ANNALS of SILVICULTURAL RESEARCH

Contemporary spatial association of genetic diversity determinants in Asian Dipterocarps: a systematic review

Journal:	*Annals of Silvicultural Research*
Manuscript ID	ASR-2022-0042.R1
Manuscript Type:	Review Paper
Date Submitted by the Author:	03-Mar-2023
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Keywords:	Genetic diversity, Dipterocarpaceae, molecular markers

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Abstract

Considering the research gaps and areas to be prioritized specifically in the forestry research sector with stress given on conservation genetics and tree improvement, we make an effort to understand the spatial patterns and identify the key determinants, which produce major effects on genetic diversity of Asian Dipterocarps. This review focuses on identifying patterns and establishing relationships between genecological parameters derived on the basis of molecular markers with factors, such as geographical range, vertical profile and IUCN categories along with recognizing research gaps pertaining to operational forestry and terrestrial ecosystems.

Corresponding to 47 research papers, meta-analysis of 50 species under subfamily Dipterocarpoideae revealed significant differences in genetic parameters, namely expected heterozygosity (H_E) and number of alleles per locus (N_A), for most genera and factors. These parameters showed significant correlations with vertical strata (r_k=-0.241; $p<0.05$) and altitude (r_s=0.283; $p<0.01$). However, on the basis of co-dominant and dominant markers, the parameters exhibited contrasting results for the species' characteristics. Further, pollen exchange and seed dispersal predominantly explained the genetic variations among the contributing factors, generally believed to be correlated with vertical strata and geographical range of the species. Conclusively, two major clusters were formed through principal component analysis (PCA), where H_E and N_A were the main deciding factors. Anthropogenic interferences, *viz.* forest fragmentation and deforestation found to be subsidising major impacts, which increase inbreeding and genetic drift, causing the loss of rare alleles and consequently, decreasing genetic variation. The study emphasizes the importance of genecological conservation and access to diverse genetic resources information, which will ensure global forest conservation and climate change mitigation network for sustainable development.

Keywords: Genetic diversity, Dipterocarpaceae, molecular markers, vertical stratification, geographical range, IUCN categories, conservation.

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Introduction

Dipterocarpaceae (often called Dipterocarps), is one of the most well-known plant families in the tropics (Appanah 1998), consisting of 16 genera and 537 species (http://www.plantsoftheworldonline.org/). It is represented by large emergent or canopy trees, generally confined to the Indo-Malayan and Afro-tropical realm with a few species extended to Papua New Guinea (*Anisoptera*, *Hopea* and *Vatica*) and Columbia (*Pseudomonotes*). Apart from being a chief timber source in various house-hold needs, many Non-Timber Forest Products (NTFP), such as resins, dammar, camphor, and butter fat, are also extracted from many of the species (Shiva and Jantan 1998), signifying their socio-economic and cultural value along with the ecological and environmental benefits. Systematically, Dipterocarps are divided into three subfamilies, namely Pakarimoideae, Monotoideae and Dipterocarpoideae (Dayanandan et al. 1999). The subfamily Pakarimoideae is confined to South America and Guyana while Monotoideae is distributed in tropical Africa and Columbia (Ashton 1982). Dipterocarpoideae is the largest subfamily, distributed throughout tropical Asia (Kostermans 1978) (except for *Vateriopsis seychellarum*, which is exclusively found in Seychelles), and are referred as Asian Dipterocarps in this paper. The details of species in this subfamily and their distribution are given in Supplementary Table 1.

In this paper, we target to establish the relationship of estimated genetic diversity measures of Asian Dipterocarps with different taxonomic, geographical, and ecological variables. The genetic diversity represents heritable variation (Ramanatha Rao and Hodgkin 2002) and acts as an important aspect in biological evolution, which allows the population or species to adapt in response to changing environment and natural selection pressure (Swingland 2001). Moreover, it supports resilience and productivity in agricultural, aquaculture, and forestry systems as well as function and structure in all ecosystems (Hoban et al. 2022). In the past few years, numerous researches highlighted the negligence of genetic diversity pertaining to various international conventions (Laikre et al. 2009, Hoban et al. 2020, Hoban et al. 2021), especially the Convention on Biological Diversity (CBD). To be specific, the convention overlooks the importance of genetic diversity in forest-based species while restricting only to the cultivated, socio-economic, and cultural species (www.cbd.int/sp/targets). Forests are the most important terrestrial ecosystem providing ecological niche to various forms of wildlife and flora, sustaining

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livelihoods for humans, and nurturing abiotic factors. Hence, playing a far more critical role than we know and think. Though, in recent times, due to anthropogenic intervention, about 9,810 species of plants come under the category of endangered or critically endangered, out of which many species are on the verge of extinction. (https://www.iucnredlist.org/). Therefore, it is essential to protect the genetic, species and ecosystem diversity concerning various biomes on Earth (Mishra et al. 2023). In view of that, genetic diversity is regarded as the foundation for forest sustainability and ecosystem stability (Rajora and Pluhar 2003). Evaluation of genetic diversity gives an insight to know the health status of a particular species and forest in general, which aids to create management techniques for conservation and tree improvement programmes specifically designed to develop new varieties and clones against biotic and abiotic threats (Salgotra and Chauhan 2023). The genetic diversity impetus and population genetics have been revolutionized by the molecular markers-based approaches, which are time saving and precisely estimating the genetic diversity measures (Wang and Szmidt 2001).

Noteworthily, maintenance of genetic diversity requires adequate implementation of conservation priorities and sustainable management programmes. However, a reduction in species distribution due to severe climate change would lead to a substantial loss of germplasm causing genetic homogenization and loss in diversity. The displacement of climatic genetic clusters due to change in interpolated genetic distances will challenge species adaptation and fundamental evolutionary potential to future climate change (Guan et al. 2021). Thus, a comprehensive study of the molecular genetic variation present in the species would be useful in determining patterns of genomic differentiation (Schierenbeck 2017, Guo et al. 2023).

Given these considerations, the synthesis roughly follows the pattern of some previous appraisals (Hamrick 1979, Hamrick et al. 1992, Moran 1992), which are also based on identifying patterns in species' genetic diversity across the globe. Though all above studies used the genetic data generated from biochemical markers (like allozymes and isozymes), the review was solely focused on the published data of genetic diversity, *via.* dominant and codominant molecular markers. Two key questions are: *(i)* Do levels and patterns of sequence variation in this family look alike under the specified area or not? and *(ii)* How do various factors and ecological effects influence their diversity? It was hypothesized that systematics and genetic variation are the two important keys

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explaining the phylogenetics, spatio-temporal distribution, physical and geographical barriers for gene flow pattern, and adaptation of species in a particular region. Thus, assist in recognizing the species' evolutionary trends. We aimed to: *(i)* evaluate factors influencing the genetic diversity of species under subfamily Dipterocarpoideae in tropical Asia; *(ii)* recognizing the patterns of genetic diversity in Asian Dipterocarps; and finally *(iii)* identification of the research gaps and provide implications on genetic diversity conservation pertaining to terrestrial ecosystems. Overall, the study encompasses geographical range, taxonomy, vertical stratification, International Union of Conservation of Nature and Natural Resources (IUCN) status of the species, to know the key factors that tend to affect the genetic diversity of Dipterocarps in Asia. The analysis and patterns of genetic variation in populations may help us in understanding their epidemiology and evolution. The important integration of the causal factors in the review that have shaped the distribution and existing genetic structure of Asian Dipterocarps will enable us to predict and prioritize the conservation of species encompassing, and areas most likely to be impacted by rapid climate change, human disturbance, and invasive species.

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Experimental procedures and analysis

Pertaining to studies allied to evaluation of genetic diversity, tribes Dipterocarpeae and Shoreae hold quite a vast and varied range. Over and above it, development of protocols, characterizations and isolation of DNA-based markers, and numerous comparisons between several species have been done and published. The studies have been cited across the geographical range of various Asian countries, where the species under these tribes predominate.

Exploration of synthesis and research articles

We have attempted to survey all the published literature on Asian Dipterocarps for which genetic interpretations could be made. However, papers fulfilling the pre-defined criteria for analysis were available in public databases for the last 27 years (1994–2020) only. The criteria chosen on the basis of which research articles were selected are: *(i)* only natural populations; *(ii)* species falling under the tribes Dipterocarpeae (8 genera) and Shoreae (5 genera); *(iii)* literature in which the values of parameters describing genetic variation, i.e., number of alleles per locus (N_A), expected heterozygosity (H_E) and number

of loci, were clearly given; and *(iv)* studies including molecular markers (dominant and co-dominant) only, ruling out biochemical markers. The keywords used to explore the papers online were mainly "genetic diversity of" + genus/species name and "population structure of" + genus/species name. Additionally, the National Forest Library Information Centre (NFLIC), Forest Research Institute (FRI), Dehradun and Northern Region Centre-Botanical Survey of India (BSI), Dehradun were reviewed comprehensively.

