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# Rain forest expansion mediated by successional processes in vegetation thickets in the Western Ghats of India

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## Abstract

**Aim** The objective of this study was to document succession from grassland thickets to rain forest, and to provide evidence for their potential as restoration tools.

**Location** The Linganamakki region (State of Karnataka) of the Central Western Ghats of India.

**Method** We selected thirty vegetation thickets ranging from 4 to 439 $m^2$ in area in the vicinity of rain forest. The area of each small thicket was estimated as an oval using its maximum length and its maximum width. When the shape was irregular (mostly in large thickets) the limits of the thicket were mapped and the area calculated from the map. Plant species were identified, the number of individuals was estimated and their heights measured.

**Results** There was a progression in the thickets from early to late successional species. Small thickets were characterized by ecotone species and savanna trees such as *Catunaregam dumetorum*. Savanna trees served as a nucleus for thicket formation. Colonizing species were mostly bird-dispersed. As succession proceeded in larger thickets, the proportion of evergreen, late-successional rain forest trees increased. The species composition of the large thickets differed depending on the species composition of reproductive adults in the nearby forested areas. The species within small thickets were also found in the large thickets. The nestedness in species composition suggested that species turnover was deterministic based on thicket size. Human disturbance (leaf and wood collection by the local populations) affected the species composition and the species–area relationship of thickets.

**Main conclusions** Vegetation thickets are nodal centres for rain forest colonization within grasslands. They expand and replace savanna. Early successional bird-dispersed species established around savanna trees followed by late-successional rain forest trees dispersed from the nearby forest by birds. Restoration programmes that reproduce natural successional processes such as those observed in thickets will be more successful and less expensive than the methods currently being employed, where trees are individually planted in grassland. Wood harvesting is the only factor that prevents thicket growth and coalescence and hampers forest expansion.

**Keywords**
Rainforest, disturbance, succession, India, thickets, nestedness.

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## INTRODUCTION

The rain forest of the Western Ghats of India is a major element of the Biodiversity Hotspot of Southern India and Sri Lanka. It contains 63% of endemic trees (Ramesh *et al.*, 1993), and endangered animal species including the tiger. Despite an extensive network of national parks and a positive annual rate of forest change (that includes tree plantations) of 0.06% year$^{-1}$ between 1990 and 2000 (FAO, 2001), the rain forest continues to be fragmented (Ramesh *et al.*, 1997; Narendra Prasad, 1998), because of the multiple services it renders to the local populations (Gadgil & Guha, 1992; Puyravaud & Garrigues, 2002). In order to increase the tree cover in abandoned pastures, fast-growing exotic tree species are usually planted. Forest restoration could be a valuable alternative that would conserve soils, water, and biodiversity, and reconnect fragmented ecosystems. However, rain forest successional processes within grasslands have not been studied in India as much as in some other areas of the tropics (Holl & Kappelle, 1999). This paper examines vegetation thickets as a potential model for rain forest restoration.

In the Western Ghats of India, vegetation thickets occur commonly in the area climatically suitable for rain forest, where they form a transition zone with grasslands (highly cattle-grazed pastures in the plains and savannas on steep slopes). Thickets have not received much attention (Pascal, 1988) probably because they represent an intermediate vegetation type, neither forest nor grassland. Vegetation thickets can locally be formed by anthropogenic fragmentation of the rain forest, or by forest succession in the grasslands (Pascal, 1988). If thickets are a result of succession, we should observe regeneration of forest species within them and successional patterns such as changes in species composition with increasing thicket area, at least when thickets are undisturbed.

