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# Do Endemic Rattans Have Lower Genetic Variability than Their Co-generic and Con-specific Non-endemic Rattans?

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## ABSTRACT

Comparisons between the population genetic variability of endemic and non-endemic species provide valuable information for the conservation of the endemic species. Comparisons between the endemic and non-endemic species are seldom carried out with con-generic and co-occurring species. In this study, we have compared three pairs of con-specific endemic and non-endemic rattan species at three locations in the Central Western Ghats, one of the global biodiversity hot-spots located in India. We have analyzed the demographic structure of these species across these three sites. We found that overall the endemic rattan species suffered from poor regeneration compared to their con-specific and con-generic non-endemic rattan species. We also used molecular markers to analyze the genetic variability of these endemic and non-endemic rattan species. Our results suggest that, except in one species, the genetic variability of the endemic species was significantly lower than the con-specific non-endemic rattan species. These results indicate the lower genetic variability of the endemic species and have important implications in prioritizing species for conservation.

**Keywords:** conservation, genetic diversity, small populations, Western Ghats, rattan demography

## INTRODUCTION

Endemic species are commonly hypothesized to have low levels of genetic variation because of inbreeding, genetic bottlenecks and other factors. Low levels of genetic variability are common for number of geographically restricted plants species (Gibson *et al.* 2008; George *et al.* 2009). Three primary factors; geographic area, ecological breadth and isolation describe the distribution of endemic species. Endemics have small effective population sizes due to smaller total population sizes than widespread species. A number of studies have documented the amount of genetic variation in small populations (Uma Shaanker *et al*. 2004; Hamrick *et al.* 1991; Gitzendanner and Soltis 2000; Gibson *et al.* 2008). In small populations, genetic drift can be a major force in reducing the genetic variation, by inducing loss of alleles. Immigration from a large source population can delay, stop or reverse such losses of genetic variation (Barrett and Kohn 1991). By increasing genetic drift and reducing gene flow, isolation of small population increases genetic differentiation between the populations (Fore *et al.* 1992; Leimu *et al.* 2006). In addition, when population size decreases, levels of inbreeding will increase due to both selfing (autogamia) and reproduction among related individuals (biparental inbreeding), which in turn will decrease the levels of heterozygosity (Karron 1991; Gitzendanner and Soltis 2000; Cole 2003). Such loss of allelic variation and heterozygosity may render a population more sensitive to ecological changes and more vulnerable to extinction.

Hamrick and Godt (1989) found that the geographic range of a species accounted for the largest amount of genetic variation in population and species levels. Species with small ranges typically have less genetic variation than regional or widespread taxa (Gottlieb 1973; Loveless and Hamrick 1988; Gitzendanner and Soltis 2000; Leimu *et al.* 2006). A number of studies have shown low levels of genetic variation in endemics and rare species than their widespread progenitor due to reduced gene flow in the endemics (Hamrick and Godt 1989; Gitzendanner and Soltis 2000). Gibson *et al.* (2008) found lower genetic diversity in the endemic *Alnus maritima* than its widespread congener *A. serrulata.* The lower genetic variability in the endemic species is attributed to higher inbreeding among the small and highly isolated populations (Gibson *et al.* 2008). However, this is not always the case and there are several studies proving contrary (Kang *et al.* 2005; Ellis *et al.* 2006; Medrano and Herrera 2008). For example, Gottlieb *et al*. (1985) show that an endemic species *Layia discodea* is genetically more variable than its closely related and widespread species *L. glandulosa.* Several studies suggest that the high levels of genetic variation sometimes exhibited by the endemic species is that they could consist of relatively large populations than their con-generic non-endemic species (Ellstrand and Elam 1993; Medrano and Herrera 2008).

Though several studies have addressed the issue of endemism, it is recommended that, to determine if endemic species exhibit lower diversity than common ones, congeneric comparisons where phylogenetic effects can be controlled are used (Gitzendanner and Soltis 2000; Cole 2003). Such comparisons of con-generic species could provide specific insights into the impacts of isolation and restricted distribution of endemic species that could be used in developing effective conservation strategies (Francisco-Ortega *et al*. 2000; Oliva-Tejera *et al.* 2006).

In India, nearly 51 of 70 rattan (Family: Palmae) taxa are endemic and are thus localized to a particular rattan-growing region (Uma Shaanker *et al*. 2004). The rattans are referred to as "canes of commerce" as they form one of the most important non-timber forest produce in South and South-east Asia (Lyngdoh *et al*. 2005). It is estimated that in

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**Table 1** Endemic and non-endemic species of rattans in the three study sites in Kodagu district, Karnataka, India.

| Site | Endemic species | Non-endemic species |
|---|---|---|
| Bhagamandala | **Calamus lacciferus* | **C. thwaitesii*, *C. pseudotenuis* |
| Makut | **C. stoloniferus*, *C. lakshmanae* | **C. thwaitesii*, *C. dransfieldii*, *C. travancoricus* |
| Sampaji | **C. lakshmanae*, *C. nagbettai* | **C. thwaitesii*, *C. travancoricus*, *C. prasinus* |

* indicate the species studied for their genetic variability.

