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Contrasting spatial patterns of distribution of genetic diversity in two important bamboo species in the Central Western Ghats, India

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Astract: Bamboo forms an important component of the tropical forests of South and Southeast Asia and provides livelihood requirements to a large number of forest fringe communities. Large-scale destruction of habitats and over-harvesting of many economically important species of bamboo has led to irreversible loss of its genetic diversity. Thus, in recent years there has been an increasing concern over the conservation of genetic resources of bamboo. However, for most species of bamboo, critical information on the extent of intra-specific genetic variability of the populations is unavailable. In this direction, we have examined the population genetic variability of *Dendrocalamus strictus* and *Bambusa bambos*, the most important species of bamboo in the Central Western Ghats, India. The study shows that the two species exhibit strikingly contrasting patterns in the distribution of genetic variability. While the diversity of *D. strictus* was higher in the northern latitudes, the diversity of *B. bambos* was higher in the southern latitudes. These findings could have important implications for conservation and management of genetic resources of bamboo in the Central Western Ghats, India.

Key words: *Bambusa bambos*, *Dendrocalamus strictus*, conservation, genetic diversity.

INTRODUCTION

Bamboos are one of the most diverse and primitive groups of plants in the family Poaceae. A number of bamboo species are economically important as they constitute one of the major non-timber forest products. India is the second richest source of

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bamboos in the world, after China, with about 18 genera and 130 species (Shanmughavel and Francis, 1996; Seethalakshmi and Kumar, 1998). The total area of bamboo in India is estimated to be about 96,000 km^2 covering approximately 13 per cent of the total forested area (Shanmughavel and Francis, 1996). Many indigenous communities living in peninsular India derive a major portion of their livelihoods from these resources. Besides, bamboos are also sought by the paper and pulp industry, which utilizes about 5 million tonnes annually (Uma Shaanker *et al.*, 2004).

In India, as in many other South Asian countries, almost all the requirements of bamboos are being met from the natural populations (Cheluvaraju *et al.*, 2001; Seethalakshmi, 2001). The extraction of bamboos over the years for both commercial interests (pulp and paper industries) and for subsistence (by the rural artisans) has imposed a tremendous pressure on the bamboo resources of the Western Ghats, a mega diversity centre (Myers *et al.*, 2000) in Southern India. These resources are also feared to be widely threatened from large-scale loss of native bamboo habitats because of forest loss and land degradation (Cheluvaraju *et al.*, 2001). In the State of Karnataka (Central Western Ghats), one of the richest bamboo areas in India, nearly two-thirds of the bamboo resources are consumed by the industrial sector (61%), while the rest (38%) is used by the cottage industries (Uma Shaanker *et al.*, 2004). In the last three decades, the extraction of bamboo resources in Karnataka has decreased by over five to nine folds presumably due to its reduced availability (Cheluvaraju *et al.*, 2001; Uma Shaanker *et al.*, 2004).

The heavy extraction pressure has taken its toll in terms of drastically reducing the bamboo stands. This has underscored the need to formulate plans for the conservation of bamboo genetic resources and to maintain ecologically sustainable populations. Many conservation programmes including *ex-situ* and *in-situ* methods have been proposed for conservation of bamboo resources (Cheluvaraju *et al.*, 2001; Seethalakshmi, 2001). However, one of the major limitations for such conservation programmes is that they lack sufficient information on what and where to conserve. Critical information on the extent of intra-specific genetic variability of the populations is a pre-requisite in formulating effective conservation strategies.

In this paper, we have assessed the genetic variability of two economically important and heavily extracted species, *Dendrocalamus strictus* and *Bambusa bambos* in the Central Western Ghats, Karnataka, India. Both the species differ in their habitat requirements and the extent of distribution. In certain regions, the populations of these two species have been rendered locally extinct (Kumar, 1991). This study attempts to quantify the population genetic variability of each of the species, and to identify patterns, if any, in the distribution of their genetic variability. Based on our findings, we discuss the approaches to conserve bamboo genetic resources in the Central Western Ghats.