Thickets can be defined as shrubby, evergreen or deciduous vegetation, often in clumps with an absent or discontinuous grass layer. They are found in a great diversity of environments world-wide, close to rain forest and in drier habitats (see references in Bourlières, 1983). They occur all over the tropics from South America to Australia. When the soil is poor in nutrients, plants or animals can contribute to the formation of an oasis that is relatively richer in nutrients, favouring the formations of thickets (Abbadie *et al.*, 1992; Ehleringer *et al.*, 1992). Single species such as *Prosopis glandulosa* Torr.[1], facilitate the establishment of woodland tree species in Texan savannas, through the formation of clumps (Archer, 1990). Savanna trees change the microclimate and provide nutrients to forest seedlings (Kellman & Miyanishi, 1982). On fertile soils, thickets are the result of a disturbance, such as fire (Scanlan & Archer, 1991) or grazing (Barrow, 1991). Overgrazing by domestic livestock reduces grass cover, thereby decreasing both fire intensity and frequency. Unpalatable, spiny or difficult-to-graze plants tend to survive and invade, resulting in patches of vegetation (Barrow, 1991).

Sacred groves, forest plots kept for religious purposes, have received considerable attention in India (Gadgil & Vartak, 1974; Ramakrishnan, 1996). They have been used as examples to argue for the sustainability of traditional biodiversity use in India (Gadgil & Guha, 1992), although the basis for this argument has been disputed (Freeman, 1999). Rain forest thickets have not been the focus of such ideological disputes nor have their species composition, biodiversity patterns, or succession been described in detail. For policy reasons they are considered to be part of wastelands and therefore amenable to land-use practices that usually result in their destruction.

In the Linganamakki region of the Western Ghats (as defined in Sinha, 1998; Garrigues & Puyravaud, 1999), thickets reach 1200 ha in total area and form 1.7% of the vegetation cover. Thickets are of great importance to villagers because they provide non-timber forest products (NTFPs) such as fruits, fire-wood, cattle fodder and green manure (Puyravaud & Garrigues, 2002). Managers consider thickets to be part of the grassland, even when they fall within the limits of a reserved forest devoid of continuous forest cover. Harvesting of NTFP in thickets is tolerated more than it is in the forest.

From 1985 onwards, the Karnataka Forest Development Project (KFDP) established exotic mono-culture tree plantations (mostly *Acacia auriculiformis* A. Cunn. Ex Benth.) in the Linganamakki region. The project had three objectives: wood production for the paper industry, restoration of degraded land and social forestry. Savanna-like vegetation and thickets were partly replaced by *A. auriculiformis* plantations.

The sociological and ecological consequences of plantations in the Linganamakki region are not necessarily positive. Cattle are not allowed into young plantations and fodder cannot be obtained from older ones. To compensate for loss of their grazing lands, the farmers collect NTFP more intensively within nearby rain forest, destroying the ecotone and opening up new grazing areas. The cash benefit accrued to farmers through these plantations is minimal. Basu *et al.* (1996) have also shown that earthworm communities are less diverse under plantations of *A. auriculiformis* than under grassland, which is considered the ultimate stage in the degradation of the rain forest (Pascal, 1988; Garrigues, 1999).

The thicket structure displays a complexity that is strikingly higher than that of the multi-species tree plantations that are established for land restoration. Because thickets persist in a highly disturbed environment, it would be useful to know whether their species composition and structure could provide guidelines for rain forest conservation and restoration. The objective of this paper is (1) to describe successional patterns within thickets bordering the rain forest in the Central Western Ghats, (2) to analyse forest dynamics in this region, and (3) to provide new insights into strategies for local rain forest restoration.

[1]Species without author names appear in Table 1.