South-east Asia, approximately half a million people are directly employed in rattan trade (Uma Shaanker *et al*. 2004). The global trade in rattans is estimated to be over US$6.5 billion a year (Uma Shaanker *et al*. 2004; Lyngdoh *et al*. 2005). Thus, there is considerable extraction of species from the wild. Consequently, these species face acute danger of becoming extinct. The Western Ghats, India, one of the richest biodiversity hot-spot in the world (Myers *et al*. 2000) is represented by only one genus *Calamus* with about 21 identified species of which, 15 are endemic (Renuka 1999; Ravikanth *et al.* 2002; Uma Shaanker *et al*. 2004). In Kodagu, a relatively small region in the Western Ghats, Karnataka, India harbors nine species of rattans, five of which are endemic (Uma Shaanker *et al*. 2004). These endemic species are often associated with small population sizes, which are often associated with low levels of genetic diversity, which might also reduce the average fitness of constituent individuals. Small populations might also lose a large amount of genetic variability due to genetic drift jeopardizing the very survival of the species (Franklin 1980). In small populations, increased selfing and mating among closely related individuals could also result in inbreeding depression among the progeny (Schaal and Leverich 1996; Young *et al*. 1996; Hommay and Jacquemyn 2006).

In this study, an attempt was made to study the population structure and regeneration status of a set of endemic and non-endemic species of rattans occurring in the Central Western Ghats. Endemic species, which are reported to have low genetic variability, could be more predisposed for low recruitment compared to the con-specific but more widespread non-endemic species. The study was designed to test the hypothesis that endemic species which are con-specific and con-generic non-endemic species will have lower recruitment than the latter. The study also addresses the genetic variability of these co-occurring species.

## MATERIALS AND METHODS

### System and study site

#### *1. Demographic analysis*

Based on the rattan species richness of South India, three study sites namely Sampaji (12° 47′ N and 75° 58′ E), Bhagamandala (12° 42′ N and 75° 60′ E) and Makut (12° 00′ N and 75° 72′ E) in Kodagu district, Karnataka, India were selected for demographic and genetic study as these sites are found to have both the endemic and non-endemic rattan species. In each of the study site, based on secondary data, a list of the endemic and non-endemic species of rattans were selected (**Table 1**) and sampled. The secondary data were collected from several published sources (Renuka 1992; Renuka 1999; Ravikanth *et al.* 2001, 2002; Uma Shaanker *et al*. 2004). At each site, 10 quadrats of 10 m × 10 m were laid and the data on demographic parameters such as density, regeneration, and number of adults (>10 m height) of endemic and non-endemic species of rattan were recorded.

Data on the number of rattan clumps per quadrat across all species and individually for each species was recorded. The mean density of the endemic and non-endemic species over all the quadrats within a site and across the three sites was computed. As an index of the regeneration, the number of seedlings was recorded for each of the endemic and non-endemic species. Based on this, the regeneration per quadrat for each species was computed. Regeneration for endemic and non-endemic species was also computed by pooling the data from all the three sites. To obtain a relative measure of the number of regenerants per adult for each of the endemic and non-endemic species, the number of seedlings of a species in a quadrat was divided by the number of adults (>10 m height) of the respective species. The assumption in this measure is that on an average the recruits in a quadrat are derived from the adults in the same quadrat.

#### *2. Genetic diversity of endemic and non-endemic species of rattans*

At each site, sampling was restricted to con-specific (to reduce extraneous errors) and con-generic (to reduce phylogenetically induced variations) endemic and non-endemic species. Since all the species studied belong to the same genus, *Calamus*, we assume that to the extent possible in this study the disparity due to phylogenetic differences have been kept to the minimum (**Table 1**).

Mature leaf samples of endemic and non-endemic rattan species were randomly collected from three regions. Leaves were collected from 10 to 15 individuals of each of the species. The harvested leaves were air dried and stored in dry place for further use. DNA was extracted from 10 randomly chosen individuals using a CTAB extraction method for each of the pairs of endemic and non-endemic species from each of the three sites. Once extracted, DNA was subjected to the polymerase chain reaction (PCR) using RAPD primers (Operon Technologies Inc., USA). In total, 60 primers were used to screen the rattan genomic DNA. The degree of utility of each primer was assessed based on the quality of the amplified products, and the amount of variation observed. Of the 60 random primers tried, 10 primers (OPF 1, OPF 14, X14, X20, V04, V05, V10, W05, W07 and W10), which showed good amplification, were selected for screening DNA from all the populations. PCR amplification was performed with 25 µl total reaction mixture volume containing one unit of *Taq* DNA Polymerase, 1 X *Taq* buffer with 15 mM $MgCl_2$, 1 mM each of dATP, dCTP, dGTP, dTTP, 3 mM of primer, and 50 ng of the template DNA. The amplification regime was performed with initial denaturation at 94°C for 5 min followed by 35 cycles of 1 min at 95°C, 10 sec 38°C, 2 min 72°C and followed by final extension at 72°C for 10 min. The PCR amplified products were electrophoresed on 1.5% agarose gels. A lambda DNA/*Eco*RI/*Hind*III double digest DNA marker (Bangalore Genei, India) was loaded on each gel to assess PCR product size. Gels were stained with ethidium bromide and visualized under UV light and photographed. Band presence was scored as 1 and the absence as 0. The presence of each band was considered as an allele. Thus, the allele frequencies were calculated under the assumption that each amplified band represented a different RAPD locus.