Accordingly, we came across a total of 69 papers with respect to different species and marker types, out of which 22 studies were omitted which did not fulfil the above given criteria or due to data inconsistency. Certain species were mentioned in multiple papers and some papers concerned multiple species. Also, some locations, such as Pasoh Forest Reserve (Malaysia), Lambir National Park (Malaysia), etc., throughout the study area were surveyed more than once, for the same or different species. Further, the variable details for selection of data are mentioned in the following sub-sections.

Genetic parameters

The genetic diversity parameters selected for analysis were N_A and H_E. These parameters were selected on the basis of their regularity in the published literature (Hamrick 1979, Hamrick et al. 1992). The parameter – number of loci for which analysis has been done, was given as absolute value in the research papers and has been mentioned as such for analysis purposes. The values of H_E and N_A were calculated by averaging across all loci for each population, whenever it was not averaged. Lastly, the life stages were not taken into consideration under this paper. Thus, the genetic data of seedling, sapling and adult trees were averaged across the same population and used for further analysis. For data of dominant markers, such as Random Amplified Polymorphic DNA (RAPD), Amplified Fragment Length Polymorphism (AFLP) and Inter-Simple Sequence Repeat (ISSR), only the value of H_E was considered.

Species characteristics

Original papers (and publications cited therein) were accessed to obtain information on the characteristics of each species, and in accordance with that, variables, namely number of populations per species, IUCN Red list category status, vertical stratification, geographical range, geo-coordinates (latitude and longitude) and elevation above mean sea level (AMSL), were selected. Variables chosen corresponding to co-dominant and

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dominant marker types were different due to irregularity and unavailability of data. The distinctive ecological variables used in this study are elaborated below.

Geographical range

For geographical range, data were derived from IUCN (https://www.iucnredlist.org/) and Global Biodiversity Information Portal (GBIF) (https://www.gbif.org/). It was divided into three categories on the basis of extent of occurrence and the total number of regions in which the particular species occurs. These categories were: *(i)* Localised – encompassing species occurring in less than 700 km range and found in 1 or 2 regions only; *(ii)* Regional – including species occurring in the range of 700–1,300 km and found in either 2 or 3 regions; and *(iii)* Widespread – including species occurring in more than 1,300 km range and found in 1–8 regions. Further, continuity of a population was also taken into consideration for this variable. For instance, species with patchy distribution or very less populations were considered as localised.

Vertical stratification

For vertical stratification, all the species were categorized according to their average heights. The categories, namely *(i)* Sub-canopy (species having tree height between 10–20 m), *(ii)* Canopy (20–50 m), and *(iii)* Emergent (>50 m), were decided on the basis of general vertical profile of the Tropical Forests (Sime Darby Property 2018). Prominently, some species which are gregarious in nature were placed in "Canopy" avoiding the consideration of their heights. Various local (Ashton 1982, Ashton 2004) and online floras, *viz.* "Plants of Southeast Asia" (https://asianplant.net/), "eFlora" (http://www.efloras.org/) and sites (https://www.iucnredlist.org/, https://www.gbif.org/), were also referred to along with the research papers.

IUCN status

Conservation status data of each species was obtained from IUCN (https://www.iucnredlist.org/) which was mainly among five categories, *viz.* Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT) and Least Concern (LC).

Geo-coordinates

Data for geo-coordinates (latitude and longitude) and altitude were derived from publications. Wherever the coordinates or elevation were not given, Google Earth Pro (Ver.7.3.3.7786; 64-bit) was used to extract that data. The variables, namely pollination

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and seed dispersal mechanism did not show any variation, as almost all the species in Dipterocarpaceae are insect pollinated and dispersed mostly by wind. Hence, not used in the analysis. Further, regional distribution (tropical/subtropical) and few other species characteristics like breeding system, habitat, etc., showed inadequacy of data; ergo they were not taken into consideration.

Statistical analysis and geospatial mapping

Mean estimates of genetic parameters (H_E and N_A) were calculated population wise for every genus and species characteristics, to compare the levels of variability. Data for co-dominant and dominant markers were analyzed and represented separately. The Analysis of Variance (ANOVA) was followed by Tukey's Honestly Significant Difference (HSD) to check pairwise differences. Additionally, to establish relationships among the genetic parameters and species characteristics or geographical variables, correlation was performed. The variables, such as geographical range, vertical stratification, and IUCN status, were converted into ordinal data (ranks) before operating correlation (Tab. 1). None of the variables (except genetic parameters) could be assumed as being normally distributed, so a non-parametric multi-collinearity test was performed to examine the cross-correlation among these variables. Spearman's rank correlation was used to check the linearity between genetic parameters and geographical variables (latitude and altitude), whereas Kendall's tau-b correlation test was used for genetic parameters and species characteristics. Also, multivariate analysis amongst the parameters and the species was done using Principal Component Analysis (PCA). All these tests were performed in the statistical software SPSS (Ver. 3.5.1).

[Here the Table 1]

For spatial mapping, a total of 210 geo-coordinates were used in software ArcMap (Ver.10.5.1) to prepare a geospatial diagram showing the geographical locations of the 8 genera of family Dipterocarpaceae, studied in this review, along with its distribution across Asia, which was finally combined with PCA.

Results

The results compiled from the reviewed literature and articles lead us to the following subheads.

Raw data inferences

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A total of 50 species corresponding to 47 publications were used for data extraction. These have been cited in the researches vis-à-vis pre-defined criterion used in this review for the selection of research papers. In total, 40 and seven articles corresponding to 45 and 14 species were attained with respect to co-dominant and dominant markers, respectively (Supplementary Tab. 2). Count of species and research papers found regarding each genus is shown in Figure 1. From the compiled data, the geographical extent of the populations ranged between 28˚48' N to 7˚43' S and 75˚52' to 124˚06' E. This covers Asian Dipterocarps almost in entirety, however, with a few regions, such as Myanmar, Laos, Cambodia, etc., (Outside extent- Papua New Guinea) were excluded. Likewise, the altitude of sampled populations varied from 4 m (*Dryobalanops aromatica* Gaertn. f.) to 1,270 m AMSL (*Shorea platyclados* Sloot. ex Foxw.). Though creating inadequacy for the analysis, data has been also extracted for species, such as *Vatica mangachapoi* Blanco, *Neobalanocarpus heimii* (King) P.S.Ashton and *Vateria indica* L., which had only one or maximum two studies related to genetic diversity.

[Here the Figure 1]

Subsequently, Supplementary Figure 1 shows the geographical locations of the populations and the number of researches done in that country. The Malaysia (14 studies) was the hotspot in terms of number of researches, owing to its high diversity in Dipterocarps, followed by Indonesia (eight studies), Vietnam (seven studies), China (five studies), India and Philippines (two studies each), and Nepal, Thailand, and Sri-Lanka with one study each.

The details of marker types (dominant and co-dominant both) revealed that an overall 569 loci were used across all the species, where maximum and minimum values of N_A was shown by *Dipterocarpus globosus* Vesque (28.70) and *Hopea hainanensis* Merr. & Chun (1.58), respectively. Similarly, the value of H_E for SSRs ranged between 0.110–0.869 with minimum and maximum value were represented by *D. costatus* G. Don and *S. platyclados* Sloot. ex Foxw., respectively. However, for dominant markers, H_E ranged between 0.097 (*S. parvifolia* Dyer) to 0.361 (*Hopea chinensis* (Merr.) Hand.-Mazz.).

A total of 23 widespread, 11 regional and localized species each, were categorized according to their geographical range among the collected data for co-dominant markers, whereas 10 widespread, two regional and localized species each, were derived for

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dominant markers. In case of co-dominant markers, most of the species were emergent (25) with a total population of 54, which are dominated in the southeast Asian region, namely Malaysia, Vietnam, Indonesia, and Philippines. This was followed by canopy (16 species, 118 populations) dominated all over Asia; and sub-canopy (four species, 16 populations) in countries like China, Vietnam, and Indonesia. However, species analyzed using dominant markers were mainly represented as canopy (seven species, 16 populations) followed by emergent (six species, 21 populations in Indonesia only) and sub-canopy (single species, four populations in China only).

