ELSEVIER

Flora 199, 351–359 (2004)
http://www.elsevier.de/flora

FLORA

Reproductive phenology of endemic understorey assemblage in a wet forest of the Western Ghats, south India

RANI M. KRISHNAN

Salim Ali School of Ecology, Pondicherry University, Pondicherry 605014, India

Submitted: Aug 15, 2003 · Accepted: Jan 3, 2004

Summary

The reproductive phenology of 60 understorey species, including 27 endemic and 33 non-endemic species, was monitored at monthly intervals for 20 months in a mid-elevation wet forest in the Southern Western Ghats. Narrow endemic species constituted 55% of the total endemic species studied. Peak flowering was observed during the dry and post-monsoon seasons for the endemic species, while the non-endemic species flowered during the dry season. Fruiting peak was observed in the dry season for endemic species and during monsoon for non-endemics. The flowering and fruiting pattern in narrow and broad endemic species was uniform. The implications of the result for conservation are discussed.

Key words: Endemics, Evergreen forests, Narrow endemics, Reproductive phenology, Understorey, Western Ghats, India.

Introduction

Information on reproductive biology of endemic, rare, endangered, and threatened species has many applications. Although important, such data are rare. Floral biology and plant-pollinator/disperser interactions of several endemic, rare, endangered, and threatened species have been studied in tropical and temperate regions (GASTON 1994), but quite selectively.

In the Western Ghats, the knowledge of local endemism patterns is applied to delimit areas of high conservation priority. Called hotspots, these areas are demarcated based on biological diversity, especially the number of endemic species (NAYAR 1996). Most studies focus on woody life forms (trees and shrubs) as the indicator ensemble to assess diversity and endemism patterns. One drawback of this method is that the understorey layers, despite being diverse and species rich, are not represented in the estimate. Although two aspects of endemism, the range and the distribution, are well studied for the tree flora in the Ghats (RAMESH 2001), little is known about whether or not the endemic flora constitutes a random assemblage with respect to taxonomy, ecology, habitat preference and biological attributes.

The understorey community in the evergreen forests of the Western Ghats is perhaps the richest in the tropics (KRISHNAN & DAVIDAR 1996). Although aspects such as growth patterns, microhabitat preference and phenology have been studied, the relative role of endemic shrubs in the overall function of the community is still poorly explored (KRISHNAN 1996, 2001, 2002). Seasonal rhythms of flowering and fruiting sustain diversity of the pollinator and disperser fauna, and ensure that the species can persist in the area. By comparing the rhythms of flowering and fruiting of the endemic species with that of non-endemic species, the contribution by each group, on a seasonal or temporal scale, can be assessed.

* **Corresponding author:** Rani M. Krishnan, Salim Ali School of Ecology, Pondicherry University, Pondicherry 605014, India, 1250 NW State #3, Pullman, WA 99163, USA, e-mail: mkrani@hotmail.com

Endemic plants are defined by their restricted geographical distribution. In the neo-tropical realm, substrate specificity has been identified as a significant factor in causing endemicity (Gentry 1992), but the underlying biological factors that cause these patterns are poorly understood. Rabinowitz (1981) identified seven types of rarity. They can be grouped under three factors: geographic range (wide distribution vs. narrow distribution), habitat specificity (generalized vs. specific) and local population size (small vs. large). Very often, species with an only narrow distribution, high habitat specifity, and occurrence in small populations are under threat of extinction. Several endemic species reported in this paper have such a narrow distribution, and are confined to evergreen forests of the Agastyamalai region in small populations. Other species, although being narrow endemics as well dominate certain valleys. Broad endemic species are defined as occuring throughout the Western Ghats.

For improving conservation efforts, information and data pertaining to the behaviour of individual species is necessary. Species richness and diversity is particularly high in Agastyamalai region of the Western Ghats, and different groups of biologically similar species can be characterized for this region. Differences between these species can be expressed in terms of life history strategy, microhabitat preference, pollinator interactions and phenology.

Phenological studies over the last four decades from the tropics show that flowering and fruiting in the canopy could be aseasonal or supra-annual (Koelmeyer 1959 a, b; Putz 1979; Yap 1982; Devy 1998; Sakai et al. 1999). Few studies have focussed on the phenology of the understorey plants although it is known that they behave differently from canopy trees (Appanah 1991), and are serviced by different pollinators and dispersers (Stiles 1978; Corlett 1998; Wesselingh et al. 2000). These differences indicate that the understorey could be an important resource base for pollinators and dispersers during periods of resource shortage in the overstorey. This paper reports the results of a pilot study undertaken in the understorey community of the southern Western Ghats, to examine the phenology of endemic and non-endemic species. If clear patterns emerge, the results of the study will provide clues about the overall phenological strategies of the endemic understorey species in the region.