MATERIALS AND METHODS

Study site

The study was carried out in the Central Western Ghats (between 11° 5'N to 15° 2'N latitude), Karnataka, India. The Western Ghats, a mountain chain running parallel to the west coast of South India, contains some of the last remaining tropical forests which are characterized by high levels of biodiversity and endemism. More than 24 species of bamboos from eight genera have been reported from the Western Ghats, of which nine species are highly threatened and endangered (Seethalakshmi, 2001) and six are endemic to this region (Uma Shaanker *et al.*, 2004).

Sampling design

Based on the distribution profiles of the two species (Cheluvaraju *et al.*, 2001), 16 sites for *D. strictus* (Table 1) and 22 sites for *B. bambos* (Table 2) were selected for the study. In each of the sites, 10-20 grids were laid and the density of the bamboo clumps was recorded. At each of these sites, young unopened leaves from 40 individuals for *D. strictus* and 20-40 individuals for *B. bambos* were sampled from an area covering 3-4 ha. A total of 640 individuals for *D. strictus* and 810 individuals for *B. bambos* were collected, wrapped in aluminium foil, frozen in liquid nitrogen (at -195 °C) and taken to the laboratory for isozyme extraction and analysis.

Isozyme analysis

In the laboratory, the young unopened bamboo leaves were homogenized in modified Chase extraction buffer containing 0.01 M EDTA, 0.001 M KCl, 0.002M $MgCl_2$, 4 per cent PVP-40, 1 per cent PEG, 1per cent PVPP, 0.027 mM NADP, 0.003 M NAD, 0.3 M DTT and 10 per cent glycerol in 0.2 M phosphate buffer (pH 7.5) (Murawaski and Bawa, 1994) and centrifuged at 10,000 rpm for 10 min at 4°C. The supernatant was absorbed on to Whatman No 3 filter paper wicks (20 mm x 1.5 mm) and stored at -70°C. The wicks were loaded on to 10 per cent starch gels (hydrolyzed, Sigma Inc., USA) and electrophoresed at 4°C at 150-200 V and 50 mA current for about 7 h. The gel buffer was 0.05 M histidine-HCl containing 1.4 mM EDTA (pH 7.0) and the tray buffer contained 0.125 M Tris buffer brought to pH 7.0 with 1 M citric acid (Cheliak and Pitel, 1984). After electrophoresis, the gels were horizontally sliced and stained by agar-overlay method (Wickneswari and Norwati, 1992). For both the bamboo species 32 isozymes were screened. Binary coding was used to score the gels. Since both the species were hexaploid in nature, the bands of isozyme were scored as an allele. Thus, each allele was given a score of '0' for absence or '1' for presence. All the distinct bands were designated with numbers, starting from the lowest migrating (cathodal) to the fastest migrating (anodal) bands.

Genetic data analysis

The data were subjected to population genetic analysis using the software POPGENE version 1.32 (Yeh and Boyle, 1997). The following genetic parameters were estimated.

Gene diversity

Nei's gene diversity index (Nei, 1973), which is equivalent to the diversity of the allele within an infinite population for both the bamboo species, was computed as, $h = 1 - \sum pi^2$; where, pi is the frequency of the occurrence of the i^{th} allele at a locus over individuals within a population.

Polymorphic percentage

The proportion of polymorphic loci was estimated for each population for both *D. strictus* and *B. bambos*. For purposes of analysis we derived two estlimates of per cent polymorphism. A locus was considered polymorphic if the frequency of the most frequent allele was below 95 per cent. Further, a locus was also considered polymorphic if it had more than one allele, irrespective of the frequency of the occurrence of the alleles.

Dice dissimilarity index

For each population (of both the species), Dice dissimilarity index was computed based on the binary coding (Sorenson, 1948). Dice dissimilarity matrix was generated by computing the Dice dissimilarity coefficient as, $D = 1- (2N_{ab}/N_a+N_b)$ where N_a = total number of bands present in lane a, N_b = total of bands in lane b, N_{ab} number of bands common to lanes a and b (Nei, 1977).