Regarding IUCN Red List category, maximum species were categorized as least concern (13) followed by vulnerable (11), endangered (one), critically endangered (seven) and near-threatened (four) for co-dominant marker. Importantly, the critically endangered 11 populations correspond to seven species belonging to the China, Indonesia, Malaysia, Sri Lanka, and Vietnam, out of which nine were localized. Dominant markers related species were reviewed mostly as critically endangered and least concern (four each) followed by vulnerable (three), endangered (two) and near-threatened (one). Here also, the critically endangered species *H. chinensis* (China) and *S. blumutensis* Foxw are localized ones, whereas *S. johorensis* Foxw and *S. palembanica* Miq. were widespread and distributed in Indonesia.

Variation among genera

The total number of entries (N) for the entire dataset was 188 (co-dominant markers) and 46 (dominant markers), which corresponded to the number of populations analyzed in different studies (Tab. 2-3). Many locations were sampled multiple times by various authors during the entire timeline. On average, the genetic diversity (H_E) for all the species of Asian Dipterocarps was 0.58 using co-dominant markers (SSRs) and 0.18 using dominant markers (ISSR, RAPD and AFLP). Mean number of alleles per locus (N_A) for all the species was 6.41, calculated only for species analyzed using co-dominant markers. The value of N_A and H_E was more in tribe Shoreae (6.93 and 0.62, respectively) than tribe Dipterocarpeae (4.52 and 0.41, respectively). The mean differences were significant at probability level less than 0.05 (Tab. 2). However, the differences in H_E were not significant ($p<0.05$) regarding dominant markers for different tribes and total species (Tab. 3). Overall, eight genera (45 species) were analyzed using co-dominant markers, whereas dominant markers were used for four genera (14 species) only.

For Review Only

[Here the Table 2 & 3]

In case of co-dominant markers, the highest value of variable N_A was shown by genus *Parashorea* (8.49) followed by *Shorea* (8.05) and *Vatica* (6.94). Whereas lowest values were obtained for *Hopea* (3.06) and *Dipterocarpus* (4.25). Importantly, the monotypic Malaysian *N. heimii* (King) P.S.Ashton showed the value for N_A equal to 11.16, which has only one population under the genus and that was insufficient to be included in the analysis for further comparison. The value for H_E varied from 0.37 (*Dipterocarpus*) to 0.71 (*Vatica*). *Neobalanocarpus heimii*, owing to a single population, revealed H_E to be 0.79. Another genus belonging to India, i.e., *Vateria*, was also sampled from only one location with N_A=7.25 and H_E=0.67. The values of genetic parameters for these two genera are higher than some of the others but data is insufficient to make any inferences. Other genera with less studied populations were *Parashorea* (4) and *Vatica* (3). Given, at least 10 populations analyzed, the highest value for mean number of loci was revealed by *Hopea* (10.90) and most populations were analyzed for *Shorea* (91). However, the mean number of populations per species was highest for *Dryobalanops* (10.33).

In case of dominant markers, *Hopea* had the highest value (0.34) of H_E, which significantly ($p<0.05$) differed from *Dryobalanops* (0.19), *Shorea* (0.15) and *Vatica* (0.21). Although, *Shorea* (30) had most populations analyzed owing to multiple studies but the mean populations per species was lesser with 2.72. Other genera had considerably lesser populations sampled for genetic analysis, as revealed by very few papers. Interestingly, *V. mangachapoi* Blanco was analyzed for five populations each using RAPD and AFLP, making the total number of entries (N) equal to ten.

Variation among factors

In natural populations, genetic diversity depends on factors, namely geographical range, vertical strata, and IUCN categories for socio-economic importance, which revealed significant outcomes for both co-dominant and dominant markers (Tab. 2-3).

In co-dominant markers, significant ($p<0.05$) differences in categories of geographical range were observed in localized and widespread species for both the genetic parameters (N_A and H_E). Here, the latter one (0.59) has more genetic diversity as compared to regional (0.56) or localized (0.50) species. The values of N_A ranged from 4.85 (localized)–6.80 (widespread) for SSRs. However, the mean number of loci per population was highest (10.04) for localized species and mean number of populations

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analyzed per species was highest (5.69) for wide-ranged species. Regarding dominant markers, localized (0.30) showed higher H_E then widespread (0.17) or regional (0.14) species. Notably, differences in H_E for dominant markers were significant ($p< 0.05$) for two pairs, *viz*. localized-widespread and localized-regional.

Among the five IUCN listed species, four and three categories in N_A and H_E showed significant differences ($p<0.05$) corresponding to co-dominant markers, respectively. The highest values for H_E (0.69) was shown by species in the least concern category. Other categories, such as critically endangered (N=11), endangered (N=74), vulnerable (N=57) and near threatened (N=12) revealed values of H_E to be 0.54, 0.60, 0.47 and 0.68, respectively. The values of N_A for different categories ranged from 4.87 (vulnerable) to 9.98 (least concern). Furthermore, the mean number of populations per species was found to be highest for the endangered category (7.4). In case of dominant markers, only 2 pairs showed significant differences ($p<0.05$). The values in H_E ranged from 0.15 (endangered and near threatened) to 0.25 (critically endangered), where minimum size (1–1.75) of the mean number of populations was observed for the two lowest categories.

The parameter vertical stratification showed significant differences ($p<0.05$) in H_E and N_A observed for co-dominant markers. For H_E, the significantly different categories were sub-canopy (0.461) and emergent (0.616) species. Canopy species (0.57) showed no significance in H_E values with either of the two other categories. In the case of N_A, sub-canopy (2.97) species showed significant differences with species in both canopy (6.35) and emergent (7.54) layers. The values for mean number of loci ranged from 8.13 in emergent to 11.63 in sub-canopy species. Also, canopy species had 118 populations analyzed with a mean value of 7.37 populations per species. For dominant markers, differences in H_E among all three categories of vertical strata were significant ($p<0.05$). The highest value of H_E was shown by species in sub-canopy (0.34) layers, followed by canopy (0.20) and emergent (0.14) layers.

Correlations

Correlation matrix was developed for co-dominant and dominant markers of the related species under subfamily Dipterocarpoideae, showing levels of correlations between genetic parameters (N_A and H_E), geographical factors (latitude and altitude) and other factors (geographical range, vertical strata and IUCN categories) (Tab. 4). Spearman's coefficient of ranked correlation and Kendall's tau-b were used to determine the same.

For Review Only

[Here the Table 4]

In the case of co-dominant markers, there was a significant correlation (r_k=0.625 and r_s=0.817; p<0.01) between N_A and H_E. The N_A was negatively correlated with latitude (r_s=-0.146; p<0.05) and altitude (r_s=-0.145; p<0.05) among the geo-coordinates, and IUCN categories (r_k=-0.248; p<0.05) and vertical strata (r_k=-0.310; p<0.01) for the species characteristics. For H_E, significant association was observed with altitude (r_s=0.283; p<0.01) and vertical strata (r_k=-0.241; p<0.05). Other correlations for both N_A and H_E were insignificant. Intended for the dominant marker, H_E was substantially correlated with latitude (r_s=0.671; p<0.01) and vertical strata (r_s=0.495; p<0.05). While other parameters with respect to H_E were not significantly associated.

Multivariate analysis

Multivariate analysis was done using PCA, to determine covariance and correlations among genetic parameters and other factors. As stated before, N_A and H_E had the highest correlation, indicating that they convey the same information. There were no other strong correlations (i.e., r>|0.5|), while a few correlations were moderate (i.e., |0.5|>r>|0.3|). All the five variables for 52 species (including both the marker types) were analyzed using the PCA. Seven species corresponding to those papers, which calculated genetic diversity using dominant markers were removed due to absence of values for N_A. A total of three components were extracted which described 84.38% of the total variation. The first principal component (PC_1) had highest loadings from genetic parameters N_A and H_E (both positive) followed by vertical strata and IUCN categories (both negative). The PC_2 had positive high loadings from geographical range and IUCN categories, while the last one (PC_3) showed the highest loadings from geographical range (negative), H_E and IUCN categories (positive). The communalities of the variables in the PCA indicate the proportion of variance as explained by the three principal axes. Here, all variables except vertical strata showed values more than 0.7.

