic variation in native tree species could help to achieve this objective.

Using a genetic-based trait-to-function framework is an effective way to increase forest functionality during reforestation to obtain multiple evolutionary, ecological, economic, and cultural objectives. In addition to growth rate as a desirable trait that can be selected to achieve multi-functional goals, genetically based trait correlations are commonly used to predict a wide array of other functions. Examples of such functions include; soil microbial diversity (Cowan *et al*., 2022; Senior *et al*., 2022), canopy arthropod diversity (Gosney *et al*., 2017), natural regeneration potential (Mamo *et al*., 2006), carbon sequestration potential (Jayawickrama, 2001), tolerance to drought and limited soil nutrients (Depardieu *et al*., 2020; Ismael *et al*., 2022), bird and mammal abundance and richness (Mann *et al*., 2012), duration of flowering to support pollinators, duration of fruiting to support animals and human communities (Nyoka *et al*., 2015), resistance to fires (Hernández *et al*., 2022), and production of fibers and craft-wood for artisans (Axelsson and Grady, 2022), among others. What our review clearly illustrates is that while such genetic-based trait-to-function frameworks are well established in temperate ecosystems, such a framework has not been well developed in ecosystems dominated by dipterocarps despite evidence of high genetic variation that could be employed to achieve forest restoration objectives.

CLIMATE-BASED REFORESTATION AND SEED SOURCE SELECTION STRATEGIES

While multi-functionality is often a goal of reforestation, there is a need to consider how to maintain functionality during climate change (Prober *et al*., 2015). Even in tropical forests, drought events, intense rain events, and seasonality is changing as a consequence of global warming and these changes are having large impacts on forest ecosystems (Axelsson *et al*., 2021; Browne *et al*., 2021; Miyamoto *et al*., 2021). Maintaining the fitness of tree populations during global warming may require interventions. How do we identify genetic resources to stabilize functionality during climate change?

One approach is to examine within population variation in functions such as drought tolerance as increasing drought events from climate change are impacting South-east Asian forests (Axelsson *et al*., 2020). Species with moderate to high FSGS are likely to have low genetic variation at small spatial scales but with increasing scale, genetic differentiation increases. Thus, if seeds are collected from mother trees separated by 1200 m, distinct phenotypes are likely to be encountered (Tito de Morais *et al*., 2015; Table 2). Such phenotypic variation may include different responses to drought as has been found in prior research (Axelsson *et al*., 2020). While FSGS may result in inbreeding at the local population level, it also implies that there is considerable genetic variation across different patches of trees and that the variation across the landscape may be high. Axelsson *et al*. (2020) found large phenotypic variation in response to water limitation among half-sib-families of *Dryobalanops keitthii* collected from mother trees within a 45 km seed collection diameter. According to this review, a large fraction of dipterocarp tree species contains moderate to high FSGS. One potential method to screen species for the presence of FSGS is to start by looking for species that are likely to have gene flow limitations, i.e., species with small flower size, small pollinators, or large seed mass (*sensu* Harata *et al*. (2012) and Tito de Morais *et al*. (2015)). For species suspected to have high FSGS, which our review indicates is a large fraction of them (92%; Table 2) simple nursery progeny experiments can identify drought tolerant genotypes and such genotypes can be increased in frequency in reforestation efforts (Axelsson et *al*., 2020). In addition to finding within population variation in drought tolerance, there is also potential for populations to vary in response to increasing aridity. Differentiation across larger geographical scales and across populations are more likely to be determined by environmental conditions than mating systems (Carvalho *et al*., 2019). We found one such study by Ng *et al*. (2021) that characterized drought-tolerant genes in *Shorea leprosula* and found that the same “drought-tolerant” genes were associated with landscape-level variation in precipitation. By incorporating drought tolerant phenotypes at high frequencies relative to the overall phenotypic composition of a seed source used in reforestation (e.g., pre-adaptation *sensu* Axelsson *et al*., 2020) and/or enhancing overall population genetic diversity as a bet-hedging strategy to allow populations to adapt to a variety of changing environmental conditions (Axelsson *et al*., 2020), we may promote restoration goals during climate change.

Another method for maintaining plant fitness during climate change is assisted migration - to move populations from drier or warmer areas to wetter or cooler areas in anticipation of climate change (e.g., if climate warming and drought are the anticipated eventuality). Similarly, Prober *et al*. (2015) propose a “climate-adjusted” provenancing strategy combining genetic diversity and adaptability, targeting projected climate change directions while allowing for uncertainty in such projections as well as unforeseen selective agents. However, for this method to be effective, we need to understand if populations are locally adapted to environmental conditions and/or if some populations are simply inherently more tolerant to resource stress. Our review reveals a paucity of studies on local adaptation to abiotic and biotic conditions in the dipterocarps (though see O’Brien and Escudero, 2022). Species with moderate to high Fst may be more likely to show patterns of local adaptation, i.e., populations that do not differ molecularly are less likely to have functional trait variation. Although common garden studies where multiple populations from differing climates are planted in home and away environments (i.e., where away environments may include drier areas that represent future conditions) have been very valuable for investigating local adaptation and the potential for assisted migration in other systems (Grady *et al*., 2015); such experiments are lacking not only in South-east Asia but are also rare around the global tropics (Chen and Schemske, 2015; Cruz *et al*., 2019; Barton *et al*., 2020; Muehleisen *et al*., 2020). These studies have provided evidence of local adaptation of tropical tree species to climatic factors (Chen and Schemske, 2015; Cruz *et al*., 2019; Barton *et al*., 2020; Muehleisen *et al*., 2020) while a lack of local adaptation has also been found (Fetched *et al*., 2000). Considering the great wealth of biodiversity in the tropics, it is surprising that more attention has not been paid to natural selection to the environment in the tropics. Summing up the few studies that do exist provides evidence for or against natural selection of tropical trees to climate for less than 20 species.