### Data analysis

#### *1. Demographic analysis*

The mean density, regeneration and regeneration per adult of the endemic and non-endemic species was compared at each site and also computed by pooling the data from all the three sites using a Student *t*-test (Snedecor and Cochran 1967).

#### *2. Mean similarity index*

As a measure of the genetic diversity, the similarity index (1-squared Euclidean index) between all possible pairs of individuals within each species (endemic and non-endemic) was computed. Based on the presence or absence of the amplification products at various loci, the similarity indices (n=45 similarity indices) was computed. The similarity index was computed as 1-squared Euclidean distance ($1-\Sigma_I (X_i-Y_i)^2$) between all possible pairs of individuals within each species at each site (Lyngdoh *et al.* 2005). The

mean similarity index was then developed for both endemic and non-endemic species of rattans respectively. The mean frequency index was statistically tested using a student's *t-test* (Snedecor and Cochran 1967).

## RESULTS

### Population structure and regeneration status of endemic and non-endemic species of rattans

#### *1. Density per quadrat*

Across all the three sites (Bhagamandala, Makut and Sampaji) the mean density of the endemic species (*Calamus lakshmanae*, *C. stoloniferus*, *C. nagbettai*, and *C. lacciferus*) was not significantly different from that of the non-endemics (*C. thwaitesii*, *C. prasinus*, *C. dransfieldii*, *C. pseudotenuis* and *C. travancoricus*) (**Fig. 1**). In Bhagamandala, on an average, the non-endemic species (*C. thwaitesii*, *C. pseudotenuis*) had higher mean density than the endemic species (*C. lacciferus*) (**Fig. 1**). At Makut, there was no significant difference between the endemic (*C. lakshmanae* and *C. stoloniferus*) and non-endemic (*C. thwaitesii*, *C. travancoricus*, and *C. dransfieldii*) species in their density (**Fig. 1**). In Sampaji, the density of the endemic rattan species *C. lakshmanae* and *C. nagbettai* were marginally higher (1.66 ± 1.08) compared to that of the non-endemic species, *C. thwaitesii*, *C. prasinus* and *C. travancoricus* (1.08 ± 2.02) (**Fig. 1**).

#### *2. Regeneration per quadrat*

Over all the sites, the mean regeneration of the endemic species (*C. lakshmanae C. stoloniferus*, *C. nagbettai*, and *C. lacciferus*) was significantly lower compared to that of non-endemic species (*C. thwaitesii*, *C. prasinus*, *C. dransfieldii*, *C. pseudotenuis* and *C. travancoricus*) (**Fig. 2**; $p < 0.006$). Even at individual sites, the regeneration of the endemic species was lower. In Bhagamandala, the regeneration of endemic *C. lacciferus* was low (0.4 ± 1.544) as compared to the non-endemic species *C. thwaitesii* (**Fig. 2**; $p < 0.05$). At Makut, *C. lakshmanae*, which is endemic to this region, had no regenerants. Interestingly, the regeneration of *C. travancoricus*, a non-endemic species, was also very poor. The regeneration pooled across the endemic species (*C. lakshmanae* and *C. stoloniferus*) was significantly less compared to that of non-endemic species (*C. thwaitesii*, *C. travancoricus*, and *C. dransfieldii*) (**Fig. 2**; $p < 0.017$). In the Sampaji region also the endemic rattan species had significantly lower regeneration compared to the non-endemic rattan species (**Fig. 2**; $p < 0.031$).