Study area and methods

Kakachi, the study site is in the Kalakad-Mundanthurai Tiger Reserve, located in the Agastyamalai region of the Western Ghats in the state of Tamil Nadu, India. The sanctuary is located 55 km east of Arabian Sea at 8° 33′ N latitude and 77° 23′ E longitude. The medium elevation evergreen forests are floristically of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum-Gluta travancorica-Nageia wallichiana* type (Ramesh et al. 1998). Ganesh et al. (1996) present a detailed floristic analysis of the study site.

Data on rainfall was obtained from the Nalmukku rain gauge (The Bombay Burma Trading Company, two kms from the study area). The annual rainfall was between 1500 mm to 3400 mm. The region receives rainfall from the south-west monsoon (June to August) and north-east monsoon (November to January). Seasons were delineated as: dry season from February to May, monsoon from June to August, and post-monsoon, or period of retreating monsoon, from September to January. Despite being categorised as a dry season, scanty rainfall was observed in February and March.

This paper presents observations on the phenological behaviour of the understorey community over 20 months, from April 1991 to December 1992. A cyclone in November 1992, left the study site inaccessible for observations.

As the study area was nearly homogenous in composition, individuals were marked along two 500 x 10 m transects, about 800 m apart. A monthly census was made to record the flowering or fruiting activity in 1249 individuals from 60 species belonging to 22 families. Representations from all habit forms in the understorey were included (Appendix 1). Phenology of species occuring in nearby disturbed forests was followed on non-marked individuals. Fruits were classified as fleshy and non-fleshy.

A species was considered to be phenologically active when at least 10% of observed individuals were flowering or fruiting. This ensured that undue weight to a small proportion of flowering and fruiting individuals was avoided when characterizing the peak for a species. Since flowers and fruits were observed throughout the study period, non-parametric chi-square test, with expected monthly (mean) values, was used to compare patterns in observed and expected flowering and fruiting phenology. Highly uniform distributions were indicated when $P > 0.95$, and a significant non-uniform distribution was indicated when $P < 0.05$ (Wheelwright 1985). Pearson's correlation was used to examine the relationship between the duration of flowering and fruiting and rainfall. To test for the proportional differences between the fruit types in narrow and broad endemic species, Kolmogrov-Smirnov test (for unequal sample size) was used.

Classification of species into endemic and non-endemic categories, and further assigning the endemics into narrow and broad, was done using the "Endemic plants of Indian region", and "The Endemic Atlas of South India" (Ahamedullah & Nayar 1986; Ramesh & Pascal 1998). Species confined to only the Agastyamalai region were classified as narrow endemics, while species distributed throughout the Western Ghats were treated as broad endemics.

Results

Endemism

Only 45% (27/60) of the total species studied were endemic. The assemblage studied had a greater proportion of shrubs (61%, 37/60) than herbs (28%, 17/60) or small trees (10%, 6/60). Shrubs had a greater proportion of endemics (48%, 13/27), whereas small trees had the

Table 1. Distribution of endemic species across life-forms.

Status	Total	Herb	Shrub	Small tree
Endemic	28	15%	23%	8%
Narrow endemic*	13	23%	18.9%	66.6%
Broad endemic*	15	29%	18.9%	16.6%
Non-endemic	32	47%	62.2%	16.6%

* Derived from endemic.

least (18%, 5/27; Table 1). When the endemics were further classified into broad and narrow groups, the percentage of narrow endemics was slightly higher (55%, 15/27) than broad endemic species (44%, 12/27). Many herbs and shrubs were broad endemics (41%, 50% respectively), while most small trees fell into the category of narrow endemics (26%).

Flowering phenology

Both endemic and non-endemic species flowered throughout the study period (mean = 11.5 and 9.7 species, respectively). Mass flowering, a phenomenon where individuals produce large number of flowers in a relatively short period of time (3 to 4 months) was confined to members of the family Acanthaceae. Only two endemic species (*Nilgirianthus perrotti* and *Barleria involucrata* var. *elata*) and three non-endemic species (*Xenacanthus pulneyensis*, *Nilgirianthus* sp., and *Nilgirianthus foliosus*) displayed this phenomenon. *Justicia diffusa*, an herb, exhibited mass flowering lasting for one month. Two species of *Strobilanthes* did not flower during the study period. Most species flowered in a 'steady state', producing a few flowers throughout the year. *Justicia diffusa*, *Plectronia neilgherrensis*, *Brysophyllum tetrandrum* and *Glyptopetalum zeylanicum* flowered only once during the study period. Among endemic species, *Aphyllorchis montana* and *Psychotria annamalyana* flowered only once. On an average 11.5 endemic species flowered throughout the study period. Maximum flowering in endemic species occurred in July 1992, when 15 species (55%) participated, while flowering was at its lowest in the months of May and December 1992, when only 7 species (25%) flowered. Peak flowering was observed during the dry and post-monsoon seasons for the endemic species, while the flowering peak for the non-endemic species was observed during the dry season (N = 27 species, $P < 0.05$; N = 33 species, $P < 0.001$ respectively).