Genetic distance and population differentiation

For both the bamboo species, Nei's genetic distance (Nei, 1972) among all pairs of populations and by partitioning the total variation into those within and among populations was computed. For all possible pair-wise comparisons, inter-population relationships were established by computing the unbiased genetic identity and distance coefficients (Nei, 1972).

Population differentiation statistics

Differentiation of populations was analyzed following Wright's F-statistics. The F-statistics measures the degree of genetic differentiation among populations relative to the total population variance. This statistics is sensitive to the total number of populations included in the analysis. F-statistics is given by $(1-F_{is})\ (1-F_{st}) = (1-F_{it})$,

where F_{it} is the total deviation from expected frequencies under Hardy-Weinberg equilibrium, F_{st} is the deviation due to population subdivision and F_{is} is the deviation within population subdivisions.

Gene flow (Nm) among populations

Gene flow of a population or the estimated number of migrants exchanged between populations per generation was calculated using Wright's method. This method is influenced by the distribution of common alleles. Nm = (1-Gst)/4Gst, where Gst = mean proportion of total gene diversity at polymorphic loci due to differences between populations.

RESULTS

Population genetic parameters

The overall mean Nei's gene diversity for the 16 *D. strictus* populations was 0.197±0.143 (Table 1). Among the populations, gene diversity index was highest for Haliyal population in the North (0.338 ± 0.154) and was least for Banavara population in the South (0.143 ± 0.131, Table 1). The mean per cent polymorphism over all the populations was 50 per cent. The percentage polymorphism ranged from 22.5 (in Banavara population) to 72.5 (in Aldur population, Table 1).

Table 1. Genetic diversity parameters for *D. strictus* in the Central Western Ghats, Karnataka, India

Study sites	N	Latitude (°N)	Longitude (°E)	Polymorphic (%)	Nei's genetic diversity		Dice's dissimilarity index	
					Mean	±SD	Mean	±SD
Banavara	40	12.580	75.850	22.5	0.143	0.130	0.022	0.021
K.Gudi	40	11.541	77.067	65.0	0.146	0.114	0.065	0.037
Burade Bangle	40	11.530	77.110	47.5	0.198	0.169	0.065	0.031
Nallikadaru	40	11.545	77.135	52.5	0.167	0.131	0.059	0.029
Kattaya	40	12.825	76.048	57.5	0.203	0.182	0.084	0.038
Doddabetta	40	12.845	75.950	55.0	0.197	0.138	0.074	0.034
Sheegekaan	40	13.277	75.415	47.5	0.211	0.150	0.067	0.028
Mudigere	40	13.117	75.600	50.0	0.212	0.118	0.072	0.037
Aldur	40	13.260	75.520	72.5	0.177	0.138	0.085	0.038
Bisgod	40	15.025	74.381	62.5	0.189	0.129	0.079	0.043
Haliyal	40	15.300	74.800	40.0	0.338	0.154	0.069	0.039
Joldal	40	13.920	75.850	57.5	0.155	0.135	0.059	0.029
Sakrebailu	40	13.800	75.480	55.0	0.220	0.156	0.073	0.032
Bhadravathi	40	13.800	75.700	50.0	0.201	0.142	0.068	0.035
Dhundsi	40	15.004	75.047	30.0	0.219	0.148	0.040	0.018
Nagaragali	40	15.380	74.366	47.5	0.185	0.154	0.063	0.031
Mean				50.78	0.197	0.143	0.065	0.032

N = Number of individuals sampled; SD = Standard Deviation

In the case of *B. bambos*, the mean overall Nei's gene diversity was found to be 0.114±0.108 (Table 2). The Nei's genetic diversity was highest for the southern populations compared to the northern populations (Table 2). The gene diversity ranged from 0.236 ± 0.091 at Anechoukar in the South to 0.015 ±0.038 in Barchi population in the North. Over all the population, the mean polymorphic percentage was 65. The northern population of Barchi (22.22%) was least polymorphic, while the KUSF and Joldal populations recorded the highest percentage polymorphism (96.3%, Table 2). The Dice's dissimilarity ranged from 0.022 to 0.085 with an overall mean of 0.065±0.032 for *D. strictus,* while for *B. bambos* it ranged from 0.019 to 0.244 with a mean of 0.101 ±0.086 (Table 2).

