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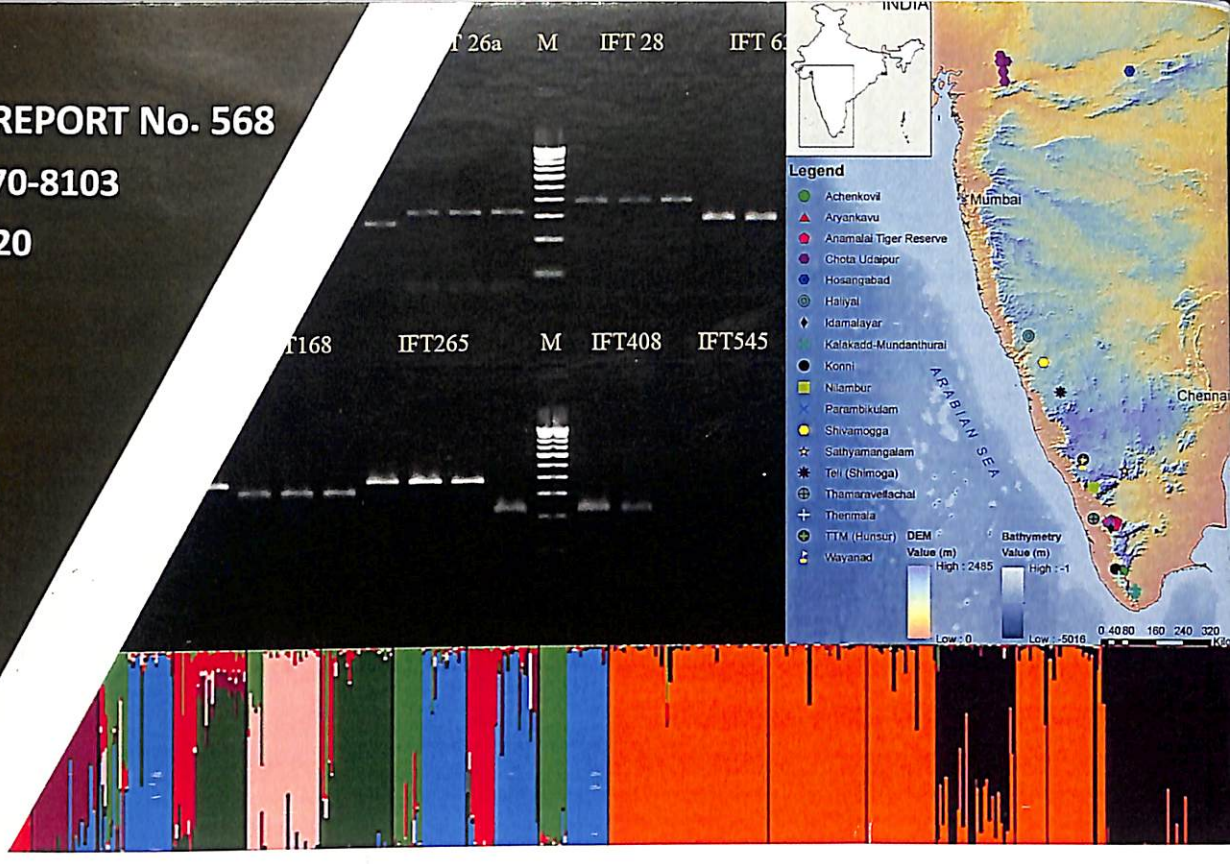

DOCUMENTATION OF POPULATION DEMOGRAPHY AND GENETIC STRUCTURE OF TEAK FOR DEVELOPING SUSTAINABLE CONSERVATION STRATEGIES AND RESOURCE MANAGEMENT

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Documentation of population demography and genetic structure of teak for developing sustainable conservation strategies and resource management

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PROJECT DETAILS

1.	Project No.	KFRI RP 718/2016
2.	Title	Documentation of population demography ai genetic structure of teak for developing sustainat conservation strategies and resource management
3.	Principal investigator	Dr. Suma Arun Dev, Senior Scientist, KFRI
4.	Associate investigator	Dr. P.K.C. Pillai, Senior Scientist (superannuated on 31.01.2018), KFRI
5.	Research Fellow	Ms. Swathi Balakrishnan
6.	Objectives	Documentation of population genetic diversity of natural teak populations using genome wide SSR markers Decipher the population genetic structure of teak using genetically divergent populations of teak
7.	Duration	4 Years
8.	Funding Agency	Department of Biotechnology (DBT), Government of India

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CONTENTS

ABSTRACT

Population genomics determines the evolutionary potential of a species by decoding the genetic structure and diversity of populations from diverse geo-ecological gradients. Teak, a tropical timber tree species distributed in diverse environmental and geographical conditions, is more responsive to local adaptation. The study investigates the extent of genetic variation and local adaptive potential of teak natural populations in India using genome-wide SSR markers, thereby identifying the role of isolation by distance and isolation by environment in shaping the genetic structure. Bottleneck effect along with genetic drift and local adaptation have played a crucial role in designing the population genetic structure which separate the population into three genecological zones namely Kerala, Tamil Nadu-Karnataka and Karnataka-central India (Gujrat and Madhya Pradesh). We have examined the genetic variability, genetic structure, allelic richness, private and unique adaptive alleles. Significant association of genetic structure to environmental factors like temperature and precipitation has revealed using linked neutral loci (locus TFGTB285 and IFGTB479b). Genetic variability of teak populations in India was also determined by geographical factors and specifically longitude (95.92 %) showed greater correlation than latitude (21.2 %). The populations/genotypes with higher private or adaptive unique alleles could be targeted for sustainable management, conservation and genetic improvement of teak genetic resources in the country. Niche modelling identified central Indian populations to be more vulnerable to climate change and probable shift in the distribution pattern of the species in the ensuing years.

Keywords: Teak. Genome wide SSR markers. Linked neutral loci. Adaptive potential. Isolation by distance. Isolation by environment

INTRODUCTION

Genetic diversity and population genetic structure provide essential basis for adaptation and resilience of plant populations to environmental adversities (Via 2009; Potter et al. 2017). Resilience could be either spatial or local system mediated where former focuses on the route of connectivity among populations while the latter on geographic distance and environmental heterogeneity. Non-neutral markers are commonly used to assess the role of environmental factors that shape the population genetic structure. However, when environmental conditions change, selective sweep affects the linked neutral loci along with adaptive loci (Smith and Haigh 1974; Sork et al. 2010; Stephen 2019). Hence, highly polymorphic neutral molecular markers have been employed to assess the distribution of genetic variation across populations of species and deduce the effect of environmental variations on the genetic structure (Holderegger et al. 2006; Sork et al. 2010). Therefore, neutral and adaptive loci play pertinent roles in inferring local adaptation through functional link between habitats, life-history variability and genotypes (Orsini et al. 2013).

Population genetic diversity is influenced mainly through mutation, migration and selection, whereas population genetic structure is greatly influenced by founder effects, population fragmentation, genetic drift, environmental and geographic factors (Heywood 1991; Kawecki and Ebert 2004). The measures such as isolation by distance (IBD), isolation by environment (IBE) and isolation by resistance (IBR) have been used to disentangle the role of multiple evolutionary forces like migration, selection and drift in local adaptation (Bradburd et al. 2013; Van Strien et al. 2015; Morente-López et al. 2018; Jiang et al. 2019). IBD leads to decrease in the gene

flow mediated either by limited pollen flow and restricted seed dispersal events or by flowering asynchrony, leading to genetic drift among isolated populations (Tonsor 1995). Whereas, IBE involves exposure of populations to heterogeneous environment and adaptive population differentiation subsequently (Sexton et al. 2014; Wang and Bradburd 2014). IBR limits gene flow and causes genetic drift via landscape features and range boundaries (McRae 2006; Spear et al. 2010; Cushman et al. 2015). Correlation of spatial genetic diversity with geographic or climatic factors to quantify the relative roles of IBD, IBE and IBR have been recently elucidated in many plant taxa including forest tree species with diverse distribution (Deacon and Cavender-Bares 2015; Constandinou et al. 2018; Morente-López et al. 2018; Pournosrat et al. 2018).

Teak is one of the highly valuable tropical forest tree species naturally distributed in India, Myanmar, Thailand and Laos covering an area of 29.035 million ha (Kaosa-ard 1981; Kollert and Cherubini 2012). In India, teak is extensively distributed along an altitudinal gradient in diverse eco-geographic regions with varied topography, vegetation, soil and diverse climatic regimes. India has about 8.9 million ha of natural teak forests predominantly covering the States of Kerala, Karnataka, Tamil Nadu, Andhra Pradesh, Telangana, Maharashtra, Gujarat, Orissa and Madhya Pradesh (Tewari 1992). Bioclimatic variables play a vital role in genetic divergence of plant populations distributed along the elevational gradients (Shi et al. 2014). Hence, conservation and sustainable management of teak genetic resources (TGRs) in the country is a serious concern as only genetically broad teak populations with unique/adaptive alleles can confront the adversities of climate change. In addition, climate change projections showed that major teak growing areas in India are vulnerable to change in climate (Gopalakrishnan et al. 2011; Deb et al. 2017).