Narrow endemic species flowered more frequently (mean = 7.1 species, std ± 1.80) than the broad endemic species (mean = 4.1 species, std ± 1.35). The narrow endemic species frequently flowered in their maximum levels (September 1991 and 1992, February, June and July 1992), while minimum flowering was observed only in December 1992 when 20% (3/15) of the species participated (Fig. 1).

In April 1991, July 1992 and October 1992, 50% of the broad endemic species flowered (Fig. 2). Lowest flowering was observed in April 1992 with only 8% of broad endemics. Uniform flowering behaviour

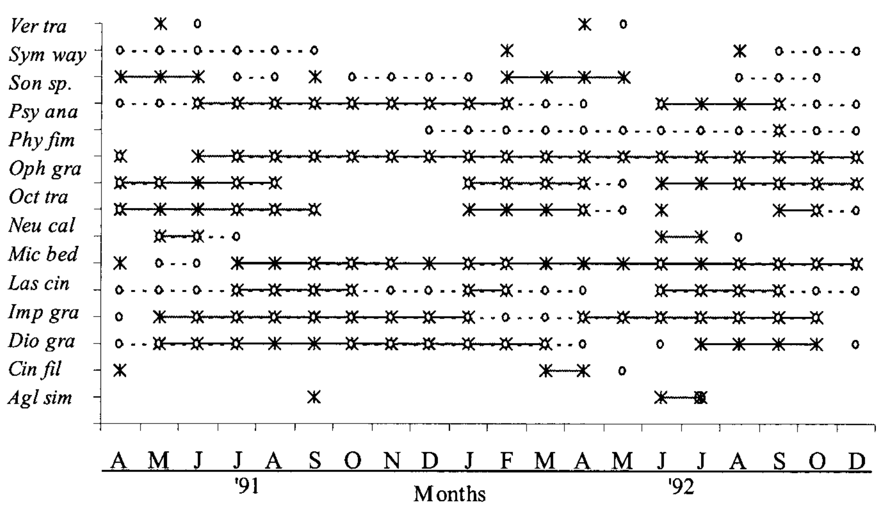

Fig. 1. Flowering (-✳-) and fruiting (--o--) phenology of narrow endemic species
Agl sim = Aglaia simplicifolia, Cin fil = Cinnamomum filipedicellatum, Dio gra = Diotacanthus grandis, Imp gra = Impatiens grandis, Las cin = Lasianthus cinnerus, Mic bed = Micrococca beddomei, Neu cal = Neurocalyx calycinus, Oct tra = Octotropis travancorica, Oph gra = Ophiorrhiza grandiflora, Phy fim = Phyllanthus fimbriatus, Psy ana = Psychotria anamalayana, Son sp. = Sonerila sp., Sym way = Symplocos wayanadense, Ver tra = Vernonia travancorica.

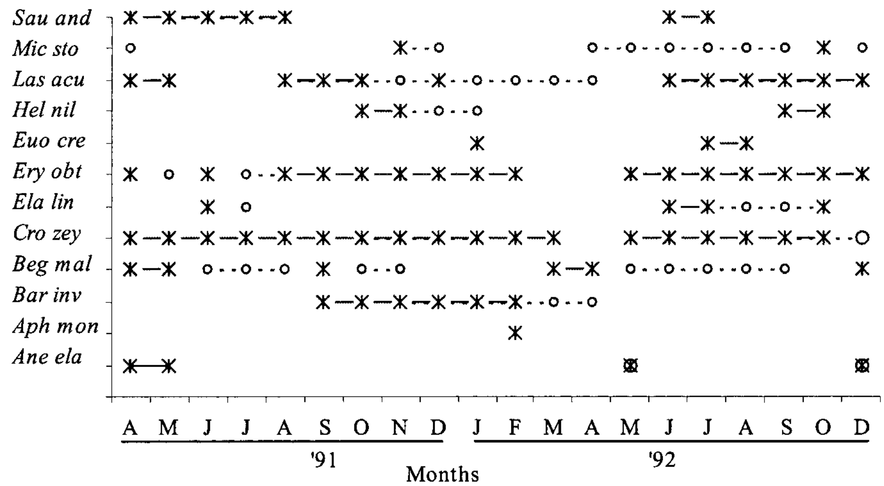

Fig. 2. Flowering (-✳-) and fruiting (--o--) phenology of broad endemic species
Ane ela = Anectochilous elatior, Aph mon = Aphyllorchis montana, Bar inv = Barleria involucrata, Beg mal = Begonia malabarica, Cro zey = Croton zeylanicus, Ela lin = Elatostema lineolatum, Ery obt = Erythroxylum obtusifolium, Euo cre = Euonymus crenulatus, Hel nil = Helicia nilagirica, Las acu = Lasianthus acuminatus, Mic sto = Microtropis stocksii, Sau and = Sauropus androgynus.

was observed in broad and narrow endemic species (N = 12 species, $P > 0.05$; N = 15 species, $P > 0.05$ respectively).

Maximum flowering for the non-endemic species occurred in February 1992 (54%, 18/33) and minimum flowering occurred in November 1991 (15%, 5/33; Fig. 3).