Further, we plotted all 52 species on a bi-plot using the PCA on three dimensional axes. It was done by extracting three PCs which explained 97.85% of variation. The species for which dominant markers were used in analysis of genetic diversity, are shown by the alphabet 'D' after their name. There are two major clusters, namely Cluster I (Bottom Right) and Cluster II (Top), spatially distributed forming the bi-plot (Fig. 2a–b). Cluster I is more compact as compared to Cluster II. As there is the highest correlation

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between N_A and H_E, the majority of the clusters forming the bi-plot can be explained using these two values.

[Here the Figure 2a-b]

The dotted spikes in the bi-plot show the distance of the points (corresponding to each species) from the PC_1-PC_3 plane. The species with the highest values of N_A and H_E are clustered near this plane (Cluster I). All the species in this cluster have mean value of N_A greater than four and H_E greater than 0.6 except for the species, namely *Parashorea tomentella* (Symington) Meijer, *Shorea xanthophylla* Symington, *Shorea acuminatissima* Symington and *Shorea laevis* Ridl., which had higher values in N_A. Further, the species with low values in N_A and H_E are farthest away from this plane and thus, forming cluster II. This cluster comprises the species which are mostly sub-canopy, localized and critically endangered or endangered with low genetic diversity (H_E and N_A) that was analyzed using dominant markers. In addition, the species *S. robusta* Roth, *D. aromatica* Gaertn. f. and *V. mangachapoi* Blanco showed large distances among their counterparts separated, *via.* both the marker types. However, the points of *H. chinensis* were quite nearby, which shows similarity in values of genetic diversity is independent for both co-dominant and dominant markers. Also, for other species, both the markers showed contrasting results, which can also be seen in Table 2 and 3. The species lying in the transition zones of cluster I and II were *Dryobalanops beccari* Dyer and *Dipterocarpus dyeri* Pierre, originated in Malaysia and Vietnam, respectively.

Importantly, *S. robusta* (using dominant markers) acts as an outlier lying parted from both the clusters, which can be explained by its distance from PC_2. The species nearest to the PC_2 are generally widespread and least concerned. The species, such as *Dipterocarpus littoralis* Blume, *H. chinensis*, *H. hainanensis* (C.C.Chang & Y.C.Tseng) Ying Liu & Q.E.Yang, and *Hopea bilitonensis* Ashton are farthest away from PC_2 owing to their localized range. Lastly, the species with more distance from PC_3 were generally widespread and least concerned. However, the overall effect of H_E and N_A had more impact on PC_3, which can be observed in the bi-plot.

Discussion

Foresters realized that tree genetic diversity can be captured and stored in the form of Forest Genetic Resources (FGRs), such as gene bank, DNA library, and so forth, in the

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biorepository, which preserve genetic material for a long-period. However, conserved FGR must be utilized to meet future global challenges in relation to food and nutritional security. A total of 50 species were used in this review, accounting for roughly 10% of the overall species in Asian Dipterocarpaceae. It revealed that there are major voids that need to be filled by more research with varied distribution coverage. In order to generalize the discoveries from genetic studies of imperative genera of Dipterocarpacae and to provide opportunities for new understanding of patterns and conservational strategies, it is crucial to investigate more prevalent genetic variation in world-wide populations, particularly in threatened species. Inadequacy of data and research gaps indicate major future prospects of genetic diversity analysis in this group, whose details are elaborated in the next sections.

Geographical extent and association of key genetic diversity determinants

Geographically, maximum studies have been conducted on the island of Borneo (in both Malaysia and Indonesia), Peninsular Malaysia and Vietnam. Thus, these places can be considered as hotspots of the research on genetic diversity of Asian Dipterocarps. The countries, namely India, Myanmar, Laos, and Philippines, however, showed severe data insufficiency considering these studies, despite holding remarkable species richness. Notably, tribe Shoreae has revealed a greater number of studies as a whole than Dipterocarpeae, which could be due to Shoreae being more diverse and holding enormous numbers with a vast range of species (Supplementary Fig. 1).

Amongst SSRs and other dominant markers, to analyse genetic diversity, the former one has proved to be a promising tool analysed through this review, since some species evaluated using SSRs for the same locations (*V. mangachapoi*, *D. aromatica*, etc.) have displayed relatively higher value of N_A and H_E (Tab. 2-3). Importantly, the SSRs characterize populations on the basis of allelic heterozygosity of both the parental types, which is lacking in case of dominant markers. Thus, showing higher value of N_A and H_E in comparison to dominant ones. Secondly, the microsatellite markers give a high number of alleles due to length mutation, which causes differences in repeat units and high variability in comparison to allozyme sequences (Schlotterer and Pemberton 1998, Ng et al. 2004). Overall, several problems and limitations while using dominant markers were highlighted in population genetic analysis (Harada et al. 1994). Hence, SSRs show impact

For Review Only

and comprehensive analysis on revealing the level of genetic diversity in most of the forest flora.

The variation in genetic diversity of a plant species generally depends on combination of factors, such as habitat type, geographical range, regional distribution, pollination mechanism, breeding system, mode of reproduction, seed dispersal, fecundity, generation length, successional and cultivation status (Hamrick 1979, Hamrick et al. 1992). Though, many of these factors can be avoided in explanation of genetic variation as the species in this review belong to the same taxa (Family Dipterocarpaceae) and may have similar values (causing influence), which might be possible that the effect of some of these factors can be essential. Dipterocarps are predominantly outcrossed species (Obayashi et al. 2002) pollinated by insects (Ashton 1982), which increases their genetic variability in comparison to other self-pollinated species. In case of seed dispersal, wind is the major precursor owing to the winged nature of the fruit (except *Vateria*) (Ashton 1982). However, a few studies mention secondary dispersal, *via.* Water (Tam et al. 2014) and rodents (Ismail et al. 2014). Consequently, seed dispersal and extent of pollen exchange plays an important role in determining the genetic diversity, increasing with the distance of seed or pollen travelled (Cao et al. 2006, Indriani et al. 2019, Vu et al. 2019).

Species diversity attributed to pollinators and seed dispersal

In this review, for co-dominant markers, the lowest genetic diversity has been shown by *Dipterocarpus* and *Hopea*. The former genus is generally pollinated by nocturnal moths of order Lepidoptera (Ashton 1982) having lesser mobility than other pollinators like bees. Therefore, pollination in *D. alatus* Roxb. ex G.Don and *D. costatus* G.Don is not far than a few kilometers (Vu et al. 2019) declining their genetic diversity. However, species like *Dipterocarpus crinitus* Dyer and *D. globosus* Vesque have shown higher diversity (Harata et al. 2012) and are known to be pollinated by *Apis dorsata* (Harrison et al. 2005). In the case of *Hopea*, the low genetic diversity can be explained by the under-canopy nature of its trees, which reduces seed dispersal (Takeuchi et al. 2004) and also affects the pollen exchange to longer distances. Unlike other dipterocarps, *V. indica* L. has wingless fruits, which might restrict its seed dispersal capabilities (Ismail et al. 2014). Still, this species shows comparably higher genetic diversity than other genera, which might be due to the other factors compensating for the seed dispersal restrictions. Yet,

For Review Only

more detailed studies are required to be done in this arena to understand the genetic variability of endemic species.

Apart from seed dispersal and pollination, the genetic variability can also be explained by range and regional distribution of the species. The genus *Shorea*, generally pollinated by tiny insects, i.e., thrips (Ashton 1982, Cao et al. 2006, Mishra et al. 2020) and beetles (Harrison et al. 2005), with very low mobility showed higher genetic diversity due to their widespread and gregarious nature. The bee pollinated *Dryobalanops* (Ashton 1982) revealed comparably higher genetic diversity than *Dipterocarpus* disclosing the sensing behaviour and evolution of pollinators in determining these variations. Importantly, the pollination mechanism (limited pollen dispersal) with the flower size was related in *P. tomentella* (Symington) Meijer, *Dipterocarpus grandiflorus* Blanco and *S. xanthophylla* Symington, where large flowered *D. grandiflorus* have more genetic diversity than other two species with comparably smaller flowers (Kettle et al. 2011). This can be positively related with the size of a pollinator, as large flowered species are pollinated by bees in comparison to thrips as the latter usually pollinate small flowers (Ashton 1982, Harrison et al. 2005). Invariably, the seed dispersal and pollination mechanism are generally dependent on other ecological and geographical factors (Takeuchi et al. 2004, Ng et al. 2019) explained in the next sub-section.