Climatic factors function as a strong selective force in forest tree populations, which adapt rapidly in lieu with the changing regimes (Lehsten et al. 2014). Species distribution and range shifts in accordance with temperature and precipitation tolerance have been cited in earlier investigations (Hickling et al. 2005; Seppä et al. 2015). Changes in environment exert a selection pressure whereby local adaptive strategies evolve, which can be determined through genecological studies (Chen et al. 2012; Mosca et al. 2014). Genecological approach would help in identifying the natural stands of similar genetic composition that could act as future seed sources for raising climate resilient populations. Hence, genecology based seed zonation would be a viable strategy to comprehend the genetic potential of Indian teak for resource management, conservation and sustainable utilization (Graudal et al. 1999).

Genetic variations of teak in its natural distribution zones have been assessed using allozymes (Kertadikara and Prat 1995; Kjaer et al. 1996), random amplified polymorphic DNA (RAPD) (Nicodemus et al. 2003), amplified fragment length polymorphism (AFLP) (Shrestha et al. 2005; Balasundaran et al. 2010; Sreekanth et al. 2012; Vaishnaw et al. 2014) and simple sequence repeat markers (SSRs) or microsatellites (Indira et al. 2008, 2010; Fofana et al. 2009; Verhaegen et al. 2010; Minn et al. 2014; Hansen et al. 2015; Huang et al. 2015). These studies documented huge genetic diversity, moderate gene flow and variation in admixture patterns among teak populations in India, that are exposed to varying bioclimatic variables. The evolution of genotyping tools like SSRs/Single Nucleotide Polymorphisms (SNPs) would enable us to locate the molecular targets under positive selection and conserve genotypes which can adapt to a changed climate (Neale and Kremer 2011). In spite of the recent

advancement in genomics of many forest tree species including teak, associating a particular genotype to specific environmental cues is often a perplexing task.

So far, no studies in teak have targeted molecular signatures as well as possible drivers of local adaptive genetic structure by partitioning of genetic variation. With this prelude, the present study aims to identify the linked SSR alleles that are positively influenced by climatic variables, to determine population genetic diversity and structure as well as partitioning of genetic variation by IBD, IBR and IBE over 18 natural teak populations in India.

OBJECTIVES

1. Documentation of population genetic diversity of natural teak populations using genome wide SSR markers

2. Decipher the population genetic structure of teak using genetically divergent populations of teak

REVIEW OF LITERATURE

Genetic diversity accounts for the genetic variation within and between a plant species, predisposed by its life history traits (Hamrick and Godt 1996). Understanding the genetic basis of population divergence and adaptive potential of species play a major role in population genetics and evolutionary biology. Environmental heterogeneity, generally defined by the climatic, edaphic and biotic factors, highly influences the genetic diversity structure of any plant species (Hanski and Ovaskainen 2003; Dubuc-Messier et al. 2017). The unique allelic composition related to the adaptive changes in the genome within each population could probably vary owing to the heterogeneity of distinct geographical areas. Geographic differences and genetic diversity are extremely relatable as each geographic location has a specific eco-geographic factors *viz.* latitude, altitude, temperature and moisture. Information on the distribution and extent of genetic diversity of species as well as the way it is structured are important to design conservation strategies. Since genetic polymorphism has important implication in conservation studies and evolution, major studies have focused on determining the genetic variations of plant species ranging from crops (Yao et al. 2007; Aci et al. 2018), medicinal plants (Yuan et al. 2010; Wei et al. 2017), woody trees (Cupertino et al. 2011; Hansen et al. 2015) etc. However, to plan a proper conservation strategy, type of markers used and the information generated are very much crucial. Neutral and adaptive markers are now used to determine the selective traits with positive selection influenced by the local adaptation.

Biochemical markers such as isozymes were introduced as the first molecular tool for genetic characterization (Tanksley and Orton 1983; Smith

1986; Soltis and Soltis 1990). Isozymes share a long history in assessing the genetic variability of forest trees within natural populations (Kertadikara and Prat 1995; Huang et al 1998; Doligez and Joly 1997; Ritland et al. 2005) and high genetic diversity of woody trees as compared to all other plant species was also observed using this marker (Hamrick and Godt 1992). However, limited availability of isozyme loci which would never allow for a genome-wide scan of variability, is its major drawback (Kassaby et al. 1991).

DNA-based markers formed perfect alternative to biochemical markers. DNA based markers can be classified into dominant and co-dominant markers. Restriction fragment length polymorphism (RFLP), Simple Sequence Repeats (SSR) and Single Nucleotide Polymorphism (SNPs) belong to the codominant markers while Amplified Fragment Length Polymorphism (AFLP), Randomly amplified polymorphic DNA (RAPD) and Inter Simple Sequence Repeats (ISSR) form the dominant markers. A good genetic marker is defined as the one showing high genetic variability and capable of generating multilocus data from the genome under study (Anne 2006). ISSR markers which makes use of microsattelite primers distributed ubiquitously across the genome with high variability. The marker is highly reproducible and cost effective when compared to RAPDs and AFLP respectively. ISSR markers have been used as ideal markers for various studies ranging from assessment of genetic variability (Wang et al. 2012), DNA fingerprinting (Shen et al. 2006), and phylogenetics (Iruela et al. 2002). Even though ISSR markers are highly relevant and sort out marker for genetic studies, report by Ng and Tan 2015 reveal the uncertainty in the banding patterns.

Simple Sequence Repeat (SSR, microsatellite) markers has gained immense popularity in genome mapping, population genetics and related areas (Ellegren

2004; Kalia et al. 2011; Zalapa et al. 2012; Mahesh et al. 2016). SSR has obvious advantages when compared to other markers such as hypervariability, co-dominance and high reproducibility (Ellegren 2004; Bhargava and Fuentes 2010; Kalia et al. 2011). One of the major advantages of microsatellite markers is its application in constructing genetic maps of large genomes even with no reference genome (Hodel et al. 2016). Further EST-SSR markers developed from the expressed sequence tags can be used to directly tag candidate genes in genetic mapping studies by correlating genotype and phenotype (Varshney et al. 2005). A rapid shift from SSR based molecular studies to SNP based was witnessed with the advent of cost effective and large scale SNP detection tools such as NGS, NGS-based Genotyping by Sequencing (GBS) and Restriction site Associated DNA Sequencing (RAD-Seq). SNP markers have become the marker of choice due to their genome wide abundance for ultra-high-throughput detection platforms (Mammadov et al. 2012). SNPs have been used in wide arena of plant research like genetic diversity assessment (Hamblin et al. 2007; Liu et al. 2017; Boakyewaa et al. 2019), QTL mapping (Wang et al. 2018) candidate gene in adaptive genetics (Zhao et al. 2017). High throughput sequencing has enabled Genome wide discovery of SSRs (Yasoda et al. 2018) and SNPs (Wang et al. 2018) along with detection of common and rare functional variants (Poland et al. 2012; Zalapa et al. 2012). Recently, transition from neutral to function markers is seen owing to the importance of detecting candidate genes influenced by local adaptation.

Rapid change in the global climate has effected the survival of biodiversity (Hoffmann and Sgro 2011). Gopalakrishnan et al. (2010) reported 30 % of teak grid to be vulnerable to climate change. Local adaptation is the strategy used by most of the species to withstand the change in environmental condition (Aitken

et al. 2008). Since range shifting and phenotypic plasticity is much faster than evolutionary process, few studies suggest phenotypic plasticity to be a more feasible option than adapt *in situ* to new condition (Ackerly 2003; Parmesan 2006). Contrary to this, number of species has shown local adaptation in response to change in environmental conditions (Franks et al. 2007). Exploring the ability of the species to respond to the spatial environmental heterogeneity will aid in understanding the adaptive divergence and evolutionary potential of the species (Pluess et al. 2016).

Landscape genomics enables to identify the adaptive potential of species in response to spatial environmental heterogeneity (Vincent et al. 2013). Adaptive genetic diversity study requires functional markers and neutral markers like RFLP, RAPD, ISSR and SSR are considered inappropriate as they provide no information on the genetic changes due to particular selection pressure (Reed and Frankham 2001; Ouborg et al. 2006). The pattern observed using non-neutral or adaptive markers vary from those observed using neutral markers (Frankham et al. 2010). Landscape genomics detects those adaptive loci under selection by a two-step process; the first being detection of the outlier loci and the second is association of the outlier loci with environmental variables. Forest trees are considered as the perfect models for adaptive genetic diversity studies owing to a wide range of environmental gradient, genetic diversity and linkage disequilibrium (Neale and Kremer 2011). Those population showing adaptive potential need to be identified especially in this climate change scenario as most of the species lacking adaptive potential might perish. Thus, for protecting and conserving the genetic resource, population with both high genetic diversity and potential for local adaptation need to be considered. Adaptive genetic diversity assessment of commercially important forest trees might be beneficial

for designing better conservation strategies. However, adaptive potential of most of the economic and valued timber trees are not yet explored. Aforementioned criteria can be employed to identify the adaptive potential of Teak natural populations.