#### *3. Regeneration per adult*

In Bhagamandala, the regeneration per adult of populations was highest for the non-endemic *C. thwaitesii* and *C. pseudotenuis* (0.19 ± 0.34) as compared to the other endemic species of rattans (*C. lacciferus*) (**Fig. 3**; $p < 0.05$), indicating that endemic species seem to have a poor regeneration per adult compared to the non-endemic species. Similarly, in Makut, significantly less regenerants per adult was observed for the endemics (*C. lakshmanae* and *C. stoloniferus*) (0.241 ± 0.457) as compared to that in the non-endemics (*C. thwaitesii*, *C. travancoricus*, and *C. dransfieldii*) (0.429 ± 0.468) (**Fig. 3**; $p < 0.05$). In Sampaji, the endemic species (*C. lakshmanae*, *C. nagbettai*) had significantly lower regeneration per adult compared to the non-endemic species (*C. thwaitesii*, *C. prasinus* and *C. travancoricus*) (**Fig. 3**; $p < 0.000001$). Over all the three sites, the regeneration of the endemic species (*C. lakshmanae C. stoloniferus*, *C. nagbettai*, and *C. lacciferus)* was significantly low compared to the con-generic non-endemic species (*C. thwaitesii*, *C. prasinus*, *C. dransfieldii*, *C. pseudotenuis* and *C. travancoricus*) (**Fig. 3**; $p < 0.05$).

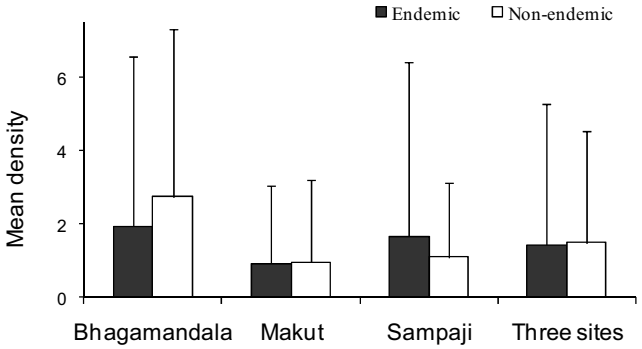


**Fig. 1 Density per quadrat of endemic and non-endemic species of rattans at different sites, Kodagu, Karnataka, India.** Bars = standard deviation (n = 10 quadrats/site).

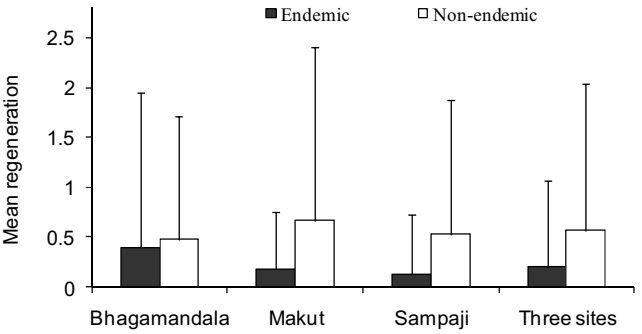


**Fig. 2 Mean regeneration per qudarat of endemic and non-endemic species of rattans at different sites.** Bars = standard deviation (n = 10 quadrats/site).

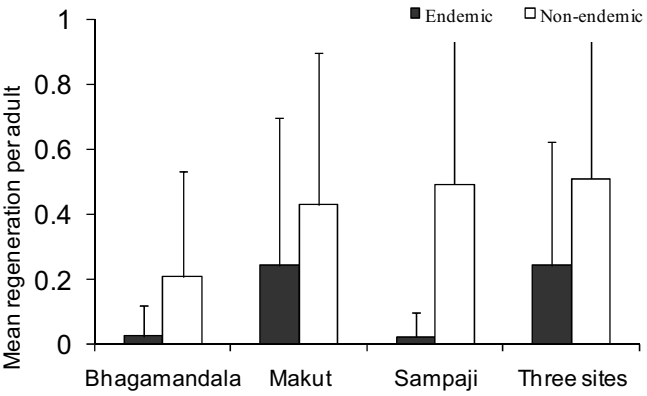


**Fig. 3 Mean regeneration per adult per quadrat of endemic and non-endemic species of rattans at different sites.** Bars = standard deviation (n = 10 quadrats/site).

### Genetic diversity

As a measure of the genetic variability, we computed the mean similarity of the individuals of both the endemic and non-endemic rattan species (Lyngdoh *et al.* 2005). Greater the similarity of the individuals, lower is the variability. We found that overall, in two of the three pairs of comparisons; the mean similarity of the endemic species was more than the non-endemic species. At Makut, the mean similarity index of the non-endemic (*C. thwaitesii*) species was significantly less (0.60 ± 0.07) compared to that of the endemic (*C. stoloniferus*) species (0.64 ± 0.06) (**Fig. 4**; $p < 0.05$). While in Bhagamandala the non-endemic species (*C. thwaitesii*) had a higher similarity index (0.71 ± 0.07) compared to the endemic species (*C. lacciferus*) (0.55±0.13) (**Fig. 5**; $p < 0.01$). At Sampaji, the endemic species (*C. lakshmanae*) showed higher similarity index (0.64 ± 0.06) compared to the non-endemic species (*C. thwaitesii*) of rattan (0.58 ± 0.90) (**Fig. 6**; $p < 0.018$).