Species diversity in association with eco-graphic factors

In case of dominant markers, there exists a large sampling sparseness, which may be attributed to the pre-eminence of co-dominant markers used in most of the studies. The meta-data analysis revealed that the *Shorea* showed the least genetic diversity when analyzed using dominant markers, while *Hopea* had the highest. The meagerness in these dataset makes it difficult to generalize the results on the basis of some factors, and thus, comparative studies are needed to know the exact pattern in this type of analysis. However, for the comprehensive explanation, other factors must be taken into consideration. Species showing higher genetic diversity, in spite of seed and pollen exchange being at a smaller distance, might dependent on other factors, e.g., regional geographical range, high fecundities, outcrossing, long life span and late succession phase are responsible for maintaining high genetic diversity (Lee et al. 2000).

Notably, geographical range acts as an essential predictor of genetic variation in a species. Generally, widespread species tend to have higher proportions of alleles and

For Review Only

genetic diversity than geographically limited species (Hamrick et al. 1992), as continuous distribution conserves genetic diversity from adverse effects of bottleneck (Ng et al. 2019), which is evident through Table 2-3. Though, in case of dominant markers, this pattern was found to be reversed as localised species showed higher diversity. It could be explained by the huge difference from attributes, *viz*. number of studies and number of populations between widespread species (N=5) and localised species (N=38), which instigated deficit sampling. Species, such as *D. littoralis* Blume, *H. chinensis*, etc., comparatively revealed lower genetic diversity owing to their restricted distribution and often occurrence in small isolated populations. This confines the gene flow resulting in reduced genetic variation, which is also explicitly found in endangered and endemic plants (Gitzendanner and Soltis 2000, Indriani et al. 2019, Rachmat et al. 2020). However, species, namely *D. alatus*, *D. costatus* and *Hopea odorata* Roxb. are exceptions as their gene diversity was found to be low despite its widespread distribution, as explained before the role of pollinators.

Moreover, vertical stratification also turned out to be playing a significant role in genetic diversity of trees. In the matter of co-dominant markers, sub-canopy species, *viz*. *H. chinensis*, *Hopea reticulata* Tardieu, etc., indicated relatively lesser value of diversity than emergent species (*Shorea acuta* P.S.Ashton, *Shorea amplexicaulis* P.S.Ashton, *Shorea guiso* Blanco (Blume), etc.; Tab. 2). It is probably due to seed dispersal depending on the height of the release point as taller trees disperse their seeds more expansively over long distances (Takeuchi et al. 2004, Nguyen et al. 2014), further strengthening their genetic diversity (Hamrick 1979, Morais et al. 2015). This result contrasts markedly in case of dominant markers (Tab. 3), which may be due to lesser number of studies/ populations in case of sub-canopy species (N=4) than the emergent (N=21) ones, as discussed previously. Most of the heterozygosity has been shown by least concern (*S. robusta* Roth, *S. acuta* P.S.Ashton , *Shorea curtisii* Dyer ex King, *D. globosus* Vesque, *S. parvifolia* Dyer, etc.) and near threatened (*S. platyclados* Sloot. ex Foxw., *N. heimii* King (Ashton), etc.) than vulnerable, endangered and critically endangered species. This low genetic diversity and allelic value is most likely due to factors, such as severe demographic bottleneck, deforestation, habitat-degradation, over-exploitation, and fragmentation (Ismail et al. 2014, Dwiyanti et al. 2014a, Duc et al. 2016, Wang et al. 2020a), associated with rare species. It is ensued by the formation of small and patchy

For Review Only

populations and lessened outcross rate (Obayashi et al. 2002), leads to inbreeding and loss of alleles by the genetic drift and enhances genetic erosion (Li et al. 2005, Ng et al. 2009). Nonetheless, not all type of rarity has the same genetic implication which could be the reason for some species, i.e., *H. bilitonensis* Ashton, *Shorea cordifolia* (Thw.) P. Ashton, etc., showing high level of genetic variation in spite of being critically endangered (Cao et al. 2009).

In addition, the factor altitude and raised topography inflicts on increasing long distance seed dispersal and pollen exchange may be enhanced by wind movements (Nguyen et al. 2020). In this review, H_E showed positive correlation with altitude (for both dominant and co-dominant markers) which might be explained by the aforesaid statement. However, there was a negative correlation (very weak) between N_A and altitude showing compensation of other factors on this generality. The correlation between latitude and H_E for dominant markers was highly positive (r_s=0.671; $p<0.01$) implying high latitude species with greater diversity. As a high latitude zone comprises more landmasses in comparison to low latitude zone (sea predominates), where ecological gradients (species distribution, seed dispersal, pollinators, distribution, biotic and abiotic components, etc.) might play a crucial role in defining genetic diversity. Additionally, in terms of latitude, the majority of the studies have been done between 10° S and 10° N and other studies throughout the extent are rather scattered to be inferred (weak and negative correlation in case of co-dominant markers) on the basis of relationship between latitude and H_E.

Other geographical features, such as ridges, mountains, and rivers, also create barriers to the gene flow (Pandey and Geburek 2009), indicating high genetic variation in the species of the plains. Here, the multivariate analysis raises two main questions: *(i)* Do species with particular combinations of traits have altered genetic variation? and *(ii)* Do certain characteristics have greater impact than others? Our PCA revealed the value of H_E and N_A were the main deciding factors in the formation of two major clusters, i.e., I and II (Fig. 2a–b), as the species with high H_E was clustered altogether. It also explained the separate clustering of species with respect to dominant and co-dominant markers. Additionally, other factors which have combined effects (with H_E and N_A) in the clustering observed were primarily IUCN categories and vertical stratification. The key

For Review Only

outcomes and important recommendations arising from this review have been elaborated in Supplementary File 1.

Conclusions

Genetic diversity delivers the building blocks for biological diversity at the levels of species, population, and ecosystem. Hence, play a vital role in populations' ability to respond to fluctuating environmental conditions. Categorically, our observations on the genetic diversity of Asian Dipterocarps have implications for filling the research gaps through more intensive studies on this aspect. The dataset is deficient in contrast to the species richness of Dipterocarpaceae. With species exhibiting immense significance, the lack of research pertaining to genetic diversity is quite alarming. First and foremost, we invoke immediate action towards the forestry implementation and conservation programmes with species specific genetic guidelines to save these taxa from fragmentation, increased inbreeding, and genetic erosion by genetic drift. We emphasize that future studies should focus on revealing other factors that may have major influence on genetic variation of these species, either solely or in combination. Such characteristics may include fecundity, fine-scale spatial genetic structure, population densities, pollen dispersal, juvenile and seedling mortality, mating system, etc. Moreover, *in situ* and to supplement it, *ex situ* conservation should be maintained to restore the regeneration of populations. This review presents indicators of patterns of diversity in Asian Dipterocarps, which may help refine prescriptions for management that would aid in reducing the damage and restoration for this globally valuable group of forest trees.

For Review Only

Acknowledgements

The authors are thankful to the Director, FRI for providing the research facility and Mr. Shivam Kishwan (FRI, Dehradun) for his generous help in the analysis. The UGC-JRF (Grant award NTA Ref. No. 210520034468; dated: 12/03/2022) provided to the researcher (first author) is duly acknowledged. Authors are grateful to the two anonymous reviewers for their positive and constructive comments.

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For Review Only

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For Review Only

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Table 1 - Summary of the genetic, geospatial and species characteristics variables used in statistical analysis.

Variables	Datatype	Converted values	Test used
Expected heterozygosity (H_E)	Continuous	-	Parametric
Mean number of alleles (N_A)	Continuous	-	Parametric
Latitude	Continuous	-	Non-parametric
Altitude	Continuous	-	Non-parametric
Geographical range	Discrete (Ordinal)	Widespread (1), Regional (2) and Localized (3)	Non-parametric
Vertical stratification	Discrete (Ordinal)	Emergent (1), Canopy (2) and Sub-Canopy (3)	Non-parametric
IUCN status	Discrete (Ordinal)	Least Concern (1), Near Threatened (2), Vulnerable (3), Endangered (4), Critically Endangered (5)	Non-parametric

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Table 2 - Levels of variability between variables w.r.t co-dominant marker (SSR) used studies.