No significant correlation was observed between rainfall and flowering among any endemic groups (r = –0.102, ns, for endemics; r = 0.205, ns for broad endemics, and r = –0.273, ns for narrow endemics). A significant negative correlation was observed with rainfall for the non-endemic species (r = –0.48, df = 19, $P < 0.05$).

Fruiting Phenology

Fruiting was observed in endemic and non-endemic species throughout the year (mean = 3.5 species and 8.4 species, respectively). Maximum fruiting in endemic species was observed in November 1991 and July 1992 (50% species), while lowest fruiting was observed in September 1991 (3.7%, 1/27). A dry season fruiting peak for the endemic species, (N = 27 species, $P < 0.05$) and monsoon fruiting peak among the non-endemic species could be distinguished (N = 33 species, P < 0.001).

For narrow endemics, the highest fruiting was observed during July 1991 and October 1992 (66%, 10/15), and the lowest in July 1992 (33%, 5/15; Fig. 1). Among the broad endemics (Fig. 2), lowest fruiting was observed during September 1991 (8%, 1/12 species), while maximum fruiting was observed in November 1991 and July 1992 (50%). The fruiting peak for the non-endemic species was observed in August 1991 (45%, 15/33), with the lowest in February 1992 (12%, 4/33; Fig. 3).

Species such as *Euonymus crenulatus* (broad endemic) and *Clausena indica* and *Glyptopetalum zeylanicum* (non-endemics) failed to fruit. A very short fruiting season was observed for *Aglaia simplicifolia*, *Cinnamomum fillipedicillatum* (narrow endemics) and *Aphyllochoris montana* (broad endemics).
Average fruiting duration was higher (10.4 months) in the narrow endemics than in broad endemics (5.3 months) and non-endemics (5.3 months; Table 2). The narrow endemic species also had greater fruiting times for fleshy and non-fleshy fruit types as compared to other groups (Table 2). More species in the understorey displayed non-fleshy fruits (53%) than fleshy fruits (46%; D = 0.057, $P < 0.05$, $n_1 = 27$, $n_2 = 33$). Non-endemic and broad endemic species also displayed a greater proportion of non-fleshy fruits (53% and 61%, respectively). The narrow endemic species displayed more fleshy fruits than the broad endemic species (46% and 38%, respectively).

Fruiting patterns for broad and narrow endemic species were found to be uniform (n = 12 species, $P > 0.05$ and n = 15 species, $P > 0.05$, respectively). Rainfall