Genetic diversity in Teak

Tectona grandis is one of the most important tropical timber species naturally occurring only in India, Myanmar, Laos, Burma and Thailand (Troup 1921; Anon 1956; Kermode 1957; Ko Ko Gyi 1972; Kaosa-Ard 1977). India has about 8.9 million ha of natural teak forest (Tewari 1992) and 5.98 million ha of teak plantations (ITTO, 2016). In order to preserve genetic resources of the species and ensure continuous supply of genetically superior germplasm for genetic improvement programs, a core collection of superior genotypes with broad genetic base is a prerequisite. Earlier genetic studies on diversity of teak in its natural distribution zones were conducted by allozyme markers in the mid-1990s (Kertadikara and Prat 1995; Kjaer et al. 1996). Allozymes were later replaced by DNA markers owing to low polymorphism and low abundance. Subsequently, many studies were reported on the genetic diversity of natural teak populations/plantations using various molecular markers such as Restriction Fragment Length Polymorphism (RFLP) (Nicodemus et al. 2003, Parthiban et al. 2003), Amplified Fragment Length Polymorphism (AFLP) (Shrestha et al. 2005; Balasundaran et al. 2010; Sreekanth et al. 2012; Vaishnaw et al. 2014) and simple sequence repeat markers (SSRs) or microsatellites (Indira et al. 2008, 2010; Fofana et al. 2009; Verhaegen et al. 2010; Minn et al. 2014; Hansen et al. 2015; Huang et al. 2016). SNPs and SSRs gained prominence soon owing to its reliability being species specific. All these studies using

various markers revealed genetic variation of teak provenances at molecular level with huge differences and variation was found to be more within population than between populations. (Keiding et al. 1986; Kjaer et al. 1999; Monteuuis et al. 2011; Chaix et al. 2011). Furthermore, Shrestha et al. (2005) studied 28 genotypes from India, Indonesia and Thailand using AFLP markers and found that 57 % of the variance occurred within populations, while 43 % occurred among populations. Hansen et al. (2015) who made first comprehensive study of the genetic resources of teak over its whole natural distribution range using SSR markers, supported Verhaegen et al. (2005) in that teak has its diversity centre in India as well as its origin. Population genetic studies with neutral markers carried out so far revealed genetic distinctiveness of central and south Indian teak populations (Katwal 2003; Nicodemus et al. 2003; Shrestha et al. 2005; Fofana et al. 2009). Molecular studies using nuclear microsatellites grouped northern and western Indian teak populations in one clade whereas Kerala and eastern Indian teak population into two separate clades. The genetic uniqueness of Nilambur provenance was also revealed (Balasundaran et al. 2010; Indira et al. 2008, 2010; Sreekanth et al. 2012). Lyngdoh (2010) positively correlated genetic dissimilarity in the population to fruit emptiness and negatively to seed germination by using ISSR markers. Higher dissimilarity of individuals within population often leads to inbreeding depression due to flower asynchronomy and close related mating (Lyngdoh et al. 2010). Studies carried on disturbed natural teak populations using SSR markers pointed out that teak prefers multi parental mating and that gene flow through pollen acts over longer distance than seed dispersal (Prabha et al. 2011). Recently, AFLP markers associated with wood property traits were identified (Vaishnav et al. 2018).

Though major work has been carried out in teak using various markers, no robust study including genome wide SSRs or SNPs have been carried out. As per literature all the studies were carried out using SSR markers with limited number of loci. Therefore, an in depth study employing genome wide SSRs/SNPs can generate information on diverse genetic resource of natural teak population, identify populations with unique alleles and diversity hot spots. This population may be used as seed source for future conservation activities or maintenance of plantation which are otherwise vulnerable to climate change. With the change in climatic condition, it is highly essential to identify those populations with adaptive potential. Candidate genes showing positive selection correlating to climate variables need to be identified for proper planning and execution of conservation strategies. Hence, identification of those natural forests both with maximum genetic diversity and local adaptation would be preferable for conservation and sustainable management of genetic resources.

MATERIALS AND METHODS

Population sampling and DNA extraction

We identified a total of 18 natural teak populations covering the areas in Kerala [Nilambur (NIL), Wayanad (WY), Parambikulam (PAR), Thamaravellachal (TH), Idamalayar (ID), Konni (KON), Achenkovil (ACH), Ariyenkavu (ARK), Themala (TEN)], Karnataka [Haliyal (HAL), Shivamoga (SHI), Thithimathi (TTM), Sakrebyle (TEL)]), Tamil Nadu (Anamalai Tiger Reserve (ATR), Satyamangalam Tiger Reserve (STR), Kalakkad-Mundandurai Tiger Reserve (KMTR)], Gujarat [Chota Udaipur (CU)] and Madhya Pradesh [Hosangabad (H)]. Natural geographic barriers, Palghat gap and Sengottai Pass divide the natural teak distribution areas were considered while sampling the Western Ghats region of India. Geographical location and the number of individuals included in the study are provided in Table 1. We prepared a population distribution map using ArcGIS 10.3 software from ESRI, Redlands, CA. Multi-point shape files were generated using GPS coordinates of the sampling locations. Georeferenced land elevation and bathymetry datasets from ETOPO1 Global Relief Model, NOAA (https://www.ngdc.noaa.gov/mgg/global/) were used to create the digital elevation model (DEM) and bathymetry layer (Fig.1). Fresh leaves were collected from all the selected individuals of 18 populations and dried on silica gel. Genomic DNA was extracted from 100 mg of leaf tissue using the modified cetyl trimethyl ammonium bromide (CTAB) method (Doyle and Doyle 1987) or ArborEasy® DNA Isolation Kit (patented product of IFGTB, Coimbatore).