Sl. no.	Categories	N[1]	Mean number of populations	Mean number of loci	N_A	H_E
					**	**
	All Species	188	4.18	9.09	6.41[b]	0.58[b]
			(0.955)	(0.266)	(0.272)	(0.013)
	Dipterocarpeae	41	4.10	9.05	4.52[a]	0.41[a]
			(1.456)	(0.209)	(0.743)	(0.037)
	Shoreae	147	4.20	9.10	6.93[b]	0.62[c]
			(1.165)	(0.335)	(0.266)	(0.011)
	Genera				**	**
1.	Dipterocarpus	37	4.625	8.73	4.25[ab]	0.37[a]
			(1.78)	(0.158)	(0.811)	(0.036)
	Dryobalanops	31	10.33	7.16	5.81[ab]	0.56[bc]
			(5.48)	(0.105)	(0.423)	(0.025)
	Hopea	20	3.33	10.90	3.06[a]	0.46[ab]
			(1.38)	(0.499)	(0.239)	(0.025)
	Neobalanocarpus*	1	1	6.00	11.16	0.79
	Parashorea	4	2	6.00	8.49[b]	0.60[bc]
			(0)	(0.816)	(2.231)	(0.072)
	Shorea	91	3.96	9.54	8.05[b]	0.68[c]
			(1.56)	(0.499)	(0.310)	(0.009)
	Vateria*	1	1	12.00	7.25	0.67
	Vatica	3	3	12.00	6.94[ab]	0.71[c]
				(0)	(0.274)	(0.015)
	Geographical range				**	**
2.	Localized	28	2.54	10.04	4.85[a]	0.50[a]
			(1.961)	(0.756)	(1.042)	(0.026)

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	Regional	29	2.63	7.72	6.13[ab]	0.56[ab]
			(1.966)	(0.726)	(0.692)	(0.028)
	Widespread	131	5.69	9.19	6.80[b]	0.59[b]
			(1.336)	(0.318)	(0.277)	(0.017)
	IUCN status				**	**
3.	Critically endangered	11	1.57	10.00	5.43[a]	0.54[a]
			(1.494)	(0.854)	(0.952)	(0.034)
	Endangered	74	7.4	11.23	5.86[a]	0.60[a]
			(2.042)	(0.435)	(0.360)	(0.017)
	Vulnerable	57	5.18	8.32	4.87[a]	0.47[a]
			(1.932)	(0483)	(0.367)	(0.030)
	Near threatened	12	3	7.75	7.80[ab]	0.68[b]
			(3.988)	(.384)	(0.876)	(0.022)
	Least Concern	34	2.61	5.91	9.98[bc]	0.69[b]
			(1.866)	(0.691)	(0.763)	(0.015)
	Vertical stratification				**	**
4.	Sub-canopy	16	4	11.63	2.97[a]	0.46[a]
			(1.693)	(0589)	(0.244)	(0.025)
	Canopy	118	7.37	9.19	6.35[b]	0.57[ab]
			(1.601)	(0.335)	(0.286)	(0.018)
	Emergent	54	2.16	8.13	7.54[b]	0.62[b]
			(1.306)	(0.532)	(0.649)	(0.021)

[1]N-Total number of populations analyzed, N_A-Mean number of alleles per locus, H_E-Expected heterozygosity.

*Not used in analysis due to insufficient data (See text for details).

**Results significant for $p<0.05$.

Superscript indicated by the same letter (a, b and c) showing non-significant differences according to Tukey HSD.

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Table 3 - Levels of variability between variables w.r.t dominant markers (RAPD, ISSR and AFLP) used studies.

Sl. no.	Categories	N[1]	Mean number of populations	Mean H_E
			NS	NS
	All Species	46	2.93	0.18
			(0.730)	(0.009)
	Dipterocarpeae	10	5*	0.21
				(0.008)
	Shoreae	36	2.77	0.18
			(0.762)	(0.012)
1.	**Genera**			**
	Dryobalanops	2	2	0.19[a]
				(.015)
	Hopea	4	4	0.34[b]
				(0.011)
	Shorea	30	2.72	0.15[ac]
			(0.905)	(0.008)
	Vatica	10	5	0.21[ad]
				(0.008)
2.	**Geographical range**			**
	Localized	5	2.5	0.30[b]
			(1.000)	(0.035)
	Regional	3	1.5	0.14[a]
			(0.408)	(0.013)
	Widespread	38	3.3	0.17[a]
			(0.863)	(0.008)
3.	**IUCN status**			**
	Critically endangered	7	1.75	0.25[c]
			(1.346)	(0.040)
	Endangered	2	1	0.15[a]
			(2.596)	(0.014)
	Vulnerable	14	3	0.19[b]
			(1.576)	(0.010)
	Near threatened	9	9	0.15[a]
				(0.010)
	Least Concern	14	3.5	0.16[a]
			(1.501)	(0.015)
4.	**Vertical stratification**			**
	Sub-canopy	4	4	0.34[c]

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			(0.010)
Canopy	21	2.28	0.20[b]
		(1.032)	(0.009)
Emergent	21	3.5	0.14[a]
		(1.335)	(0.007)

[1]N-Total number of populations analyzed, N_A-Mean number of alleles per locus, H_E-Expected heterozygosity.

*Only one study for *V. mangachapoi* using RAPD and AFLP taking 5 populations.

** Results significant for $p<0.05$.

Superscript indicated by the same letter (a, b and c) showing non-significant differences according to Tukey HSD.

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Table 4 - Correlation among the variables for co-dominant and dominant markers.

	N_A	H_E	Latitude	Altitude	Range	V. Strata	IUCN Cat.
Co-dominant marker							
N_A	-	-	-	-	-	-	-
H_E	0.625**[k] 0.817**[s]	-	-	-	-	-	-
Latitude	-0.146*[s]	-0.136[s]	-	-	-	-	-
Altitude	-0.145*[s]	0.283**[s]	0.111[s]	-	-	-	-
Range	-0.009[k]	-0.081[k]	NC	NC	-	-	-
V. Strata	-0.284*[k]	-0.256[k]	NC	NC	0.121[k]	-	-
IUCN Cat.	-0.248*[k]	-0.194[k]	NC	NC	0.218[k]	0.377**[k]	-
Dominant markers							
H_E	NC	-	-	-	-	-	-
Latitude	NC	0.671**[s]	-	-	-	-	-
Altitude	NC	0.270[s]	0.351*[s]	-	-	-	-
Range	NC	0.253[k]	NC	NC	-	-	-
V. Strata	NC	0.495*[k]	NC	NC	0.366[k]	-	-
IUCN Cat.	NC	0.085[k]	NC	NC	0.470[k]	0.405[k]	-

*Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).
[s]Spearman's correlation coefficient, [k]Kendall's tau-b coefficient.
NC: Not calculated.

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Figure 1 - Number of species and papers w.r.t each genus.

Figure 2 - Geographical distribution of populations analyzed in Asian dipterocarps; (a) the 920 colors of the coordinates spatially correspond to the PCA results, and (b) 3D bi-plot 921 showing all species analyzed using PCA.

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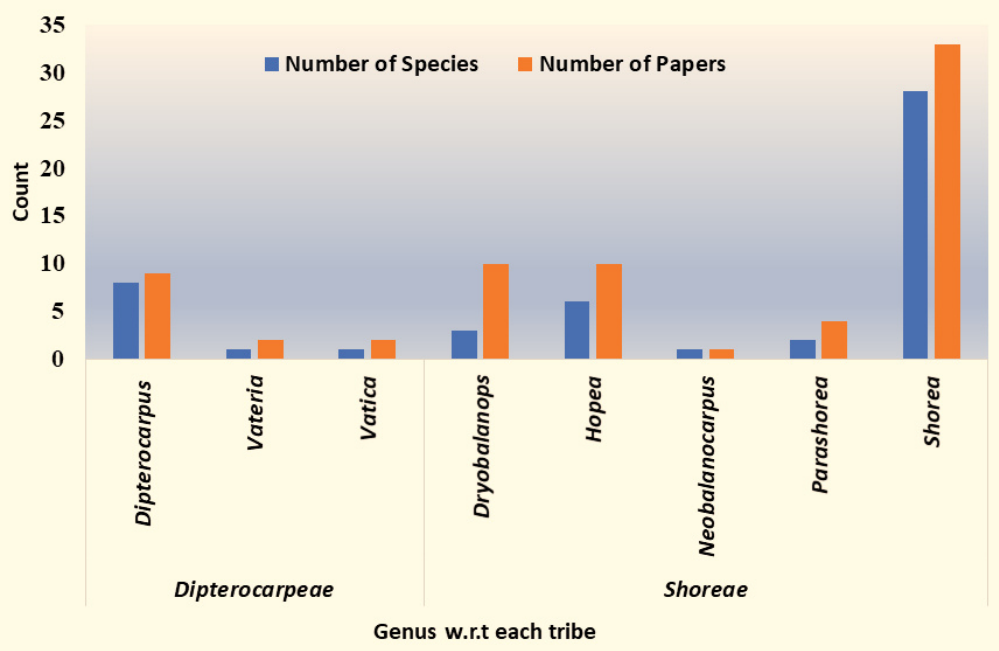