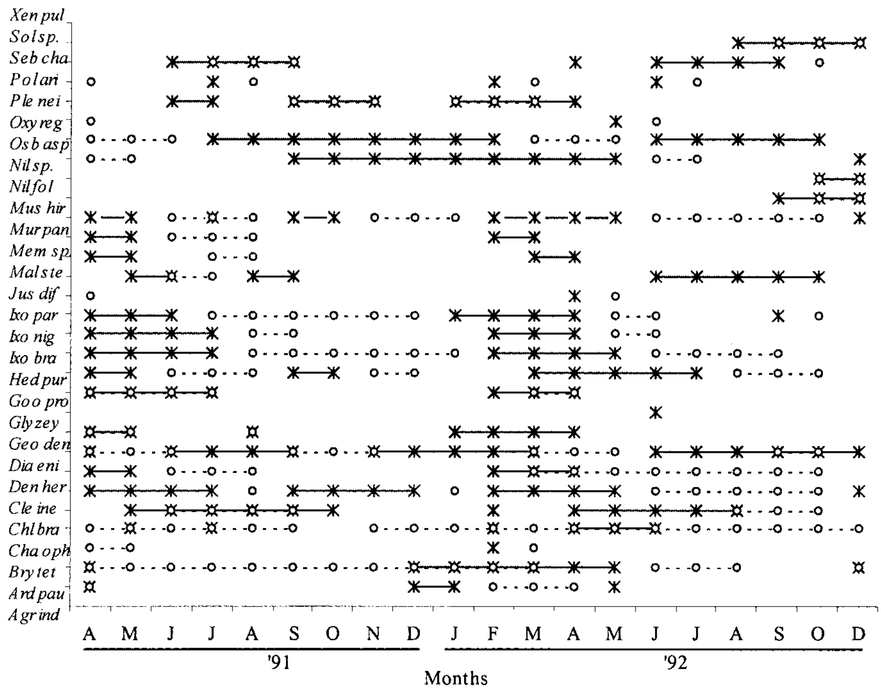

Fig. 3. Flowering (-✳-) and fruiting (--o--) phenology of non-endemic species
Agr ind = Agrostistachys indica, Ard pau = Ardisia pauciflora, Bry tet = Brysophyllum tetrandrum, Cha oph = Chassalia ophioxyloides, Chl bra = Chloranthus brachystachys, Cle ine = Clerodendron inerme, Den her = Dendrobium herbaceum, Dia eni = Dianella enisifolia, Geo den = Geodorum densiflorum, Gly zey = Glyptopetalum zeylanicum, Goo pro = Goodyera procera, Hed pur = Hedyotis purpurascens, Ixo bra = Ixora brachiata, Ixo nig = Ixora nigircans, Ixo par = Ixora parviflora, Jus dif = Justicia diffusa, Mal ste = Mallotus stenanthus, Mem sp. = Memecylon sp., Mur pan = Murraya paniculata, Mus hir = Mussanda hirsutissima, Nil fol = Nilgirianthus foliosus, Nil sp. = Nilgirianthus sp., Osb asp = Osbeckia aspera, Oxy rug = Oxyceros rugulosus, Ple ne i = Plectronia neilgherrensis, Pol ari = Polygala arillata, Seb cha = Sebastiana chamaelea, Sol sp. = Solanum sp, Xen pul = Xenacanthus pulneyensis.

influenced fruiting in the broad endemic species (r = 0.447, df = 19, $P < 0.05$). No significant correlation could be observed for the other groups (r = 0.386 ns, for endemics; r = –0.059, ns, for non-endemics; r = 0.051, ns, for narrow endemics).

Discussion

The relative rate of endemism in evergreen forests of the Western Ghats is higher in understorey shrubs (77%) than in the case of trees (65%) (Krishnan & Davidar 1996, Ramesh 2001). The rate of endemism is comparable to the shrublands of Venenzuelan Guayana, which have quite a high amount of endemic taxa, although endemic genera (30 of the 40) represented in these sites are even higher as compared to Western Ghats (Steyermark 1986).

Table 2. Average fruiting duration (in months) among the understorey groups.

Status	Overall	Fleshy	Non-fleshy
Non-endemic	5.3	8.6	3.9
Narrow endemic*	10.4	9.5	11.1
Broad endemic*	5.3	6.4	4.6

* Derived from endemic.

Ramesh & Pascal (1991) attribute much of the narrow endemism to bioclimatic factors – rainfall, number of dry months and temperature. Based on these factors, it is often concluded that the narrow endemics persist due to the particular microclimates in certain valleys. Additional factors like light levels reaching the forest floor, the density of trees, and the availability of microsites can affect the persistence and survival of species in the understorey conditions. Rabinowitz (1981) observed that for narrow endemic species, competitive abilities are more critical for survival than regulation of abundance.

Microhabitat preferences of narrow endemic species in the investigated community indicate that they are able to persist under challenging understorey conditions, with different mechanisms maintaining diversity and increasing density. Species richness was highest in tree-fall gaps and maximum diversity could be found under low tree density conditions, while under high tree density dominance of certain taxa became more obvious (Krishnan 2001).

Flowers were detectable throughout the year. Despite a low average monthly variation in flower availability in the understorey, the peak flowering periods for endemic and non-endemic species in the community are distinctly different. The average number of endemic species in flower was 11.5, as compared to 9.7 species for the non-endemics. Two flowering peaks were observed for the endemics (dry and post-monsoon season), while dry season flowering was observed for the non-endemics. This is similar to the predominant flowering in the dry season reported also in other seasonal tropical sites (Opler et al. 1980; Booj & Ramakrishnan 1981; Augspurger 1983; Koptur et al. 1988; Sivaraj & Krishnamurthy 1989; Heideman 1989; Lovejoy & Bierregaard 1990; Terborgh 1990; Leigh & Wright 1990; Murali & Sukumar 1994; Bhat & Murali 2001).

The higher frequency of flowering by the endemic species could be due to preference for localized pollinators. Pollinator availability has been considered as a probable reason for differential flowering times in some tropical communities (Stiles 1978, Bawa et al. 1985). Although a number of pollinator groups are observed, the understorey community of the investigated forest is predominately bee-pollinated. The high amount of endemic species pollinated by them contributes towards maintaining a continued flower (and fruit) availability in the understorey throughout the year.

The differences between the broad and narrow endemics are more evident in their dispersal strategies rather than in flowering. Flowering was uniform for both the groups, although narrow endemic species had greater number of species flowering throughout the study period. Like flowers, fruits were also available throughout the year. But there was a segregation of fruiting times in Kakachi sanctuary, leading to a dry season peak of fruit availability by the endemics and a wet season peak for the non-endemic species. Wet season fruiting has been reported also from other tropical sites (Leigh & Wright 1990; Terborgh 1990; Lovejoy & Bierregard 1990).

Within the endemic groups some differences in the fruiting were evident in two aspects: The species-specific fruiting was, to some extent, dependent on rainfall, and the majority of the fruits was non-fleshy. It is probable that, for the broad endemics and the non-endemic species, survival of seeds and seedlings may critically dependent on moisture availability. In general, the narrow endemic species had a longer fruiting duration (10.4 months) and a greater proportion of fleshy fruits. The longer fruiting duration probably brings two kinds of advantages to the narrow endemic species. First, they are able to dominate available microsites throughout the year ensuring greater seed and seedling survival. Second, they can be serviced by local, unspecialised frugivores, such as small birds. This strategy is similar to the situation in the tree strata. Most canopy trees in the community are not highly specialised in their dispersal of diaspores, and they depend on very few vectors for seed dispersal (Ganesh & Davidar 2001).