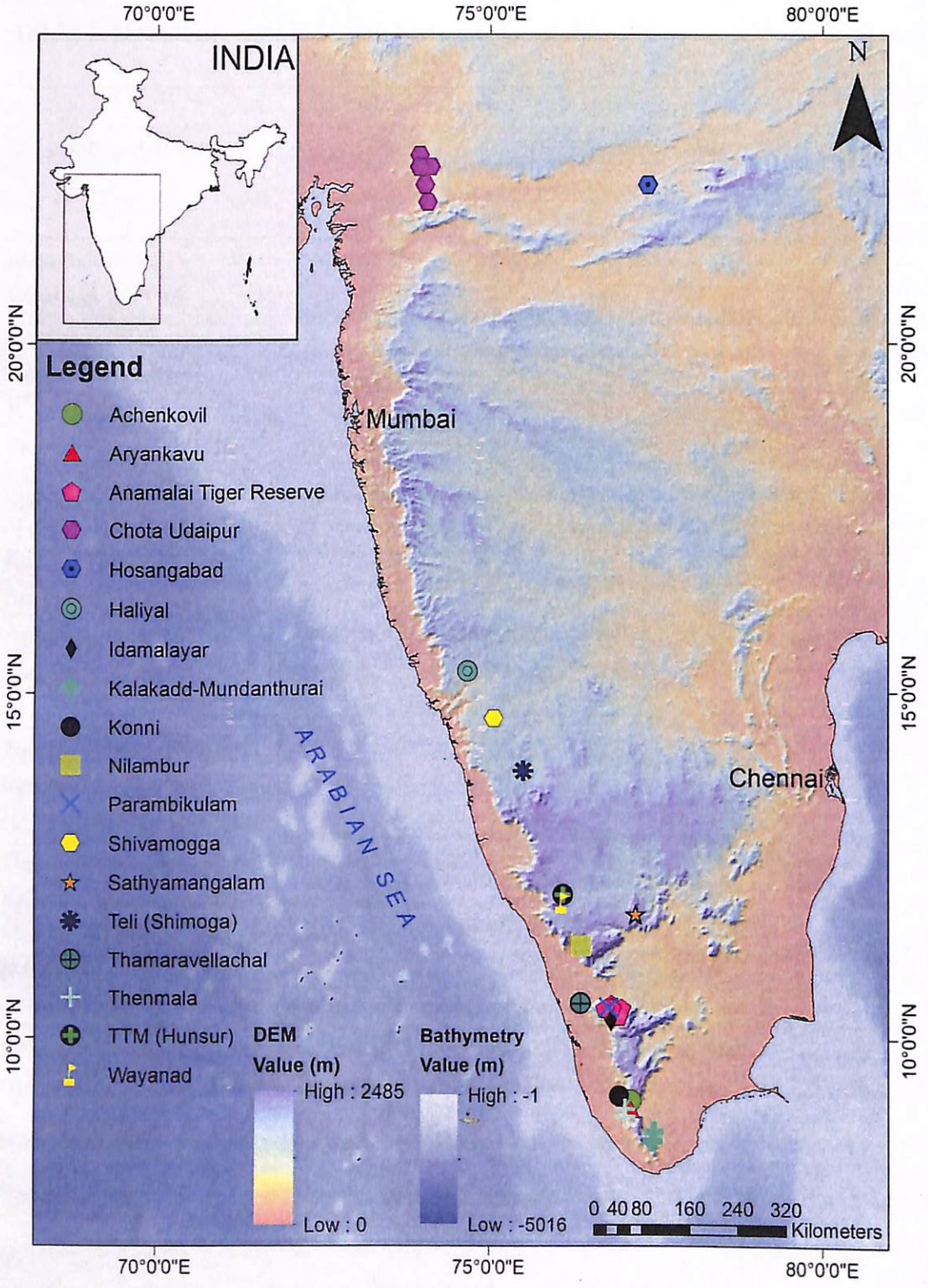

Fig. 1. GIS distribution map of natural teak populations sampled in India

Table 1. Details of sampled Teak Natural populations

Populations	GPS		Elevation range(m)	Veg. type	No.of sampled individuals
	Lat (N)	Long (E)			
		KERALA			
Nilambur (NIL)	11°20'02.8"	076°23'12.2"	55-112	MDF	25
Wayanad Wild life sanctuary (WY)	11°15'13.0"	076°05'28.0"	853-867	MDF	23
Parambikulam Tiger Reserve (PAR)	10°26'50.5"	076°48'10.2"	539-578	MDF	25
Thamaravellachal (TH)	10°30'19.0"	076°22'21.9"	70-209	MDF	25
Idamalayar (ID)	10°15'56.1"	076°50'17.6"	318-369	Semi vergreen	10
Konni (KON)	09°10'33.7"	076°57'38.6"	186-268	Deciduous	25
Achenkovil (ACH)	09°06'26.3"	077°07'50.3"	314-392	MDF	25
Ariyenkavu (ARK)	08°59'08.4"	077°07'46.4"	304-373	MDF	25
Thenmala (TEN)	08°53'24.7"	077°02'24.7"	202-241	MDF	25
		TAMIL NADU			
Topslip, Anamalai Tiger Reserve (ATR)	10°27'39.6"	076°51'06.3"	597-1116	MDF	55
Gethesal, Satyamangalam Tiger Reserve (STR)	11°47'05.3"	077°12'01.2"	1058-1112	Deciduous	34
Kalakkad R.F., Kalakkad - Mundandurai Tiger Reserve (KMTR)	08°32'31.3"	077°28'04.5"	315-619	Dry deciduous	24
		KARNATAKA			
Haliyal (HAL)	15°18'05.4"	074°40'27.0"	498	MDF	13
Anavatti, Shivamoga (SHI)	14°36'52.7"	075°04'05.7"	591	MDF	14
Hunsur, Thithimathi (TTM)	12°04'39.2"	076°06'38.3"	835	Dry deciduous	11
Sakrebyle (TEL)	13°50'29.6"	075°30'33.3"	650	MDF	20
		GUJRAT			
Chota Udaipur (CU)	22°41'12.7"	073°56'13.8"	193-348	Dry deciduous	35
		MADHYA PRADESH			
Hoshangabad (H)	22°15'27.2"	077°22'43.7"	362-364	MDF	12

MDF- Moist deciduous forest

Simple sequence repeats (SSRs)

Twenty-five genome wide polymorphic SSR loci reported from whole genome sequence of *Tectona grandis* (Yasodha et al. 2018) were considered for the present study (Table 2). The forward primers were fluorescently labeled with HEX or FAM. Polymerase chain reaction was performed using 20 µl reaction containing 5-10 ng DNA, 10X Taq buffer with 1.5 mM $MgCl_2$, 200 µM dNTPs, 10 pm of each primer and 2U Taq DNA polymerase (Invitrogen, Bangalore). Amplifications were carried out with an initial denaturation at 95°C for 5 min, followed by 35 cycles at 94°C for 45 secs, specific annealing temperatures ranging from 53.5°C-56°C for 60 secs, extension at 72°C for 45 secs, and final extension period for 10 min at 72°C. SSR genotyping was performed using ABI 3500/3730XL Genetic Analyzer (Applied Biosystems, USA) and allele size was evaluated using GENEMAPPER software Version 4.0 (Applied Biosystems, USA).

Genetic diversity and Structure analysis

We estimated genetic variability among 18 populations by evaluating the following parameters *viz.* observed and effective number of alleles (*Na & Ne*), number of private alleles (*Np*), observed heterozygosity (*Ho*), expected heterozygosity (*He*), Shannon's genetic diversity index (*I*) (Lewontin 1972), genetic differentiation coefficient (F_{st}), gene flow (*Nm*), Nei's genetic distance (*Gd*) and principal component analysis (PCoA) using GenAlEx 6 software (Peakall and Smouse 2006). Unbiased genetic distance was used to construct dendrogram using UPGMA (Unweighted Pair Group Method with Arithmetic Mean) as implemented in Power Marker v3.25 (Liu and Muse 2005).

Table 2. Microsatellite markers used for PCR amplification (Yasodha *et al.*, 2018)

Locus	Repeat motifs	Primer Sequence	Annealing temperature (°C)
IFGTB4a	(ATAC)7	F (HEX)GAAGTAGGACGGAGCCCTAAAT R AACCCCTCAACCCTTTCTACTC	55.3
IFGTB5	(TG)23	F (FAM)CTGATGGGGTTAATTCTTCTCG R ATCCTCCTCACTAAACCGAACA	54
IFGTB28	(AAAG)6	F (FAM)CAGCCTCTGCATGTCAAATAAA R TTAGAGCTGGATATGCCATTGA	54.8
IFGTB83	(AG)21	F (HEX)AATTGGCATAAAGCGTGCTACT R CGCACGTCCTATTTTGGTTTAT	53.5
IFGTB101	(CCG)11	F (FAM)GTGCTCCTCTCTATTGGGATTG R TGTATCCATCATCTGCATCCTC	55.3
IFGTB165	(GAA)7	F (HEX)ATATCCCTCGTCACCTTCAATG RTTCTGCAAAGTCGAAGTTGTTC	54.2
IFGTB509	(ATTGA)6	F (FAM)TCCTTCAGAACTGTGAACCAAA R TCACCCACTGCTATATATGTTCC	54
IFGTB777	(TCAGG)6	F (HEX)TACTAACCGGAAGAGGGAAACC R TGTCGCTATGGACAGTTCATCT	55.3
IFGTB821	(AC)24	F (HEX)CCCCAATTATGTCAACCGACT R GGCATTATCTAAGATCGCAAGG	56.1
IFGTB479b	(GGA)11	F(FAM) GTGAAGATTCGGGTATGGAGAG R TACTCCCAGATTTCCCAATCAC	55.3
IFGTB4b	(TC)21	F (FAM) CAGCAATTTACCCTTGTTTTCC R TTTGTTCCACCACTTCTGTTTG	53.4
IFGTB439	(CA)13	F (FAM)AGGAGACAAAAACGATCCGATA R TTGGGATCCTATGGTGAATGAT	53.4
IFGTB14	(TTCT)9	F (FAM) TGTGGTATTGGACCATCTGAAA R GGTAACCCACCAACAAATATGC	54.4
IFGTB61	(AT)12	F (FAM)GTTGAACCAATCGAAACAGATG R CATGTCCATGTCTTGTCCCATA	53.5
IFGTB285	(AC)21	F (HEX)CTAAGGGGTTTTCCCAAATCTC R CTTGCAAGTTTGGGCTTTAGAA	55
IFGTB416	(CTT)12	F (FAM)CAGGGCACATTTGAATTTCCT R GCCCTTTCATTACTTATGGTTCC	53.7
IFGTB26b	(TTAA)5	F (HEX)GTCCAGAGTGAAAACCAGGAAG R AAAACCCATAACCTAGGCCAAT	56.3
IFGTB149	(CT)21	F (FAM)GTCCTCAAATCGAACGAAAAAC R TACCCCAACCTCTCAAACCTTA	55.2
IFGTB264	(CGTGG)5	F (HEX)GCACATGATAAGTTGGGTTTGA R GTGGGCTTTTTAATGCTACGAC	55
IFGTB215	(GATGG)5	F (FAM)TATACTGTGCCGATGGTGATTC R AGGATGAAATCAAGAACGTGGT	56
IFGTB382	(TATG)7	F (FAM)TACTCATCACTGTCCCCAGTTG R GAACGGGAATCTAGAGTTGTGG	56.3
IFGTB168	(TCT)12	F (FAM)ATCTTCAGCAGAGGAGGCTATG R GTGCCCTTTTCTCTCTTCTTCA	55.2
IFGTB135	(GCTG)6	F AGCAAACATAGAGCCCAGAGAG R ACAATGTAAAAGGCCCTACCAA	55.5
IFGTB63	(ATG)12	F (FAM)CCCAAAGCGAATAATATCCTACC R ATGACTTGTTCGATGGGCTAAT	54
IFGTB245	(ATGT)6	F(HEX) AACCACATGCTTTAAGGTTTCC R TATCACCTGAAAAGCTGGGAAG	54

An admixture model in the Bayesian analysis tool, STRUCTURE version 2.3 (http://pritch.bsd.uchicago.edu/structure.html) was used to determine the subpopulations of *Tectona grandis* genotypes. A burn-in period of 10^5 and 10^6 Markov Chain Monte Carlo (MCMC) repetitions after burn-in was set with an admixture model. The K value was set from 2-20 followed by 25 independent runs for each simulated values of K. Optimal K value was determined by simulation method (Evanno et al. 2005) using the software Structure Harvester Core vA.2 (Earl and vonHoldt, 2012). Outputs of 25 iterations at each K (2-20) were run in CLUMPP v1.1.2 (Jakobsson and Rosenberg 2007) to align clustering results, and visualized using DISTRUCT v1.1 (Rosenberg 2004).