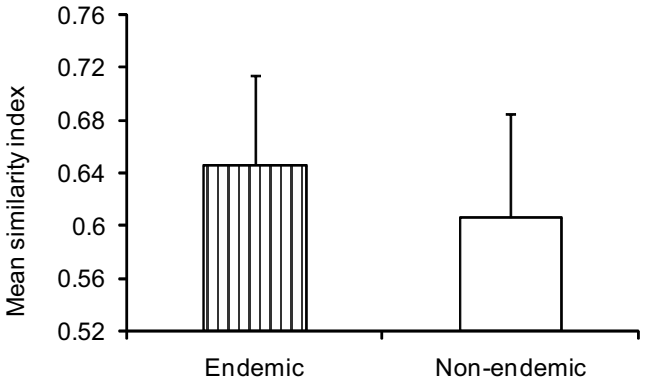


**Fig. 4 Mean similarity of endemic *Calamus stoloniferus* and non-endemic *C. thwaitesii* at Makut ($p < 0.05$).** Bars = standard deviation (n = 45).

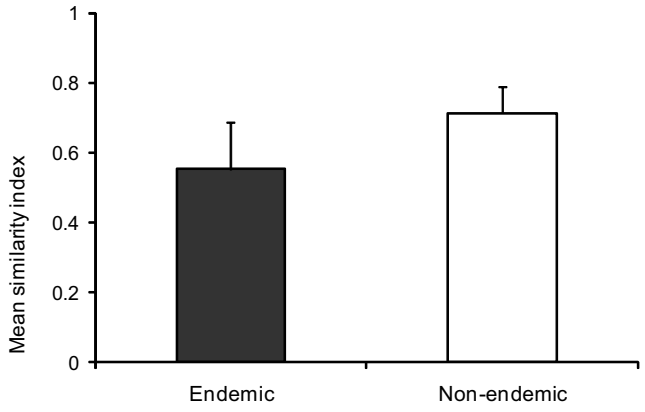


**Fig. 5 Mean similarity of endemic *Calamus lacciferus* and non-endemic *C. thwaitesii* at Bhagamandala ($p < 0.01$).** Bars = standard deviation (n = 45).

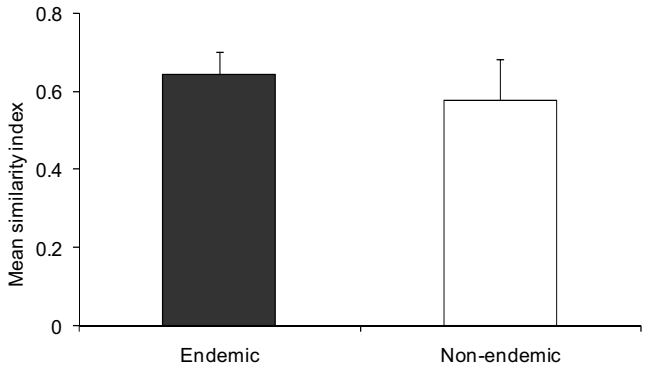


**Fig. 6 Mean similarity of endemic *Calamus lakshmanae* and non-endemic *C. thwaitesii* at Sampaji ($p < 0.018$).** Bars = standard deviation (n = 45).

## DISCUSSION

Most of the studies carried-out in addressing the differences in the population structure and genetic variability across the endemic and non-endemic species, have deficiencies in the methodology adopted. In most studies, the endemic and the non-endemic species were collected across different sites and analyzed. Many of the existing reviews including that of Hamrick and Cole (Hamrick and Godt 1990; Hamrick *et al*. 1991; Cole 2003) are based on the lumping of endemic and non-endemics across taxa and thus treating each of them as a homogenous unit of sample. Existing studies rarely have considered both con-specific and con-generic species for comparison. Thus, the parameters measured are influenced by the spatial variation more in the non-endemic compared to the endemic species and could potentially mislead comparisons of the genetic variability parameters between the endemics and non-endemics. In this study, we have made an attempt to overcome the above shortcomings by taking into account the phylogenetic relationship of the species and sampling in the same geographical area using *Calamus* as an example.

Our results seem to support the commonly held notion that endemics could be more endangered than the more widespread, non-endemic, species. The lower levels of regeneration of the endemics could be viewed both as a cause and a consequence of their restricted distribution. In the former it is argued that because of their poor regeneration due to low competitive ability, endemic species are outcompeted by their more widespread species and thus restricted to small habitats (Hamrick *et al*. 1992, Loveless 1992; Gitzendanner and Soltis 2000; Gibson *et al.* 2008). Alternatively, because of their restricted distribution, it could be argued that endemic species could suffer from reproductive failure and hence incur inbreeding depression, both of which could result in the progressive loss of regeneration of the species.