Thus the narrow and broad endemic species, which have a similar flowering strategy, have different fruiting strategies, while the broad endemic and non-endemic species with different flowering strategies have a similar fruiting strategy. The narrow endemic species seem to be a unique group due to their long fruiting duration, predominance of fleshy fruits, and long fruit retention times of non-fleshy fruits.

The phenological patterns observed for the endemics in Kakachi suggest that the understorey interactions are complex and probably directional. Maximising density in preferred microhabitats, life history constraints and biological attributes all add up to aid in the persistence of many endemic species in the area. Darwin (1859) observed that rarity is inseparably linked with extinction process. Conservation biologists have established that, all else being equal, the rare species are more susceptible to the risk of extinction than widespread taxa (Gaston 1994). For narrow endemics, disturbance directly can affect the survival of the species. Any manipulation of the overstorey cover (such as in thinning operations), or clearing the understorey (if cardamom is planted or cane and other minor forest products are collected) will have a significant negative effect on the survival of the endemic species in the region.

Acknowledgements

This work was made possible due to a JRF research grant No. 6/6/88 from DOEn, Government of India. I would like to acknowledge Dr. Priya Davidar for her guidance and Jayakrishnan Surendran for field assistance. Critical inputs from Dr. J-P. Sutra, Dr. S. Iyer, and two reviewers improved an earlier version of the manuscript.

References

Ahamedullah., M. & Nayar, M. P. (1986): Endemic plants of Indian Region. – Botanical Survey of India, Calcutta.

Appanah, S. (1991): Plant-pollinator interactions in Malaysian Rain Forests. In: Bawa, K. S. & Hadley, M (eds.):