Table 2. Genetic diversity parameters for *B. bambos* in the Central Western Ghats, Karnataka, India

Study sites	N	Latitude (°N)	Longitude (°E)	Polymorphic (%)	Nei's genetic diversity		Dice's dissimilarity index	
					Mean	±SD	Mean	±SD
Kulve	40	14.38	74.46	74.07	0.106	0.088	0.057	0.083
Hulakal	20	14.40	74.45	51.85	0.105	0.131	0.076	0.062
Manchikere	20	14.47	74.46	40.74	0.104	0.143	0.058	0.044
Dandeli	40	15.17	74.40	88.89	0.236	0.091	0.244	0.370
Virnoli	40	15.08	74.34	33.33	0.025	0.060	0.021	0.030
Barchi	40	15.21	74.37	22.22	0.015	0.038	0.019	0.023
Jagalpet	20	15.18	74.30	29.63	0.068	0.130	0.050	0.026
Bhadravati	40	13.51	75.48	62.96	0.116	0.168	0.074	0.040
KUSF	40	13.49	75.55	96.30	0.110	0.121	0.160	0.267
Joldal	40	14.05	75.51	96.30	0.159	0.148	0.132	0.204
Umblebail	40	13.47	75.34	51.85	0.159	0.176	0.085	0.044
Nayakankere	40	13.48	75.32	66.67	0.159	0.188	0.103	0.055
Lakkavalli	40	13.37	75.39	66.67	0.109	0.149	0.092	0.046
Doddabetta	40	11.40	77.05	88.89	0.189	0.130	0.159	0.083
Gundalhalla	40	11.48	77.05	77.78	0.167	0.152	0.143	0.070
Kadigerebetta	40	11.40	77.05	70.37	0.190	0.170	0.163	0.073
Irpu	38	12.09	76.00	74.07	0.207	0.191	0.140	0.070
Devimachi	38	12.18	76.00	62.96	0.209	0.186	0.116	0.051
Anechoukur	38	12.16	76.03	81.48	0.239	0.148	0.141	0.072
Gundya	40	12.55	74.51	59.26	0.120	0.056	0.047	0.053
Hassan	38	12.52	75.58	62.96	0.114	0.148	0.059	0.041
Muthodi	38	13.05	75.41	77.78	0.107	0.121	0.080	0.078
Mean				65.319	0.114	0.108	0.101	0.086

N = Number of individuals sampled; SD = Standard Deviation

Patterns of genetic variability

Genetic diversity of *D. strictus* populations was significantly positively correlated with the latitude at which they occurred ($r = 0.498$ $P < 0.05$; Fig. 1). Nei's gene diversity of populations was significantly negatively correlated with temperature ($r = -0.57$, $P < 0.05$) and positively with relative humidity ($r = 0.56$, $P < 0.05$). On the