The reproductive output (in terms of regeneration per adult) seen in rattans is comparatively very low in endemics probably because of their small population size. Lack of reproductive individuals in the endemic species could also contribute to lower fitness due to mating among few related individuals. Poor establishment of the seedlings could be further due to the inbreeding depression. Ravikanth *et al.* (2001) have shown that even for the wide spread species *C. thwaitesii* inbreeding depression was high and this could be severe in the endemic species. A number of studies have shown that small or isolated populations often have decreased fruit set, or seed germination relative to large populations (Menges 1991; Byres and Meagher 1992; Hendrix 1994; Heschel and Paige 1995; Agren 1996).

Apart from being endemic with low population sizes, many of the rattan species are also threatened because of their economic importance (Uma Shaanker *et al.* 2004; Ramesha *et al.* 2007). At all the three study sites, the economically important and endemic species of rattans such as, *C. stoloniferus*, *C. lakshmanae* and *C. nagbettai* are known to be harvested. Similarly, *C. thwaitesii* a non-endemic species is also intensely harvested in these areas (Uma Shaanker *et al.* 2004). However, our result also showed a high standard deviation with respect to the demographic parameters. This is due to the fact that in some quadrats some species were absent. Thus, both the endemic and non-endemic species seem to have equal harvesting pressures. Despite that, the results indicate that endemic species as a group have a poor regeneration ability compared to the co-occurring and congeneric non-endemic species. This could also be attributed to the fact that there is huge demand for endemic species of rattans such as *C. stoloniferus*, *C. lakshmanae* and *C. nagbettai.* This leads to indiscriminate extraction of individuals before they reach the reproductive stage. Thus, despite having similar densities, the endemic species have lower regeneration.

### Genetic variability of endemic and non-endemic rattan species

The mean similarity index based on all loci indicated that the endemic species (*Calamus stoloniferus* and *C. lakshmanae*) at Makut and Sampaji are more similar than the non-endemic species (*C. thwaitesii*) of rattan (**Fig. 4** and **6**; $p < 0.049$ and $p < 0.0018$). However, at Bhagamandala, the non-endemic species (*C. thwaitesii*) were more similar among themselves (less genetic diversity) as compared to the endemic species (*C. lacciferus*) ($p < 0.01$). Thus, our studies seem to also point at the fact that endemic species are generally less genetically diverse than the co-occurring non-endemic species, though the data is not overwhelmingly supportive. These studies reinforce the existing concern of the threat and therefore the need for conserving the genetic resources of endemic species.

Compared to the more widespread species, endemic

species are reported to have generally low levels of genetic variability (Ledig and Conkle 1983; Waller *et al*. 1987; Hamrick and Godt 1989; Soltis *et al.* 1991; Hamrick *et al.* 1992; Loveless 1992; Gitzendanner and Soltis 2000; Gibson *et al.* 2008). Hamrick *et al.* (1992) reported significantly lower levels of genetic diversity in the endemic species. Several population genetic parameters such as percent polymorphism and number of alleles per locus were more in the widespread compared to the endemic species (Hamrick *et al*. 1992). Loveless (1992) has also shown a strong correlation between the geographical distribution of populations and the levels of variability contained in them. Many of these studies are based on the differences in the allozyme variation. Recent studies have shown that the gene diversity as measured by DNA based markers also show low variability in endemic species (Smith and Pham 1996).

The low levels of genetic variability have been explained to result from enforced inbreeding in the small and often fragmented populations of the endemic species. Indeed, many endemic species have been reported to have higher rates of self-pollination resulting in greater inbreeding (Karron 1987, 1991; Inoue and Kawahara 1990). Besides, the endemic species could also be losing alleles due to processes of random drift and genetic fixation. Notwithstanding the above reports, there are, however, few studies suggesting a higher level of genetic variability in the endemic compared to the non-endemic species as well (Karron 1987; Hamrick and Godt 1990; Karron 1991; Ranker 1994; Lewis and Crawford 1995; Kang *et al.* 2005; Ellis *et al.* 2006; Medrano and Herrera 2008). Grasses of the genus *Orcuttia*, endemic to parts of California, appear to be as variable as other more widespread species of Grammineae (Griggs and Jain 1983). *Layia discodea* and its closely related and widespread *L. glandulosa* have comparable levels of variability (Gottlieb *et al.* 1985). There is as yet no clear explanation for these results.

Nevertheless, it is now generally accepted that endemics with restricted distribution have lower levels of genetic variability than the non-endemics. The lower levels of genetic variability could be both a cause for, and consequence of, the restricted distribution of the species. In our study, we found that both the regeneration as well the genetic variability was low in the endemic species than their con-specific non-endemic species. Based on the results of this study, it is suggested that conservation strategies should be developed separately for endemic and non endemic species.