Reproductive ecology of tropical forest plants. Man and Biosphere series. – Parthenon, London, 85–101.
AUGSPURGER, C. K. (1983): Phenology, flowering synchrony, and fruit set of six neotropical shrubs. – Biotropica **15:** 257–267.
BAWA, K.S.; BULLOCK, S. H.; PERRY, D. R.; COVILLE, R. E. & GRAYUM, M. H. (1985): Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. – Am. J. Bot. **72:** 346–356.
BHAT, D. M. & MURALI, K. S. (2001): Phenology of understorey species of tropical moist forest of Western Ghat region of Uttara Kannada district of South India. – Cur. Sci. **81:** 799–805.
BOOJ, R. & RAMAKRISHNAN, P. S. (1981): Phenology of trees in a subtropical evergreen montane forest in north-east India. – Geo-Eco-Trop. **5:** 189–209.
CORLETT, R. T. (1998): Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. – Biol. Rev. Camb. Phil. Soc. **73:** 413–448.
DARWIN, C. (1859): On the origin of species by means of natural selection or The preservation of favoured races in the struggle for life. – John Murray, London.
DEVY, M. S. (1998): Breeding systems in bee-pollinated canopy forests of South Western Ghats, India. In: Forest canopies, Global perspectives. – Marie Selby Botanical Gardens, Florida.
GANESH, T. & DAVIDAR, P. (2001): Dispersal modes of tree species in wet forests of southern Western Ghats. – Cur. Sci. **80:** 394–399.
GANESH, T.; GANESAN, R.; DEVY, M. S.; DAVIDAR, P. & BAWA, K. S. (1996): Assessment of plant biodiversity at a mid-elevation evergreen forest of Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. – Cur. Sci. **71:** 379–392.
GASTON, K. J. (1994): Rarity. Population and community biology series 13. – Chapman & Hall, New York.
GENTRY, A. H. (1992): Tropical forest biodiversity: distributional patterns and their conservational significance. – Oikos **63:** 19–28.
HEIDEMAN, P. D. (1989): Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. – J. Ecol. **77:** 1059–1079.
KOELMEYER, K. O. (1959a): The periodicity of leaf change and flowering in the principal forest communities of Ceylon. Part I. – Ceylon Forester **4:** 157–189.
KOELMEYER, K. O. (1959b): The periodicity of leaf change and fruiting in the principal forest communities of Ceylon. Part II. – Ceylon Forester **4:** 308–364.
KOPTUR, S.; HABER, W. A.; FRANKIE, G. W. & BAKER, H. G. (1988): Phenological studies of shrub and treelet species in tropical cloud forests of Costa Rica. – J. Trop. Ecol. **4:** 323–346.
KRISHNAN, R. M. (1996): Ecology of understorey shrubs in a wet forest of south India. – Ph.D. thesis. Pondicherry University, India.
KRISHNAN, R. M. (2001): Microsites and diversity of understorey shrubs in southern Western Ghats, India. – J. Trop. For. Sci. **13:** 258–269.
KRISHNAN, R. M. (2002): Reproductive phenology of a wet forest understorey in the Western Ghats, south India. – Gl. Ecol. and Biogeogr. **11:** 179–182.
KRISHNAN, R. M. & DAVIDAR, P. (1996): The shrubs of Western Ghats (South India): floristics and status. – J. Biogeogr. **23:** 783–789.
LEIGH, E. G. & WRIGHT, S. J. (1990): Barro Colorado Island and Tropical Biology. In: GENTRY, A. H. (ed.): Four neotropical rainforests. – Yale Univ. Pr., New Haven, CT, 28–47.
LOVEJOY, T. E. & BIERREGAARD, JR., R. O. (1990): Central Amazonian forests and the Minimum Critical Size of Ecosystems Project. In: GENTRY, A. H. (ed.): Four neotropical rainforests. – Yale Univ. Pr., New Haven, CT, 60–74.
MURALI, K. S. & SUKUMAR, R. (1994): Reproductive phenology of a tropical dry forest in Mudumalai, Southern India. – J. Ecol. **82:** 759–767.
NAYAR, N. (1996): Hot spots of endemic plants in India, Nepal and Bhutan. – Tropical Botanic Garden and Research Institute, Kerala, India.
OPLER, P. A.; FRANKIE G. W. & BAKER, H. G. (1980): Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. – J. Ecol. **68:** 167–188.
PUTZ, F. E. (1979): Aseasonality in Malaysian tree phenology. – Malaysian Forester **42:** 1–24.
RABINOWITZ, D. (1981): Seven forms of rarity. In: SYNGE, H (ed.): The biological aspects of rare plant conservation. – Wiley, Chichester, 205–217.
RAMESH, B. R. (2001): Patterns of richness and endemism of arborescent species in the evergreen forests of the Western Ghats, India. In: GANESHAIAH, K. N.; UMA SHANKER, R. & BAWA, K. S. (ed.) Proc. Internat. Conf. on Tropical Ecosystems. – Oxford-IBH, New Delhi, 539–544.
RAMESH, B. R. & PASCAL, J.-P. (1991): Distribution of endemic arborescent evergreen species in the Western Ghats. – Proc. Sympos.on Rare, Endangered and Endemic Species of the Western Ghats, Tiruvananthapuram, India, 1–7.
RAMESH, B. R. & PASCAL, J.-P. (1998): Atlas of endemics of the Western Ghats (India): Distribution of tree species in the evergreen and semi-evergreen forests. – French Institute of Pondicherry.
RAMESH, B. R.; DEFRANCESCHII D. & PASCAL J.-P. (1998): Vegetation map of Tiruvananthapurm-Tirunelveli. – French Institute of Pondicherry and the Forest Department of Karnataka, Kerala and Tamil Nadu, French Institute, Pondicherry.
SAKAI, S.; MOMOSE, K.; YUMOTO, T.; NAGAMITSU, T.; NAGAMASU, H.; HAMID, A. & NAKASHIZUKA, T. (1999): Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. – Am. J. Bot. **86:** 1414–1436.
SIVARAJ, N., & KRISHNAMURTHY, K. V. (1989): Flowering phenology in the vegetation of Shevaroys, Southern India. – Vegetatio **79:** 85–88.
STILES, G. F. (1978): Temporal organization of flowering among the hummingbird foodplants in a tropical forest. – Science **198:** 1177–1178.
STEYERMARK, J. A. (1986): Speciation and endemism in the flora of the Venenzuelan tepuis. In: VUILLEUMIER, F. & MONSASTERIO, M. (eds.): High altitude tropical biogeography. – Oxford Univ. Pr., New York–Oxford, 317–373.

TERBORGH, J. (1990): An overview of research at Cocha Cashu biological station. In: GENTRY, A. H. (ed.): Four neotropical rainforests. – Yale Univ. Pr., New Haven, CT, 48–59.
WHEELWRIGHT, N. T. (1985): Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. – Oikos **44:** 465–477.
WESSELINGH, R. A.; BURGERS, H. C. M. & DEN NIJS, J. C. M. (2000): Bumblebee pollination of understorey shrub species in a tropical montane forest in Costa Rica. – J. Trop. Ecol. **16:** 657–672.
YAP, S. K. (1982): The phenology of some fruit tree species in a lowland dipeterocarp forest. – Tree Physiol. **45:** 21–35.

Appendix

The reproductive traits of the understorey species in Kakachi
Habit: H = herb, S = Shrub, ST = Small tree, O = orchid
Fruit nature: F = fleshy, NF = non-fleshy
Status: B = Broad endemics, N = Narrow endemics, n = non-endemics