Developing an understanding of the extent and causes of intraspecific variation in traits and function within the dipterocarps would help in designing seed-sourcing campaigns in a strategic way. For example, including a range of genetic material in reforestation could hedge bets that genetic material suited for future conditions is included in restoration and hence “pre-adapt” developing forests for future conditions (Axelsson *et al*., 2020). Furthermore, in cases where genetic variation occurs as a consequence of evolutionary adaptation to certain environmental conditions (Li *et al*., 2021; Ng *et al*., 2021) such knowledge could be used to direct seed-sourcing campaigns (Prober *et al*., 2015).

This is currently being done in non-tropical forests; e.g., via assisted migration (Grady *et al*., 2015; Zucchi *et al*., 2017) and low-intensity breeding (Pastorino and Marchelli, 2020). Despite good evidence that evolutionary knowledge can increase the effectiveness of reforestation (Thomas *et al*., 2014), a strategic use of genetic resources is not currently being widely applied to the restoration of native tropical forests. This review suggests that developing such strategies would require a better knowledge of what type of selection pressures are influencing intraspecific variation in these forests and how they are distributed across abiotic and biotic environmental gradients.

SEED SOURCING FOR IMPROVING GENETIC DIVERSITY AND GENETIC CONNECTIVITY

Given that many species of dipterocarps are shown to have FSGS, there are likely special considerations needed for effective seed sourcing for restoration in the face of climate change. Forest degradation commonly results in a loss of genetic diversity in tree populations that can cause inbreeding as has been demonstrated in several dipterocarp tree species (Obayashi *et al*., 2002; Wickneswari *et al*., 2004; Ng *et al*., 2009; Ang *et al*., 2016; Widiyatno *et al*., 2016; Widiyatno *et al*., 2017). Populations of species with FSGS are more likely to experience inbreeding as neighboring individuals tend to be genetically related. As a consequence, we often find decreased performance and fitness of subsequent generations of trees (Ismail *et al*., 2014; Nutt *et al*., 2016; Tito de Morais *et al*., 2020; Takeuchi and Diway, 2021). For example, the study by Widiyatno *et al*. (2016) demonstrates that genetic diversity decreases with degradation from logging, especially with respect to sensitive genetic parameters such as the numbers of rare alleles. Furthermore, species with known limitation in dispersal or that are pollinated by immobile insects (e.g., species with high FSGS) may be extra sensitive to isolation and forest disturbance and hence need extra care in restoration. Designing restoration projects that explicitly consider genetic connectivity may help minimize inbreeding and also promote adaptation to environmental change by maintaining gene flow (Ismail *et al*., 2014; Nutt *et al*., 2016; Tito de Morais *et al*., 2020; Takeuchi and Diway, 2021). This may be especially important in cases when competing land use objectives are causing fragmentation that limits gene flow.

Conclusions

We conclude that there are broad differences among tree species in their levels of intraspecific molecular and phenotypic variation with a high proportion of dipterocarp species having fine-scale genetic structure (92%). The occurrence of FSGS suggests that trees aggregated in a forest patch are highly genetically related to each other with high inbreeding potential. Studies of FSGS also suggest that intraspecific variation occurs across relatively short distances (e.g., from 50 to 1200 m between patches). This would also mean that species with FSGS might need special consideration in seed sourcing to prevent inbreeding but also that such species may contain large phenotypic and functional variation on quite small spatial scales. If mother trees for species with FSGS are separated by at least 1200 m, then for 92% of dipterocarps, we would expect phenotypic variation. We suggest that species with high genetic differentiation (high Fst or occurrence of FSGS) are those that are most likely to be usefully employed for increasing multi-functionality and being used in an adaptive capacity either through within population identification of desirable traits for species with high FSGS or through identification of populations that may be pre-adapted to future conditions and used in assisted migration for species with high Fst. By selecting traits such as high tolerance to drought and/or using assisted migration, we can help maintain fitness during climate change. Maintaining genetic diversity and high genetic connectivity also has likely fitness benefits during climate change. However, our major finding that we emphasize here is that there is a major research gap in the understanding of functional variation and the presence of local adaptation within the dipterocarps – this lack of research is consistent globally across tropical forests where very little evolutionary research is applied to ecological restoration despite the clear benefits that have been demonstrated in non-tropical forests. A strategic use of evolutionary science applied to tropical reforestation can improve forest multi-functionality, adaptation to climate change, and the prioritization of native species over exotic species for wood production. While there is still a long way to go to understand how natural selection and other evolutionary factors drive intraspecific genetic variation in the tropics (with research on 20 out of 40,000 known tropical tree species), we suggest that the overwhelming majority of dipterocarp species have both moderate to high Fst and FSGS and that finding species that have useful intraspecific traits to improve reforestation should be relatively easy and immediately useful.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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