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## REFERENCES

**Agren J** (1996) Population size, pollinator limitation, and seed set in self incompatibility herb *Lythrum salicaria*. *Ecology* **77**, 1779-1790

**Barrett SCH, Kohn JR** (1991) Genetic and evolutionary consequences of small population size in plants: implication for conservation. In: Falk DA, Holsinger KE (Eds) *Genetics and Conservation of Rare Plants*, Oxford University Press, Oxford, pp 3-30

**Byers DL, Meagher TR** (1992) Mate viability in the small population of plant species with homomorphic sporophytic self-incompatibility. *Heredity* **68**, 353-359

**Cole CT** (2003) Genetic variation in rare and common plants. *Annual Reviews of Ecology, Evolution and Systematics* **34**, 213-237

**Ellis JR, Pashley CH, Burke JM, McCauley DE** (2006) High genetic diversity in a rare and endangered sunflower as compared to a common congener. *Molecular Ecology* **15 (9)**, 2345-2355

**Ellstrand NC, Elam DR** (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* **24**, 217-242

**Fore SA, Hickey RJ, Vankat JL, Guttman SI, Schaefer RL** (1992) Genetic structure after forest fragmentation: a landscape ecology perspective on *Acer saccharum*. *Canadian Journal of Botany* **70**, 1659-1668

**Francisco-Ortega J, Santos-Guerra A, Kim SC, Crawford DJ** (2000) Plant genetic diversity in the Canary Islands: A conservation perspective. *American Journal of Botany* **87**, 909-919

**Franklin IR** (1980) Evolutionary change in small populations. In: Soule ME, Wilcox BA (Eds) *Conservation Biology: An Evolutionary, Ecological Perspective*, Sinauer, Sunderland, pp 134-150

**George S, Sharma J, Yadon LV** (2009) Genetic diversity of the endangered and narrow endemic *Piperia yadonii* (Orchidaceae) assessed with ISSR polymorphisms. *American Journal of Botany* **96**, 2022-2030

**Gibson JP, Rice AS, Stucke MC** (2008) Comparison of population genetic diversity between a rare, narrowly distributed species and a common, widespread species of *Alnus* (Betulaceae). *American Journal of Botany* **95 (5)**, 588-596

**Gitzendanner MA, Soltis PS** (2000) Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany* **87**, 783-792

**Gottlieb L** (1973) Enzyme differentiation and phylogeny in *Clarkia franciscana*, *C. rubicunda* and *C. amoena*. *Evolution* **27**, 282-290

**Gottleib LD, Warwick SI, Ford VS** (1985) Morphological and electrophoretic divergence between *Layia discoidea* and *L. glandulosa*. *Systematic Botany* **10**, 484-495

**Griggs FT, Jain SK** (1983) Conservation of vernal pool plants in California, II. Population biology of a rare and unique grass genus *Orcuttia*. *Biological Conservation* **27**, 171-193

**Hamrick JL, Godt MJW, Murawski D, Loveless MD** (1991) Correlations between species traits and allozyme diversity: implications for conservation biology. In: Falk D, Holsinger K (Eds) *Genetics and Conservation of Rare Plants*, Oxford University Press, Oxford, pp 75-86

**Hamrick JL, Godt MJW** (1989) Allozyme diversity in plant species. In: Urbanska K (Ed) *Differentiation Patterns in Higher Plants*, Academic Press, New York, pp 53-67

**Hamrick JL, Godt MJW** (1990) Allozyme diversity in plant species. In: Brown AHD, Clegg MT, Kahler AL, Weir BS (Eds) *Plant Population Genetics, Breeding and Germplasm Resources*, Sinauer, Sunderland, MA pp 43-63

**Hamrick JL, Godt MJW, Sherman-Broyles SL** (1992) Factors influencing levels of genetic diversity in woody plant species. *New Forests* **6**, 95-124

**Hendrix HD** (1994) Effects of population size on fertilization, seed production and seed predation in two prairie species. In: Wickett RG, Dolan-Levis P, Woodlife A, Pratt (Eds) *The 13th North American Prairie Conference: Spirit of Land, Our Prairie Legacy*, Preney Print and Lotho, Ontario, Canada, pp 115-121

**Heschel M, Paige KN** (1995) Inbreeding depression, environmental stress and population size variation in scarlet garlia (*Ipomosis aggregata*). *Conservation Biology* **9**, 126-133

**Honnay O, Jacquemyn H** (2006) Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* **21 (3)**, 823-831

**Inoue K, Kawahara T** (1990) Allozyme differentiation and genetic structure in island and mainland Japanese populations of *Campanula punctata* (Campanulaceae). *American Journal of Botany* **77**, 1440-1448

**Kang M, Jiang M, Huang H** (2005) Genetic diversity in fragmented populations of *Berchemiella willsonii* var. *pubipetiolata* (Rhamnaceae). *Annals of Botany* **95**, 1145-1151

**Karron JD** (1987) A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* **1**, 47-58

**Karron JD** (1991) Pattern of genetic variation and breeding systems in rare plants species. In: Falk DA, Holsinger KE (Eds) *Genetics and Conservation of Rare Plants*, Oxford University Press, Oxford, pp 3-30

**Ledig FT, Conkle MT** (1983) Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus torreyana* Parry ex Carr.). *Evolution* **37**, 79-85