Partitioning of genetic variation

The genetic, geographic and environmental relationships shared among the 18 natural teak populations were investigated. Nineteen environmental variables of the respective sampling sites were obtained from CHELSA (http://chelsa-climate.org/downloads/). Spatial distance was obtained from the GPS coordinates of the sampled populations. Significance was determined by comparing the observed correlation to random permutation of the data. Pairwise genetic and geographic distance matrices were calculated using GenAlex software (Peakall and Smouse 2006). Environment standard Euclidean distance for the populations was calculated for all 19 bioclimatic variables and altitude using SPSS v21 (SPSS Inc., Chicago, IL, USA; http://www.spss.com). We investigated the correlation between three matrices [genetic, environmental (bioclimatic variables + altitude) and geographic distances] through Mantel and partial Mantel tests using the *vegan* package in R v3.6 (Oksanen et al. 2015) and

significance was tested with 10000 permutations. Partial redundancy analysis was performed to identify the contribution of latitude and longitude in determining the population structure using the *vegan* package in R v3.6 (Oksanen et al. 2015).

Association of markers (alleles) with environmental variables

All the 23 SSR loci were subjected to latent factor mixed model (LFMM) as implemented in LEA package in R (Frichot and François 2015) to check for association of SSR loci with the environmental variables, if any. LFMM identifies the effects of linkage by using hidden factors, if environmental associations are present (François et al. 2016). However, PCoA analysis was done to identify only those environmental factors with strong load on each principal component axis and subjected to LFMM. Allelic information was converted into binary data as per the acceptable format of LFMM. Marker-environmental variables associated based on the Z-score was estimated using Gibbs sampler algorithm by running 10,000 sweeps with a burn-in length of 5000 for every sweep. The number of latent factor was placed between 1 and 8 for any K and the program was run 5 times. Genomic inflation factor (λ) was calculated based on the concept of Devlin and Roeder (1999). The lambda value was further used to calculate the adjusted p-value which determines if the association is significant. We used Benjamini-Hochberg correction of the adjusted p-value to calculate the significant threshold of Z- scores. The markers with Z-score showing a false discovery rate of q=0.05 or less were considered significant. The DNA sequence containing the respective SSR loci with environmental association was further subjected to BLAST similarity search.

Ecological Niche Modelling (Maxent)

Ecological Niche Modelling (Maxent) explores the potential distribution of a species (Phillips et al. 2006). The unique occurrences were collected through field survey and the points were geo referenced in GIS to mark the present localities. The 19 "bioclimatic" variables available from globally interpolated datasets of monthly temperature and precipitation of the WorldClim dataset (Hijmans et al. 2005) was used as the environmental background for the modelling. The derived bioclimatic variables of temperature and precipitation were presumed to be maximally relevant to plant survival and reproduction. In addition to that, elevation, slope, aspect, and compound topographic index from the USGS Hydro-1K dataset (USGS 2001) were also included. The Area under the Receiving Operator Curve (AUC) was used to evaluate the model's goodness of fit and the model with highest AUC value was considered as the best performer. The final potential species distribution map had a range of values from 0 to 1 which was regrouped into four classes of potential habitats *viz.* highly suitable (>0.6), suitable (0.4–0.6), moderately suitable (0.2–0.4) and least suitable (<0.2). The Jackknife test (Wu 1986) was used to assess the importance of the variables.

RESULTS

Genetic diversity

Since two primers could not amplify a majority of the samples, results obtained from 23 primers were used for data analysis. The number of observed alleles (*Na*) per locus ranged from 4.09-10.44 with a mean of 7.70. Effective number of alleles (*Ne*) ranged from 2.75-5.90 with mean of 4.30. Shannon's information index (*I*) ranged from 1.03-1.81 with an average of 1.49. Average observed and expected heterozygozities were 0.614 and 0.668, respectively (Table 3). A total of 195 private alleles (*Np*) were identified. Among the analyzed 18 populations in India, highest amount of genetic diversity was observed in the very moist populations of Kerala (Na 9.106; Ho 0.664; He 0.710) followed by moist/ dry Tamil Nadu (7.53, 0.571, 0.669) and Karnataka (5.935, 0.554, 0.662) populations. Dry populations of Gujarat (6.17, 0.572, 0.599) and Madhya Pradesh (4.09, 0.581, 0.543) were observed to have almost similar genetic diversity measures. Inbreeding coefficient (*Fis*) within population ranged from -0.079 (H) to 0.151 (ATR). Mean genetic differentiation coefficient for overall population (F_{st}) was 0.202. Thus, ~80 per cent of the genetic diversity was distributed within populations and 20 per cent across populations. More than one migrant per generation (Nm=1.054) was observed among populations (Table 3).

Table 3. Population Diversity Parameters

Pop	Na	Ne	I	Ho	He	Fis	Private alleles	Fst	Nm
ID	5.74	3.59	1.37	0.687	0.654	-0.044	7		
WY	9.48	5.01	1.69	0.624	0.713	0.139	19		
KON	9.96	5.55	1.77	0.666	0.732	0.122	22		
NIL	9.96	5.24	1.69	0.647	0.701	0.085	28		
ARY	8.65	4.63	1.59	0.657	0.696	0.071	18		
PAR	9.17	4.47	1.63	0.692	0.700	0.004	17		
TEN	9.04	4.66	1.67	0.643	0.716	0.099	9		
TH	10.44	5.90	1.81	0.651	0.734	0.129	19		
ACH	9.52	5.23	1.75	0.709	0.751	0.033	11		
ATR	9.39	4.48	1.56	0.582	0.686	0.151	18	0.202	1.054
STR	7.13	9.79	1.40	0.582	0.658	0.090	5		
KMTR	6.09	3.68	1.34	0.550	0.664	0.146	2		
HAL	5.22	3.38	1.23	0.511	0.618	0.103	3		
SHI	6.17	3.96	1.35	0.512	0.655	0.160	6		
TTM	5.09	3.75	1.29	0.595	0.668	0.068	1		
TEL	7.26	4.17	1.50	0.599	0.706	0.104	5		
CU	6.17	3.21	1.23	0.572	0.599	0.030	5		
H	4.09	2.75	1.03	0.581	0.543	-0.079	0		
Mean	7.70	4.30	1.49	0.614	0.668	0.013			

Na, number of different alleles; Ne, number of effective alleles, Ho; Observed heterozygosity; He,expected heterozygosity; I, Shanon's diversity index; Fis, Fixation index; Fst, inbreeding coefficient among population; Nm, Gene flow

Population genetic structure

The peak of ΔK value was highest when K=8 (ΔK=18.5401) (Fig. 2), indicating the presence of a minimum of 8 distinct clusters (ancestral populations) and 425 genotypes were inferred and assigned into clusters as shown in Fig. 3. Maximum genetic admixture was observed in nine Kerala populations which were totally different from the admixture pattern of Tamil Nadu, Karnataka, Gujarat, and Madhya Pradesh populations. Identical population structure was shared among a few populations namely, Thenmala, Achenkovil and Konni populations of Kerala, between Tamil Nadu (ATR, STR, KMTR) and Karnataka (TTM and TEL) populations, between two Karnataka populations (HAL and SHI) and between Gujarat (CU) and Madhya Pradesh (H) populations. The genotypes of Ariyenkavu, Wayanad and Idamalayar populations (Kerala) clearly differed from the other populations in their genetic admixture pattern. Population structure analysis of all populations excluding Kerala (Fig. 4) showed 5 subpopulations wherein ATR, KMTR populations had minimum admixture and TTM and TEL had maximum admixture pattern. Tamil Nadu populations and TTM as well as TEL had maximum gene flow when compared to other Karnataka populations. CU (Gujrat) and H (Madhya Pradesh) showed a population structure entirely different from the remaining populations with least admixture. STRUCTURE analysis of the two central Indian populations alone showed three sub populations (K=3), with least admixture in Madhya Pradesh (H) population. Population H had one of the three ancestral subpopulations in larger quantity than CU (Fig. 5). Genetic and geographic distances among the analyzed populations displayed a significant positive correlation. Geographically closer Konni and Thenmala populations in Kerala

showed the least amount of genetic differentiation with highest gene flow (>10) while distant populations such as Idamalayar in Kerala and Haliyal in Karnataka showed the highest amount of genetic divergence with least gene flow (0.73).