Fig. 1

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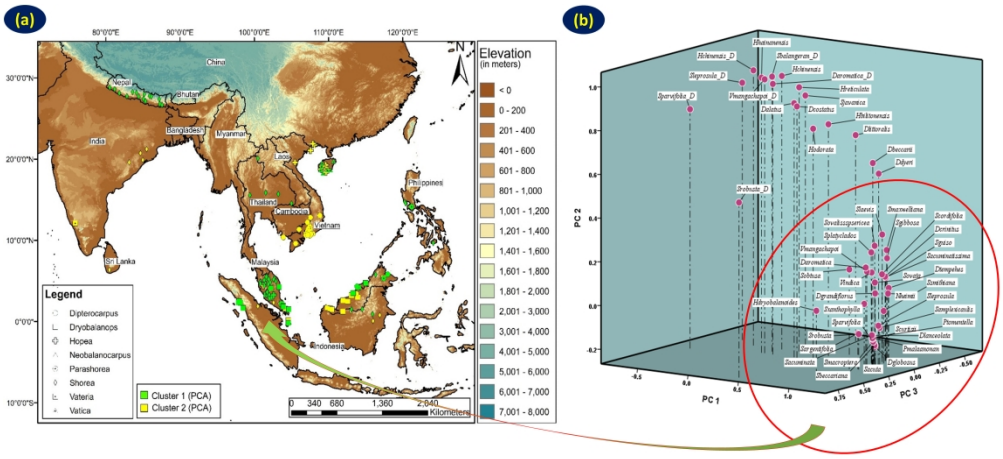

Fig. 2

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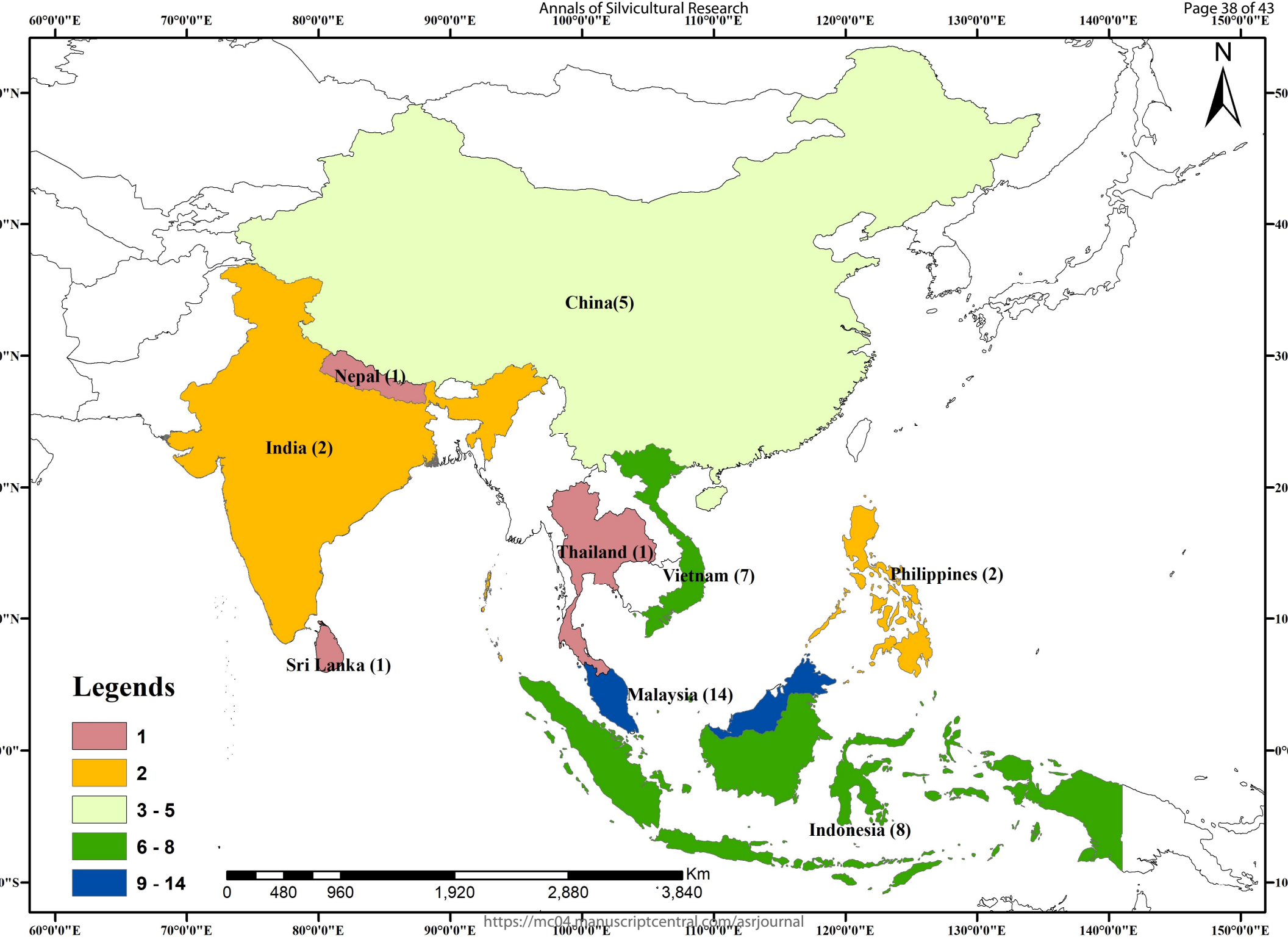
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N
China(5)
Nepal (1)
India (2)
Thailand (1)
Vietnam (7)
Philippines (2)
Sri Lanka (1)
Malaysia (14)
Indonesia (8)
Legends
1
2
3 - 5
6 - 8
9 - 14
0
480
960
1,920
2,880
3,840
Km

Supplementary Table 1. Systematics and general distribution of subfamily Dipterocarpoideae (Ashton 1982, Dayanandan et al. 1999, Ashton et al. 2004; www.plantsoftheworldonline.org).

Subfamily	Tribes	Genera	No. of species	Distribution(s)
Dipterocarpoideae	Dipterocarpeae	*Dipterocarpus*	65	Sri Lanka to the Philippines, Borneo and Sumbawa
		Anisoptera	10	Bangladesh and Indo-China to New Guinea
		Upuna	1	Borneo
		Cotylelobium	5	Sri Lanka, Peninsular Thailand, Malaysia, Sumatra and Borneo
		Vatica	77	Sri Lanka to New Guinea
		Stemonoporus	26	Sri Lanka
		Vateria	3	Southern India and Sri Lanka
		Vateriopsis	1	Seychelles
	Shoreae	*Dryobalanops*	7	Peninsular Malaysia, Sumatra and Borneo
		Neobalanocarpus	1	Peninsular Malaysia and extreme south-east Peninsular Thailand
		Hopea	112	Sri Lanka to New Guinea
		Shorea	189	Indo-China to the Philippines
		Parashorea	13	Indo-Burma to Sumatra, Borneo and the Philippines

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Supplementary Table 2. Data on variables for 50 species w.r.t. both the marker types.