**Leimu R, Mutikainen P, Koricheva J, Fischer M** (2006) How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology* **94**, 942-952

**Lewis PO, Crawford DJ** (1995) Pleistocene refugium endemics exhibit greater allozymic diversity than widespread congeners in the genus *Polygonella* (Polygonaceae). *American Journal of Botany* **82**, 141-149

**Loveless MD, Hamrick JL** (1988) Genetic organization and evolutionary history in two North American species of *Cirsinx. Evolution* **42**, 254-265

**Loveless MD** (1992) Isozyme variation in tropical trees: Patterns of genetic organization. In: Adam WT, Strauss SH, Copes DL, Griffin AR (Eds) *Proceedings of the International Symposium on Population Genetics of Forest Trees*, July 31-August 2, Corvalis, Oregon, USA, pp 67-94

**Lyngdoh N, Santosh SH, Ramesha BT, Nageswara Rao M, Ravikanth G, Narayani Barve, Ganeshaiah KN, Uma Shaanker R** (2005) Rattan species richness and population genetic structure of *Calamus flagellum* in North-Eastern Himalaya, India. *Journal of Bamboo and Rattans* **4 (3)**, 293-307

**Medrano M, Herrera MC** (2008) Geographical Structuring of Genetic Diversity across the whole distribution range of *Narcissus longispathus*, a habitat-specialist, Mediterranean narrow endemic. *Annals of Botany* **102**, 183-194

**Menges ES** (1991) Seed germination percentage increases with population size in a fragmented prairie species. *Conservation Biology* **5**, 158-164

**Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J** (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858

**Oliva-Tejera F, Caujape J, Navarro-Deniz J, Reyes-Betancort A, Scholz S, Baccarani-Rosas M, Cabrera–Garcia N** (2006) Patterns of genetic divergence of three Canarian endemic *Lotus* (Fabaceae): Implications for the conservation of the endangered *L. kunkelii*. *American Journal of Botany* **93**, 1116-1124

**Ramesha BT, Ravikanth G, Nageswara Rao M, Ganeshaiah KN, Uma Shaanker R** (2007) Genetic structure of rattan, *Calamus thwaitesii* in core, and buffer and peripheral regions of three protected areas at central Western Ghats, India: Do protected areas serve as refugia for genetic resources of economically important plants? *Journal of Genetics* **86 (1)**, 9-18

**Ranker TA** (1994) Evolution of high genetic variability in the rare Hawaiian fern *Adenophorus periens* and implications for conservation management. *Biological Conservation* **70**, 113-118

**Ravikanth G, Ganeshaiah KN, Uma Shaanker R** (2001) Mapping genetic diversity of rattans in the Central Western Ghats: Identification of hot-spots of variability for *in-situ* conservation. In: Uma Shaanker R, Ganeshaiah KN, Bawa KS (Eds) *Forest Genetic Resources: Status, Threats and Conservation Strategies*, Oxford and IBH Publishing Co. Pvt. Ltd., India, pp 69-83

**Ravikanth G, Ganeshaiah KN, Uma Shaanker R** (2002) Identification of hot spots of species richness and genetic variability in rattans: an approach using geographical information systems (GIS) and molecular tools. *Plant Genetic Resources Newsletter* **132**, 17-21

**Renuka C** (1992) *Rattans of the Western Ghats: A Taxonomic Manual*, Peechi, India. Kerala Forest Research Institute, Peechi, pp 1-96

**Renuka C** (1999) Indian rattan distribution – an update. *The Indian Forester* **25**, 591-598

**Schaal BA, Leverich WJ** (1996) Molecular variation in isolated plant populations. *Plant Species Biology* **11**, 33-40

**Smith JF, Pham TV** (1996) Genetic diversity of the narrow endemic *Allium aaseae* (Alliaceae). *American Journal of Botany* **83**, 717-726

**Snedecor GW, Cochran WG** (1967) *Statistical Methods*, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, pp 1-165

**Soltis PS, Soltis DE, Tucker TL, Lang FA** (1991) Allozyme variability is absent in the narrow endemic *Bensoniella oregnona* (Saxifragaceae). *Conservation Biology* **6**, 131-134

**Uma Shaanker R, Ganeshaiah KN, Srinivasan K, Ramanatha Rao V, Hong LT** (Eds) (2004) *Bamboos and Rattans of the Western Ghats: Population Biology, Socio-economics and Conservation Strategies*. Published by Ashoka Trust for Research in Ecology and Environment, International Plant Genetic Resources Institute and University of Agricultural Sciences Bangalore, India, pp 1-199

**Waller DM, O'Malley DM, Gawler SC** (1987) Genetic variation in the extreme endemic *Pedicularis furbishiae* (Scrophulariaceae). *Conservation Biology* **1**, 335-340

**Young AG, Boyle T, Brown AHD** (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution* **11**, 413-418