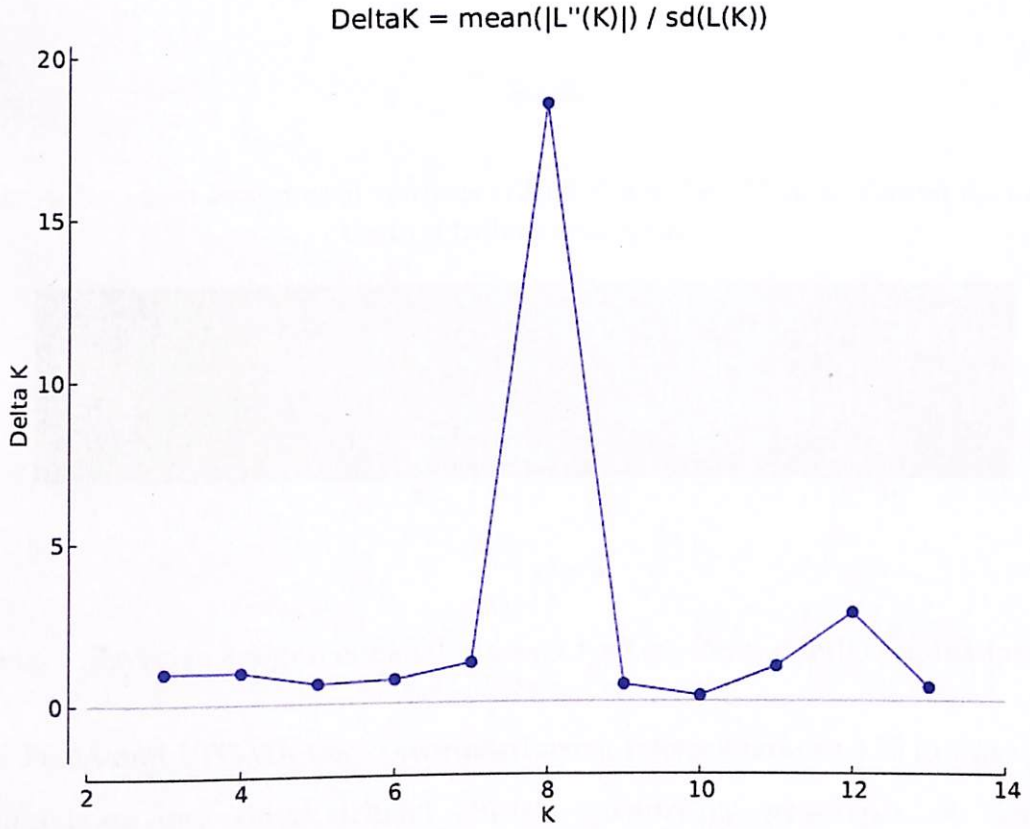

Fig. 2. Bayesian assignment analysis with K = 8 for all 18 teak populations

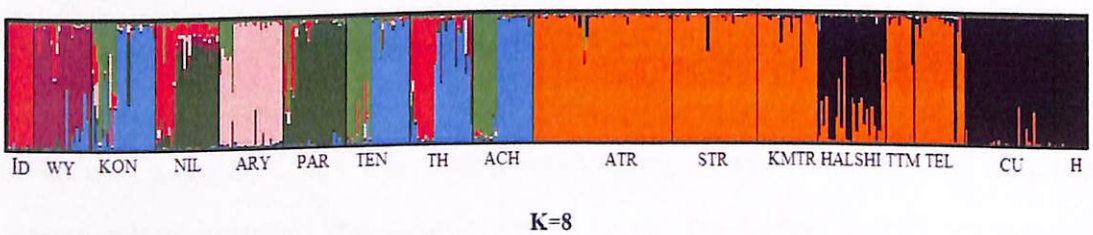

Fig. 3. Population structure pattern of 18 teak populations using DISTRUCT for K=8

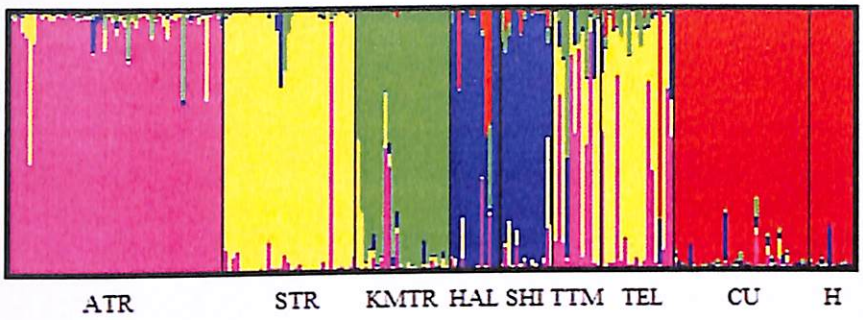

Fig. 4. Bayesian assignment analysis with K=5 for Tamil Nadu/Karnataka and Central India populations.

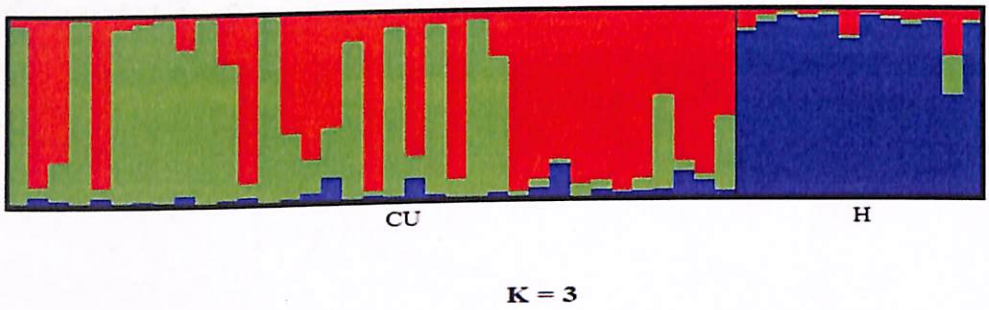

Fig. 5. Bayesian assignment analysis with K=3 for Central India populations

PCoA and UPGMA tree constructed using Power Marker v3.25 grouped 18 populations into three distinct clusters comprising genotypes of Kerala (Nilambur, Wayanad, Idamalayar, Thamaravellachal, Parambikulam, Konni,Ariyenkavu, Thenmala and Achenkovil), Madhya Pradesh-Gujarat-Karnataka (CU, H, HAL and SHI) and Tamil Nadu-Karnataka (ATR, ATR, KMTR, TTM and TEL) populations (Fig. 6). The first co-ordinate axis in the PCoA analysis accounted for 17.36 per cent of the variance and 4.30 per cent in the second axis. UPGMA tree constructed using Power Marker v3.25 showed clear overlaps between the populations, and the clustering was in accordance with PCoA and structure analysis (Fig. 7).

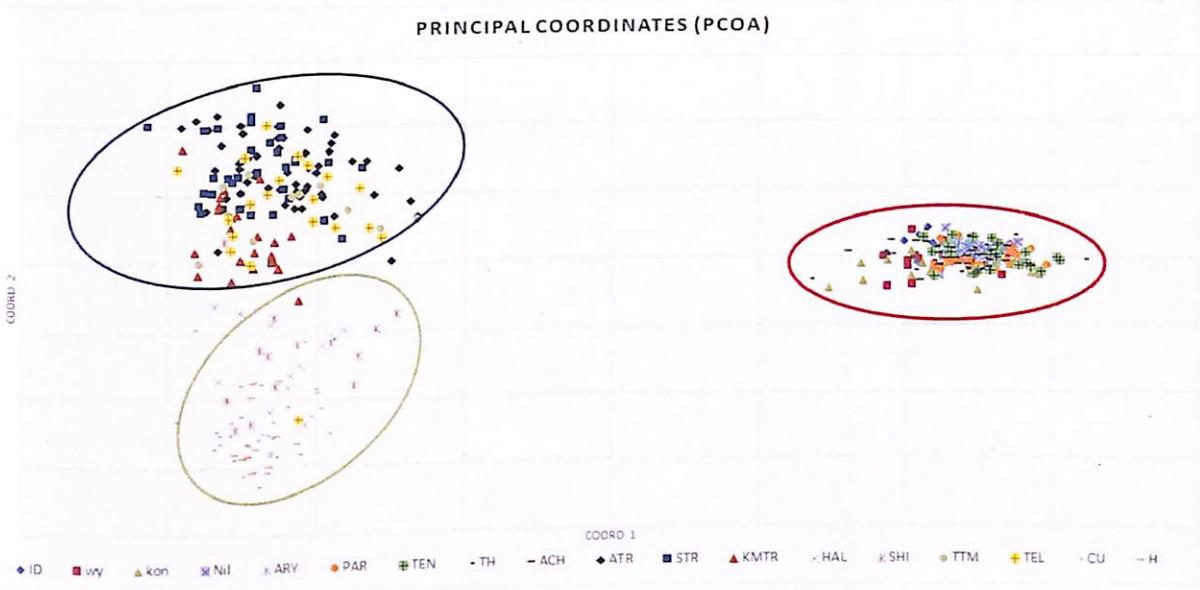

Fig. 6. Two dimensional plot of PCoA of 18 teak populations

PCoA grouped 18 populations into three distinct clusters comprising genotypes of Kerala (Nilambur, Wayanad, Idamalayar, Thamaravellachal, Parambikulam, Konni.

Fig. 7. UPGMA dendrogram of individuals per population clustering pattern using Power marker

Partitioning of genetic variation by environmental and geographic distance

Mantel and partial Mantel tests were performed to investigate the correlation between eco-geographical variables and genotypic data (Table 4). The highest correlation value was between environmental and geographical distances (r = 0.6198). Both environmental and geographical distances significantly but weakly correlated with the genetic distance (r = 0.21 and r = 0.2078, respectively). Since environmental and geographical distances were correlated, partial Mantel test was performed to investigate pure relationships, isolation by environment (IBE) and isolation by distance (IBD). The results showed that genetic distance had a small but significant correlation with both geographical and environmental distances (r = 0.1012 and r = 0.1058, respectively). However, the correlation between geography and environment retained high value (r = 0.6024). Thus, the inference can be drawn that the genetic structure of teak populations in India is probably affected by joint influence of both environmental and geographical factors. The geographical variable, longitude showed greater (95.92 %) correlation than latitude (21.2 %) as estimated using partial redundancy analysis.