Sl. no.	Species	Marker	Number of loci	Measures of genetic variation		Species characteristics			References
				N_A	H_E	Geographical range	Vertical stratification	IUCN red list status	
1.	*D. alatus*	SSR	9	2.20	0.234	1	2	3	Tam et al. 2014, Vu et al. 2019
2.	*D. costatus*	SSR	9	2.30	0.151	1	2	3	Duc et al. 2016, Vu et al. 2019
3.	*D. crinitus*	SSR	7	6.60	0.673	1	1	3	Harata et al. 2012
4.	*D. dyer*	SSR	9	3.85	0.604	2	1	4	Tam et al. 2019, Nguyen et al. 2020
5.	*D. globosus*	SSR	6	28.7	0.843	3	1	1	Harata et al. 2012
6.	*D. grandiflorus*	SSR	6	12.49	0.683	1	2	4	Kettle et al. 2011, Tito de Morais et al. 2015
7.	*D. littoralis*	SSR	10	3.27	0.432	3	1	5	Dwiyanti et al. 2014b
8.	*D. tempehes*	SSR	10	10.30	0.777	2	1	4	Isagi et al. 2002
9.	*D. aromatica*	SSR	7.8	6.82	0.637	1	2	3	Lim et al. 2002, Nanami et al. 2007, Harata et al. 2012, Dwiyanti et al. 2014b, Harada et al. 2018
		RAPD	10	1.68	0.191				Ritonga et al. 2018
10.	*D. beccarii*	SSR	7	3.70	0.404	2	1	4	Harada et al. 2018
11.	*D. lanceolata*	SSR	8	6.80	0.601	2	1	1	Harata et al. 2012
12.	*H. bilitonensis*	SSR	14	4.65	0.604	3	3	5	Lee et al. 2004a, Lee et al. 2013
13.	*H. chinensis*	SSR	9	2.80	0.398	3	3	5	Trang and Triest 2016
		ISSR	10	1.68	0.337				Tang et al. 2015
14.	*H. dryobalanoides*	SSR	5	5.6	0.678	1	1	1	Takeuchi et al. 2004
15.	*H. hainanensis*	SSR	12	2.46	0.424	3	3	4	Wang et al. 2020a
16.	*H. odorata*	SSR	9	2.70	0.356	1	2	3	Nguyen et al. 2014

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17.	*H. reticulata*	SSR	7	3.42	0.533	3	3	5	Wang et al. 2020b
18.	*N. heimii*	SSR	6	11.16	0.793	2	1	4	Iwata et al. 2000,
19.	*P. malaanonan*	SSR	6	8.56	0.631	1	1	1	Abasolo et al. 2009, Ang et al. 2016
20.	*P. tomentella*	SSR	6	8.41	0.580	2	1	1	Kettle et al. 2011, Tito de Morais et al. 2015
21.	*S. acuminata*	SSR	4	6.75	0.63	1	1	1	Takeuchi et al. 2004
		AFLP	42	NA	0.1				Cao et al. 2009
22.	*S. acuminatissima*	SSR	8	7.245	0.459	3	1	3	Tito de Morais et al. 2015
23.	*S. acuta*	SSR	7	14.1	0.806	3	1	1	Harata et al. 2012
24.	*S. amplexicaulis*	SSR	10	11.5	0.739	2	1	2	Harata et al. 2012
25.	*S. argentifolia*	SSR	8	8.12	0.694	2	2	1	Tito de Morais et al. 2015
26.	*S. balangeran*	RAPD	42	1.74	0.125	2	2	3	Indriani et al. 2019
27.	*S. beccariana*	SSR	10	18	0.792	2	1	1	Harata et al. 2012
28.	*S. blumutensis*	AFLP	53	NA	0.165	3	2	5	Cao et al. 2009
29.	*S. cordifolia*	SSR	7	12	0.723	3	2	5	Stacy et al. 2001
30.	*S. curtisii*	SSR	9.6	8.83	0.650	1	1	1	Ujino et al. 1998, Ng et al. 2006, Harata et al. 2012
31.	*S. dasyphylla*	AFLP	47	NA	0.164	2	1	4	Cao et al. 2009
32.	*S. gibbosa*	SSR	10	9.3	0.622	1	1	5	Tito de Morais et al. 2015
33.	*S. guiso*	SSR	6	6.5	0.747	1	1	3	Tinio et al. 2014
34.	*S. javanica*	SSR	7	2.45	0.437	3	2	4	Rachmat et al. 2012
35.	*S. johorensis*	AFLP	47	NA	0.115	1	1	5	Cao et al. 2009
36.	*S. laevis*	SSR	10	4.6	0.518	1	1	3	Masuda et al. 2010
37.	*S. leprosula*	SSR	11.5	10.	0.748	1	1	2	Lee at al. 2004b, Ng et al. 2004, Ng et al. 2006, Ang et al. 2016
		AFLP	NA	NA	0.153				Cao et al. 2006, Cao et al. 2009
38.	*S. macroptera*	SSR	5	10.9	0.715	1	1	1	Ng et al. 2006
		AFLP	45	NA	0.155	1	1	1	Cao et al. 2009

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39.	*S. maxwelliana*	SSR	12	6.7	0.692	1	1	4	Masuda et al. 2010
40.	*S. obtusa*	SSR	5	4.68	0.663	1	2	2	Senakun et al. 2011
41.	*S. ovalis* ssp. *sericea*	SSR	7	8.9	0.643	1	2	5	Ng et al. 2004
42.	*S. ovata*	SSR	7	10.4	0.774	1	2	4	Harata et al. 2012
43.	*S. palembanica*	AFLP	52	NA	0.149	1	2	5	Cao et al. 2009
44.	*S. parvifolia*	SSR	10	11.07	0.719	1	1	1	Lee et al. 2004, Takeuchi et al. 2004, Harata et al. 2012
		AFLP	NA	NA	0.132				Cao et al. 2006, Cao et al. 2009
45.	*S. platyclados*	SSR	12	7.58	0.697	1	2	4	Ng et al. 2013, Muhammad et al. 2016, Ng et al. 2019
		AFLP	56	NA	0.144				Cao et al. 2009
46.	*S. robusta*	SSR	4.5	9.16	0.687	1	2	1	Pandey and Geburek 2009, Pandey and Geburek 2010
		ISSR	16	1.79	0.234				Surabhi et al. 2017
47.	*S. smithiana*	SSR	8	11.685	0.679	2	1	3	Tito de Morais et al. 2015
48.	*S. xanthophylla*	SSR	9	6.96	0.590	2	2	2	Kettle et al. 2011, Tito de Morais et al. 2015
49.	*V. indica*	SSR	12	7.25	0.675	3	2	3	Ismail et al. 2013
		SSR	12	6.94	0.713				Guo et al. 2017
50.	*V. mangachapoi*	RAPD	20	1.69	0.219	1	2	3	Zhang et al. 2012
		AFLP	10	1.29	0.196				Zhang et al. 2012

[a] Data on all the variables were obtained for the 50 taxa listed above. Two variables describe genetic variation: N_A = Mean number of alleles per locus and H_E = Expected heterozygosity.

[b] Categories for each species characteristic are indicated by numbers. Geographical Range: 1=Widespread, 2=Regional, 3=Localised; Vertical Stratification: 1=Emergent, 2=Canopy, 3=Sub-canopy; IUCN Red List Status: 1=Least Concern, 2=Near-Threatened, 3=Vulnerable, 4=Endangered, 5=Critically Endangered.

[c] NA: Not Applicable (Data Deficient).

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Supplementary File 1

Perspectives

As mentioned in the discussion of conservation implication of Dipterocarps in various sections and sub-heads, it is opined that the advancements in genome-based molecular tools relatively ease out the complexity of tropical forests where the family probably originates. Genetic diversity research advancement not only lies in the evaluation of H_E but changing single nucleotide base change may also govern the allelic variability. The key outcomes and important recommendations arising from this review are as follows:

1. Presence of genetic variability in trees are essential for their further improvement by providing options to the breeders to develop new varieties and hybrids. This can be achieved through phenotypic and molecular characterization of FGRs for which understanding patterns of genetic diversity is essential.
2. The review helped refine prescriptions for management that would aid to reduce the damage and restoration in specifically dynamic forest-based ecosystems. These genetic patterns interpretations are of great significance for scientifically and comprehensively formulating reasonable conservation strategies for family Dipterocarpaceae.
3. Variation in the population's gene pool allows natural selection to act upon traits that allow the population to adapt to changing environments. Understanding of these variations will aid to supplement the genetic diversity that increases the likelihood of the population to adapt and survive.
4. These findings provide important information for future allele/gene identification using genome-wide association studies (GWAS) and marker-assisted selection (MAS) to enhance genetic gain in conservation and breeding programmes of Dipterocarps and other forestry species. Conservation policy makers may need to focus their efforts below the species level to stem further losses of genetic resources with development of site-specific biotechnological solutions for restoration and rehabilitation of fragile forest ecosystems.
5. Furthermore, review creates a database for patterns of Asian Dipterocarps which is essential to enhance cyber-bioprospecting-based infrastructure in forest biotechnology combined with tree genomics, as genomic analysis, transcriptomics, metabolomics, and image analysis become accessible tools for genetic engineering and systems biology of forest trees.
6. The accelerated climatic changes result in the range contraction of Asian Dipterocarps and affect the genetic connectivity across the landscape, and could potentially lead to a great loss of genetic variation; which require time bound mitigation measures and conservation plans.

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