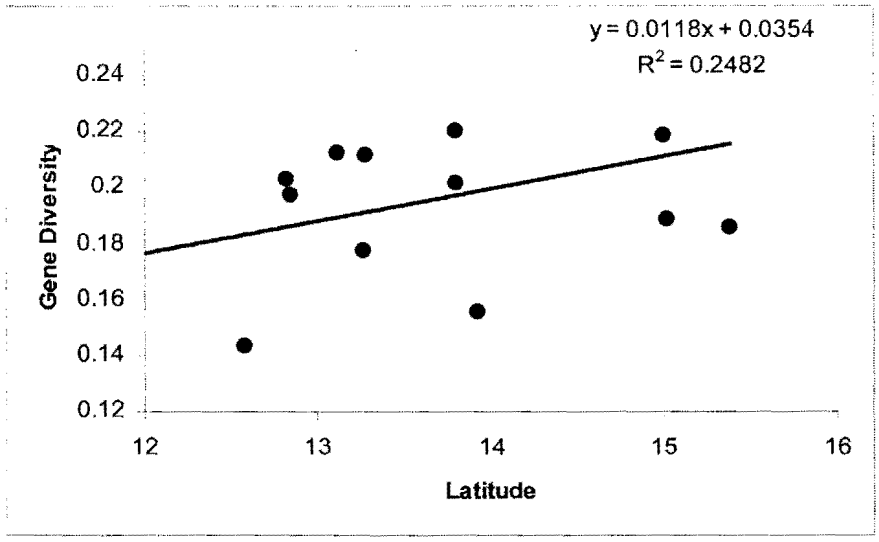

Figure 1. Relationship between latitude and gene diversity for *D. strictus* populations (n = 16; r = 0.498; $P < 0.05$).

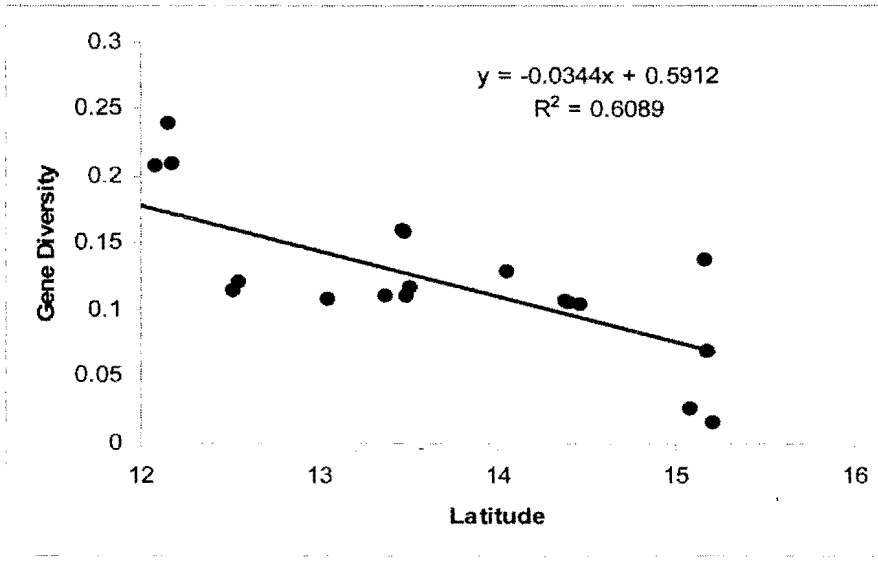

Figure 2. Relationship between latitude and gene diversity for *B. bambos* populations (n = 22; r = - 0.78; $P < 0.05$).

other hand, Nei's gene diversity for *B. bambos* populations was found to decrease significantly with latitude (r = – 0.78; $P < 0.05$, Fig. 2). However, no significant relationship was found with either temperature or with humidity.

Genetic differentiation and gene flow

The population differentiation of *D. strictus* and *B. bambos* was examined by (a) computing pair-wise Nei's genetic distance and examining its association with geographical distance and by (b) partitioning the total genetic variability due to within and among population variation. For both species, there was a clear genetic differentiation of the populations based on the geographical origin of the population.