Table 4. Simple and partial Mantel test demonstrating correlation between Geographic (Geo), Genetic (Gen) and Environmental (Env) distance of Teak natural populations

	Mantel Test		Partial Mantel Test	
	R	p-value	R	p-value
Gen, Geo	0.2078	0.001	0.1012	0.001
Gen, Env	0.21	0.001	0.1058	0.001
Geo, Env	0.6198	0.001	0.6024	0.001

Gen,Genetic; Geo, Geographic; Env, Environmental

Association of markers (SSR alleles) with environmental variables

All loci were subjected to LFMM to check for correlation with environmental variables. PCA analysis identified three bioclimatic variables with maximum load (Appendix 1). The first three principle components showed that BIO-7 (Annual temperature range), BIO-1 (Annual mean temperature), and BIO-13 (precipitation of the wettest month) were the major loadings on PCA1, PCA2, and PCA3 and accounted for 43 %, 28.95 % and 17.76 % of total variation. These bioclimatic variables were used to further detect the possibility of any relationships between allelic variations and environmental variables. Two loci IFGTB285 and IFGTB479b showed alleles associated with bioclimatic variables BIO-1 and BIO-13, and BIO-1 and BIO-7, respectively. In the case of IFGTB285 locus, two of the alleles associated with BIO-1 (331, 333, 335 and 338) were also found to be associated with BIO-13 (331 and 333) i.e., both with temperature and precipitation. Of these, 331, 333 and 335 alleles were seen only in Kerala populations whereas the allele 338 was found in Karnataka and Tamil Nadu populations. The SSR loci IFGTB479b has three alleles associated with temperature i.e., BIO-1 (375) and BIO-7 (336, 342, and 375). Allele 375 associated with both BIO-1 and BIO-7, was present only in Kerala population while allele 336 exists in Kerala, Karnataka, Tamil Nadu, Gujarat and Madhya Pradesh populations. Likewise, allele 342 was present only in Gujarat and Madhya Pradesh populations. BLAST similarity search of IFGTB285 locus sequence showed a 58 % sequence coverage and 86 % identity to *ABA-Insensitive 5*, which happens to play a key role in regulating targets associated with stress adaptation genes like LEA proteins (Skubacz et al. 2016). In contrast, locus IFGTB479b could not be related to any genes.

Niche modelling

The unique 18 points were recorded from India which covers the State of Kerala, Tamil Nadu, Karnataka, Gujarat and Madhya Pradesh. The predicted potential distribution is high in the southern and central Western Ghats regions and sparsely seen along the crest line of the northern Western Ghats (Fig 8). The area in red depicts the localities that have higher probabilities. The main factors influencing the potential distribution of this species are maximum temperature of warmest month, annual precipitation, precipitation of wettest month and minimum temperature of coldest month, etc. (Table 5). The simple probability test conducted from the jack knife procedure confirmed that the prediction is significantly better than at random ($P < 0.05$) and gave an estimate between 0 and 1 of probability of presence. The test and training Area under Curve (AUC) values were also higher (0.971) which implies the model accuracy and justifies the construction of final niche model with all the available points

Table 5. Variable Contributions – Maxent modeling of *T. grandis*

Variable	% contribution	Permutation Importance
Max. Temperature of Warmest Month	33.9	2.1
Annual Precipitation	20.6	1.5
Precipitation of Wettest Month	13.9	33.6
Min. Temperature of Coldest Month	10.4	34.3
Precipitation of Driest Month	10.1	1.7
Elevation	6.3	3.5
Slope	2.9	0

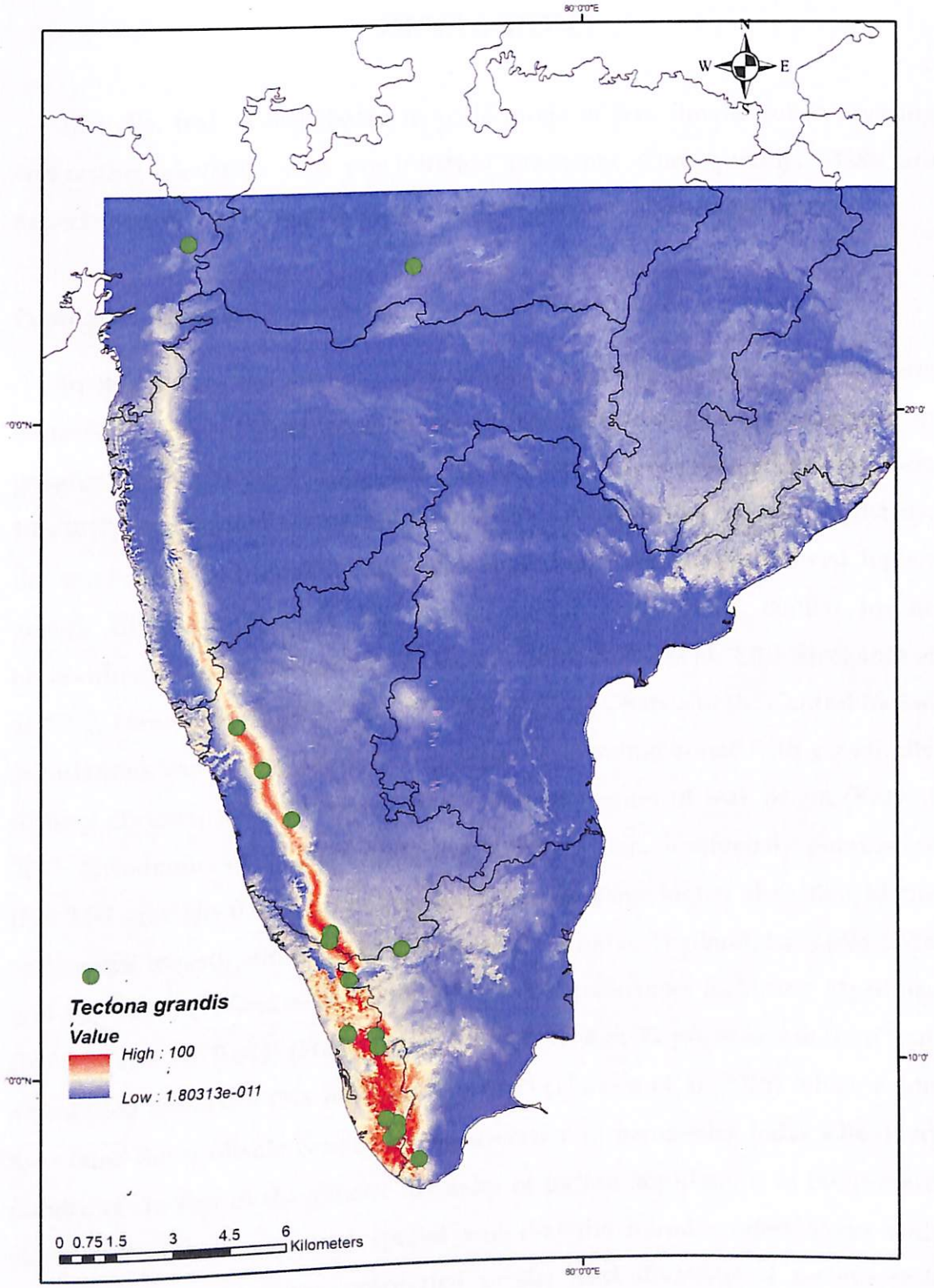

Fig. 8. Prediction of potential distribution of natural populations of *Tectona grandis* in India

DISCUSSION

In India, teak is distributed in wide range of eco-climatic zones covering contrasting elevation and precipitation gradients. Consequently, TGRs are expected to display a huge genetic variability owing to local adaptations.

Population Genetic diversity

In this study, we analyzed the genetic variability of teak using genome wide SSRs for the first time to assess the adaptive genetic variations in geographically distinct natural teak populations of India (annual precipitation 106-3617 mm; annual temperature 9.8-27.7°C; altitude 65-1100 m). Primarily, the semi-moist/moist deciduous peninsular teak populations showed higher genetic diversity than the dry central Indian populations, similar to the observations in earlier studies (Fofana et al. 2009; Indira et al. 2010; Sreekanth et al. 2012; Hansen et al.2015). Secondly, the Western Ghats and the Central Indian populations were designated as two separate breeding zones with genetically distinct clusters, with Western Ghats being the center of teak origin (Katwal 2003; Nicodemus et al. 2003; Indira et al. 2010). Genetic diversity parameters (Na 7.70 and Ho 0.614) of Indian provenances were higher than that of the earlier SSR investigations; 17 provenances from India, Thailand, Laos (Na 4.614 and Ho 0.514) (Fofana et al. 2009), 18 native provenances including Myanmar (Na 6.04 and Ho 0.644) (Huang et al. 2015) as well as 29 provenances from four distributed countries (Na 6.78 and Ho 0.61) (Hansen et al. 2015) which again ascertains the probable origin of teak diversity in peninsular India. Observed pattern of decline in the genetic diversity of Indian populations in the present study indicates an eastward spread and that the founder effect along with genetic drift might have contributed to the least diversity of eastern teak population in Maharashtra. Earlier observations on teak distribution had also corroborated eastward movement of TGR from India to Laos (Hansen et al. 2015).