Species	N	Habit	Fruit nature	Flowering duration (mo)	Fruiting duration (mo)	Status
Acanthaceae						
Barleria involucrata var. elata Nees.	30	*S*	NF	6	6	B
Diotacanthus grandis (Bedd.) Benth. ex Clarke	70	*S*	NF	15	13	N
Justicia diffusa Willd.	30	*H*	NF	1	2	n
Nilgirianthus foliosus (Wight) Bremek.	25	*S*	NF	3	2	n
Nilgirianthus perrottetianus (Nees) Bremek.	20	*S*	NF	0	0	n
Nilgirianthus sp.	5	*S*	NF	2	2	n
Strobilanthus sp. 4	20	*S*	NF	0	0	n
Strobilanthus sp. 5	20	*S*	NF	0	0	n
Xenacanthus pulneyensis (Clarke) Bremek.	10	*S*	NF	4	3	n
Balsamaceae						
Impatiens grandis Heyne	10	*H*	NF	16	18	N
Begoniaceae						
Begonia malabarica Lam.	6	*H*	NF	6	10	B
Celastraceae						
Euonymus crenulatus Wall. ex W. & A.	70	*S*	F	3	0	B
Glyptopetalum zeylanicum Thw.	4	*S*	NF	1	0	n
Microtropis stocksii Gamble	35	*S*	F	2	10	B
Chloranthaceae						
Chloranthus brachystachys BI.	15	*S*	F	12	7	n
Compositae						
Vernonia travancorica	4	*St*	NF	2	2	N
Erythroxylaceae						
Erythroxylum obtusifolium (Wt.) J. Hk.	10	*S*	F	16	4	B
Euphorbiaceae						
Agrostistachys indica Dalz.	70	*S*	NF	4	4	n
Croton zeylanicus M. Arg.	13	*S*	NF	18	8	B
Mallotus stenanthus M. Arg.	25	*S*	NF	9	2	n
Micrococca beddomei (H. f.) Prain	35	*S*	NF	18	12	N
Phyllanthus fimbriatus (Wight) Muell.-Arg.	70	*S*	NF	19	18	N
Sauropus androgynus Merr.	10	*H*	NF	7	5	B
Sebastiana chamaelea Muell.	8	*H*	NF	3	4	
Lauraceae						
Cinnamomum filipedicellatum Kosterm.	5	*St*	F	3	1	N

Liliaceae						
Dianella enisifolia Red.	10	*H*	F	16	11	n
Melastomataceae						
Memecylon sp.	10	*S*	F	4	2	n
Osbeckia aspera (L.) Blume	15	*S*	NF	10	4	n
Meliaceae						
Aglaia simplicifolia (bedd.) Harms	8	*St*	F	3	1	N
Myrsinaceae						
Ardisia pauciflora Heyne ex. Roxb.	70	*S*	F	8	16	n
Orchidaceae						
Anectochilous elatior Lindl.	15	*O*	NF	4	2	B
Aphyllorchis montana Reichb.	5	*O*	NF	1	1	B
Dendrobium herbaceum Lindl.	10	*O*	NF	5	11	n
Geodorum densiflorum Schlechter.	10	*O*	NF	7	3	n
Goodyera procera Hook.	25	*O*	NF	7	6	n
Polygalaceae						
Polygala arillata Ham.	20	*S*	NF	9	6	n
Proteaceae						
Helicia nilagirica Bedd.	5	*St*	F	4	3	B
Rubiaceae						
Brysophyllum tetrandrum H. f.	3	*S*	F	1	3	n
Chassalia ophioxyloides (Wall.ex Kurz.) Thw.	35	*S*	F	6	19	n
Hedyotis purpurascens H. f.	10	*S*	NF	9	8	n
Ixora brachiata Roxb.	6	*St*	F	8	10	n
Ixora nigircans W. & A.	3	*S*	F	7	4	n
Ixora parviflora Vahl.	5	*S*	F	8	9	n
Lasianthus acuminatus Wt.	8	*S*	F	12	15	B
Lasianthus cinnerus Gamble	62	*S*	F	10	19	N
Mussanda hirsutissima (H. f.) Hutchinson ex Gamble	8	*S*	F	10	11	n
Neurocalyx calycinus (R. Br.ex Benn.) Robins	10	*H*	NF	4	4	N
Octotropis travancorica Bedd.	10	*St*	F	13	8	N
Ophiorrhiza grandiflora Wight.	10	*H*	NF	15	13	N
Oxyceros rugulosus (Thw.) Tiruvengadum	10	*S*	F	13	6	n
Plectronia neilgherrensis Bedd.	5	*H*	NF	1	2	n
Psychotria anamalayana Bedd.	70	*S*	F	1	12	N
Saprosma corymbosa (Bedd.) Bedd.	70	*S*	F	13	17	N
Rutaceae						
Clausena indica (Dalz.) Oliver	10	*S*	F	0	0	n
Murraya paniculata (L.) Jack	6	*S*	F	4	3	n
Solonaceae						
Solanum sp.	10	*H*	F	9	4	n
Sonalariaceae						
Sonerila sp.	5	*H*	NF	8	9	N
Symplocaceae						
Symplocos wayanadense (Kuntze) Nooteb.	70	*S*	F	2	9	N
Urticaceae						
Elatostema lineolatum var.linearis Wight.	10	*H*	NF	4	5	B
Verbenaceae						
Clerodendron inerme Gaertn.	10	*S*	F	13	7	n