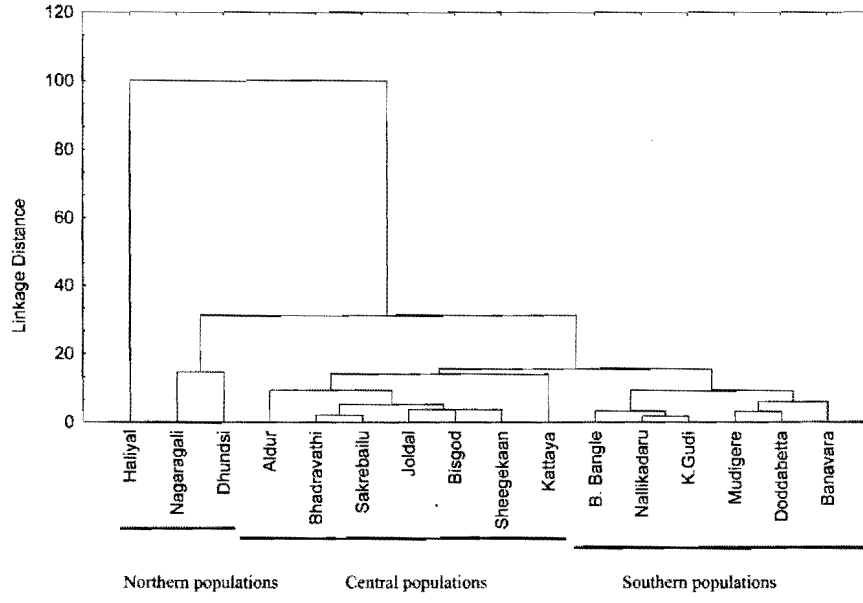

Figure 3. Dendrogram for *D. strictus* populations

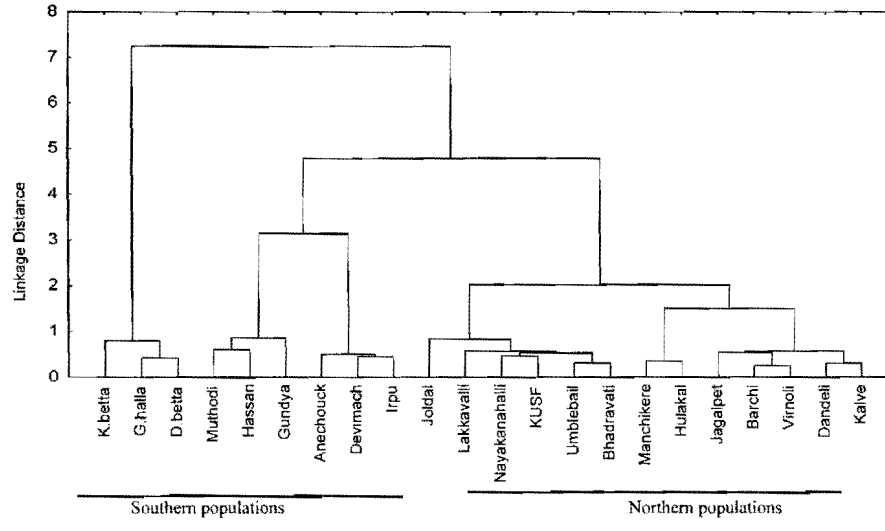

Figure 4. Dendrogram for *B. bambos* populations

The average Nei's genetic distances among populations were 1.189 and 0.91 in *D. strictus* and *B. bambos* respectively. Based on the distance values, a cluster analysis was conducted. The cluster analysis revealed clear segregation of the populations based on their geographical origin (Figs. 3 and 4). The estimates of gene flow (Nm) across the populations was 0.9237 and 1.32 for *B. bambos* and *D. strictus* respectively.

DISCUSSION

Based on measures of population genetic analysis, very contrasting spatial patterns in the distribution of genetic diversity in the two species of bamboo were observed. *D. strictus* populations from the northern latitudes were genetically more diverse than those from the southern latitudes. In contrast, *B. bambos* populations in the southern latitudes were found to be genetically more diverse than those in the northern latitudes (Fig.1). Such type of positive associations between genetic diversity parameters along the latitudinal gradients have also been shown for few other forest species in the Western Ghats (Nageswara Rao *et al.*, 2001, 2007; Ravikanth *et al.*, 2002). Huh and Huh (2002) reported such trend of low genetic diversity in northern populations of *Pseudosasa japonica,* a heavily extracted bamboo species in Korea, as compared to the southern populations.