Fundamentally, allelic richness indicates strong potential of populations to evolve according to the changing environment (Allendrof 1986; Allendrof et al. 2012; Caballero and Gracia-Dorada 2013) and serve as indicators of gene flow (Slatkin 1985; Barton and Slatkin 1986; Butcher et al. 2006). According to our study, allelic richness and private alleles were maximum in Nilambur population followed by other Kerala populations, Tamil Nadu, Karnataka and central Indian populations. Occurrence of private alleles in these populations support the origin of teak and its migration from southwestern India to the rest of its natural distribution limits (Volkaert et al. 2008). Further, absence of private alleles and least genetic diversity seen in the eastern Madhya Pradesh population, again authenticates the migration route. The observed differences in the allelic richness and private alleles from the source population might be due to adaptational selection or migrational allele loss followed by genetic drift (Nei et al. 1975; Slatkin and Takahata 1985). Climatic conditions also differ in these distribution zones, which may have resulted in adaptive divergence among the populations. Accordingly, populations with higher number of private alleles represent genetic distinctness and deserve effective conservation measures and breeding programs.

Population genetic structure and genecological zonation

According to the STRUCTURE analysis, eight ancestral populations can be divided into three groups; nine Kerala populations in one group with high genetic diversity and admixture pattern, three Tamil Nadu and two Karnataka populations as another group with comparatively lower genetic diversity and admixture pattern and finally, two Karnataka and Central India (Gujarat and Madhya Pradesh) populations with least genetic diversity and admixture. Maximum admixture and unique genetic composition of Kerala populations indicates high gene flow between geographically closer populations. Even

though, IBR plays a significant role in determining the structure of populations by considering the ecological barriers and landscape patterns which hinders the gene flow (McRae 2006; Spear et al. 2010; Cushman et al. 2015), our study has not shown the effect of natural breaks (Palghat gap and Sengottai pass) in the Western Ghats on genetic differentiation and gene flow among Kerala populations (Nm=2.622). Another interesting feature is high gene flow and similar population structure in two Kerala populations (Wayanad and Konni) irrespective of its geographical distance which could be attributed to historical origin. According to our data, genetic diversity and structure of TGRs in India could be explained through migration and dispersal route probably from northern Kerala (Nilambur) to other Kerala populations, followed by dispersal to Tamil Nadu and Karnataka and to Gujarat and then Madhya Pradesh indicating an eastward movement. Additionally, teak populations in Tamil Nadu which are on the eastern side of the Western Ghats showed more genetic affinity towards Karnataka populations. The eastward movement of teak natural resource is in agreement with earlier studies (Volkaert et al. 2008; Hansen et al. 2015) wherein a global picture was also drawn considering all the natural distribution zones (Hansen et al. 2015).

Based on the population differentiation and structure analysis, teak natural populations can be very well segregated into three genecological zones wherein a strong connect could be drawn to geographic and environmental factors. Firstly, very moist Kerala populations with high annual precipitation formed a genecological zone which had least gene flow (<1) with Tamil Nadu as well as Karnataka populations. Secondly, the moist/semi-dry teak populations of Tamil Nadu and Karnataka maintained a gene flow of more than 5 migrants per generation preventing genetic differentiation among them creating a zonation. Finally, populations of Tamil Nadu (KMTR), Gujarat (CU), Madhya Pradesh (H) and Karnataka with less annual rainfall and high temperature also

maintained a gene flow of >5 migrants per generation and showed more or less similar genetic makeup. UPGMA and PCoA cluster analysis for 18 teak populations were consistent with structure analysis indicating a distinct differentiation among Kerala, Karnataka/Tamil Nadu and central Indian populations further pointing out to possible strong adaptations to the changing local climate. Similar views were shared in the earlier investigations on natural populations of teak (Nicodemus et al. 2000; Fofana et al. 2009; Verhaegen et al. 2010; Sreekanth et al. 2012; Ansari et al. 2012; Vaishnaw et al. 2014).

Evidence for isolation by distance and isolation by environment

Mantel test showed a strong correlation between geographical and genetic distances while partial mantel test showed significant albeit reduced correlation between environment or geography (Table 4). This study has shown the joint influence of both environment and geography in shaping the genetic structure of teak which is reported in other species as well (Pournosrat et al. 2018). As for the influence of geographic factors, redundancy analysis has shown greater contribution of longitude over latitude (supplementary table 1). Additionally, phenological phases observed across the populations might also have contributed to the genetic separation as pollen and stigma maturation are not overlapping across the distribution zones limiting the gene flow along the altitudinal gradient (Hirao and Kudo 2004). Further, our study has also identified the role of precipitation and temperature in influencing the genetic architecture of teak populations in India which is consistent with the clusters obtained via STRUCTURE and PCoA analysis. Restricted gene flow and genetic drift due to geographic distance and adaptability owing to environment heterogeneity are the key elements shaping the genetic structure among populations (Nosil et al. 2009) which was evident in this study. Though adaptive potential of tree species' has been explored in large (Prunier et al. 2011;

Zhou et al. 2014; Wang et al. 2016; Zhang et al. 2019), till date, no study has been undertaken on teak natural populations with respect to its adaptive potential.

Association of alleles with environmental variable

Distribution of any species is influenced by climatic and geographical factors at large spatial scales (Pearson and Dawson 2003; Soberon and Peterson 2005). In India, teak grows naturally in wide eco-geographic zones from sea level to an altitude of about 1200 m, diverse range of rainfall (700-2500 mm) and temperature of up to 48°C with a minimum of up to 20°C in central India (Kaosa-ard 1981). This makes teak an ideal candidate for exploring its adaptive potential owing to the environmental heterogeneity in its distribution. According to the LFMM analysis only two loci (IFGTB285 and IFGTB479b) positively correlated with environmental variables. BIO-1 (annual Mean temperature), BIO-7 (Annual Temperature range) and BIO-13 (Precipitation at the wettest month). The correlation analysis also provided a clear representation of the distribution pattern of the populations in three different clusters (geographic zones) as observed via PCoA and STRUCTURE analysis. The difference between temperature during the coldest and hottest months have definitely influenced the alleles wherein minimum range was found in Kerala populations and maximum in other teak populations. Role of temperature and precipitation in influencing the adaptive potential of candidate genes have already been reported in various studies (Prunier et al. 2011; Zhou et al. 2014; Wang et al. 2016; Zhang et al. 2019). Though the SSR loci identified cannot be considered as candidate genes, we could identify sequence upstream to the locus IFGTB285 shared sequence similarity with *ABA-Insensitive 5* like gene. ABI5 protein integrates with various phytohormone pathways and enables appropriate plant stress response (drought and salinity) (Skubacz et al. 2016). Thus, our study could infer the possibility of local adaptation of teak population to stress.

Ecological Niche Modelling

Ecological niche modelling widely used in conservation biology, describes ecological niche of a species using the species occurrence points and related environmental variables (Peterson et al. 2007; 2011). In this era of changing climate, ecological niche modelling plays a crucial role in understanding the bioclimatic variables critically affecting the spatial distribution of forest tree species. Especially in teak with predicted shifts in species distribution, projected climate changes are likely to affect the distribution of species (Gopalakrishnan et al. 2011; Deb et al. 2017). Therefore, for the sustainable management and conservation of TGRs in the country, selection of populations with appropriate level of genetic diversity and climate resilience alone may not be sufficient. Hence, identification of perfect location and microclimate for its plantation is crucial wherein location good enough at present may not be suitable for tree growth in the coming years of changed climate (Gopalakrishnan et al. 2011; Sork et al. 2011). The present study identified environment variables such as maximum temperature of the warmest month (33.9 %) followed by precipitation (20.6%) as the key predictor variables that contribute to the temporal and spatial variation of teak distribution. As per this study, central Indian provenances are found to be much more vulnerable to climate change as evident from the Fig. 5, which is consistent with the previous studies (Gopalakrishnan et al. 2011; Deb et al. 2017). Thus, niche modelling allows forest managers to implement conservation and sustainable management programmes in the predicted suitable niches which will enhance the resilient potential of the species.

CONCLUSIONS

Genome wide SSR markers used to analyze the genetic diversity and structure of teak natural populations from varying geographical locations, distributed along an altitudinal gradient could identify the role of IBD, IBE in shaping the genetic structure and genetic diversity of Indian teak natural populations. Both IBD and IBE could have influenced the genetic makeup of the natural teak populations in India separating them into three gene ecological zones namely Kerala, Tamil Nadu-Karnataka and Karnataka-Central India (Gujrat and Madhya Pradesh). Bottleneck effect along with genetic drift and local adaptation might have resulted in varying admixture pattern and genetic structure. Association of the linked neutral markers with bioclimatic variables were also ascertained wherein precipitation and temperature seemed to have greater influence. Thus, the adaptive potential of teak natural populations by means of linked neutral SSR markers could be identified wherein selective sweep played a crucial role. The populations/genotypes with higher private alleles could be targeted for sustainable management, conservation and genetic improvement programs. Genecological zonation representing a complete genepool of genotypes with adaptive potential and transplantation of high risk genotypes would be viable options to enhance environmental resilience of teak genetic resources in the changed climate. Detailed studies focusing on gene specific SNPs linked to abiotic stress related genes would identify teak populations/genotypes which has undergone local adaptation and has greater possibility to withstand the adverse effects of climate change.

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