The observed spatial patterns of genetic diversity in the two bamboo species correspond well with their underlying spatial distribution patterns (Uma Shaanker *et al.*, 2004; Cheluvaraju *et al.,* 2001). In other words, our studies show that the genetic diversity

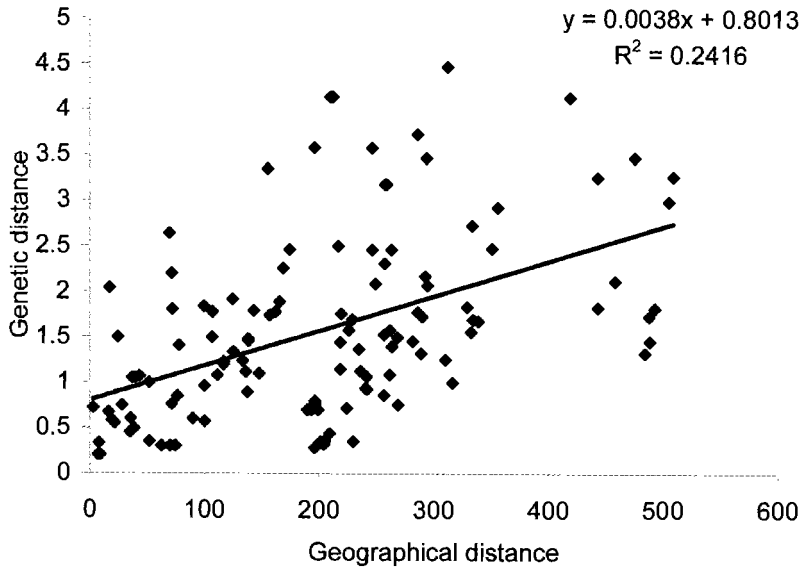

Figure 5. Relationship between genetic distance and geographical distance (kilometres) for *D. strictus* populations ($r = 0.49$; $P < 0.05$).

in *D. strictus* seems to be associated with the hotter and drier climate in northern latitude compared to *B. bambos,* where the diversity is associated with the cooler and humid climate in the southern latitude.

The observed estimates of geneflow in our study was comparable to other bamboo species, *Sasamorpha borealis* ($N_m = 0.56$; Lee and Chung, 1999) and *P. japonica* ($N_m = 1.39$; Huh and Huh, 2002). The genetic differentiation of populations in both the species could partly be attributed to the restricted gene flow caused among other factors by their gregarious flowering behaviors coupled with a high degree of asynchrony in the flowering episodes among populations (Uma Shaanker *et al.*, 2004). Thus, populations even in close proximity, can effectively be reproductively isolated leading to differentiation of populations over time and their genetic segregation. These problems would further be accentuated by the large-scale perturbations in their habitat that may effectively hinder the pollen and/or seed dispersal.

In the case of *D. strictus*, there was a strong association between Nei's genetic diversity and the population size ($r = 0.54$, $P<0.05$) confirming that small patches may be at the risk of losing their genetic diversity. While assessing sandal population genetic diversity, Nageswara Rao *et al.* (2007), also highlighted such strong association of loss in genetic diversity due to increased anthropogenic pressure and reduced population size. There appears to be unanimous agreement that the larger the population size, the better would be the status of the genetic resources (Gilpin and Soule, 1986; Prober and Brown, 1994). Earlier studies have shown that the demographic status of a species could be used as an appropriate indicator of the status of the genetic diversity of the populations (Lande, 1988; Quattro and Vrijenhoek, 1989). The genetic differentiation of the bamboo population, in this study, is also evident from the high values of G_{ST} (0. 35 in *B. bambos* and 0.27 in *D. strictus*) suggesting that the total variation observed in both the species was due to variation among the populations. In fact, in case of *D. strictus*, the Nei's genetic distance was found to be significantly positively correlated with their geographic distance ($r = 0.49$, $P< 0.05$, Fig 5). A significant positive association between genetic and geographic distance and their consequences have been documented in *P. japonica* (Huh and Huh, 2002). The geographic range has been shown to be strongly associated with the levels of variation maintained within the population and at the species level in various other forest species as well (Hamrick and Godt, 1989).

The study presented here holds important implications for the conservation and management of the two most economically important bamboos in the Central Western Ghats. Our study indicates a clear genetic differentiation of the populations of two species. The 'hot-spots' of genetic diversity for *B. bambos* are in southern latitude, and for *D. strictus* in northern latitude. Thus, separate conservation protocols need to be evolved to maximize the conservation efforts for the two economically important bamboo species.

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