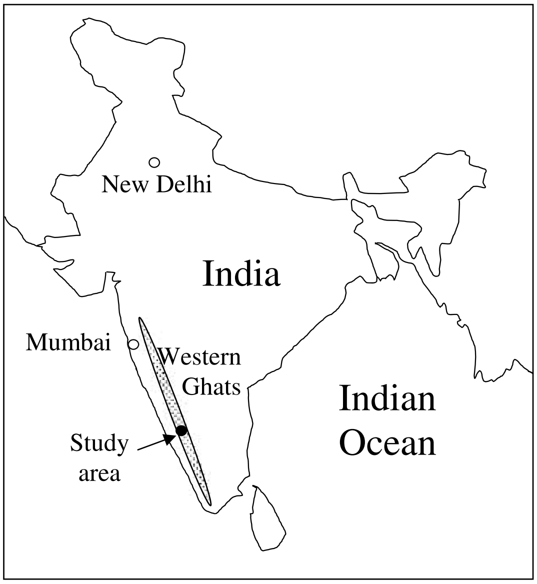


**Figure 1** Map of the study area.

## STUDY AREA

The study was carried out in south-west India (Fig. 1), between the crest of the Western Ghats and the Linganamakki reservoir (14°00′ N, 74°45′ E). This area, is a humid and hilly region of Karnataka State (Shimoga District). Its elevation varies between 550 and 1100 m. The climate is tropical with a rainy season from May to September as a result of the south-west monsoon, and with a dry season from October to May. Mean annual rainfall is 5000 mm on the crest of the Ghats and decreases eastward to 3000 mm. Mean annual temperature ranges between 16 and 23 °C according to elevation (Pascal, 1988). The bed-rock is composed of Greywacke and covered by weakly or moderately desaturated ferrallitic soils (Bourgeon, 1989).

The forests, which occupy the valleys, are sometimes degraded and derive from the *Dipterocarpus indicus* – *Diospyros candolleana* – *D. oocarpa* type (Pascal, 1988). Savannas in this area are structurally and floristically homogeneous and are composed of a continuous grass layer interspersed with deciduous trees rarely exceeding 5–6 m in height. They occur on steep slopes. The grazing lands of the plains are a mosaic of isolated and degraded patches of forest and thickets. The grass layer is thin, with abundant annual Poaceae (Breton, 1994). Because of human exploitation, grazing lands have replaced much forest and savanna (Mariotti & Peterschmitt, 1994; Puyravaud *et al.*, 1994).

Clumps of thickets in grassland along the limit of the lowland dipterocarp rain forest were chosen for the study. The thickets were lessthan 5 km apart and less than 500 m from the edge of the rain forest. Thickets formed by successional processes can be distinguished from those formed by recent rain forest fragmentation by the presence of tall remnant trees in the latter. No recent forest fragment was detected during this study.

Thickets have been opened up by local villagers to gain access for gathering wood and other products. Villagers exploit vegetation that is as close as possible to their settlement and productive enough to enhance harvest efficiency (Garrigues, 1999; Puyravaud & Garrigues, 2002). This pattern follows the adjacency principle according to which people have a tendency to exploit areas next to their already developed land. Therefore, clumps of several thickets are exploited if they satisfy these requirements or not exploited until they satisfy the requirements for efficient harvest. As a consequence, it is impossible to find thickets near others that are intact. Thickets were therefore lumped into two categories: 'undisturbed thickets' with no or little evidence of recent wood cutting, and 'disturbed' thickets were those obviously harvested.

## METHODS

### Thicket characteristics

The area of each small thicket was estimated as an oval using its maximum length and its maximum width when they had a regular shape. When the shape of the thicket was irregular, as is often happens with larger thickets, the limits of the thicket were mapped on tracing paper and the area calculated from the map. In each thicket, all woody plants above 10 cm in height were identified using the Flora of Karnataka (Saldanha, 1984), recorded, and their height measured. Most authors estimating $\alpha$-diversity, sample trees above 10 cm diameter at breast height (DBH). This size limit is usually chosen because trees are easier to identify. However, the flora of the Western Ghats is well described and most species were known to us from the seedling stage onward. Moreover, as shown by Condit *et al.* (1998), for a given number of plant individuals, the number of species is nearly independent of the minimum size of trees sampled. As thickets may contain a few plants, it was important to decrease the size of plants sampled as much as possible in order to increase the number of individuals and life-forms taken into consideration. Because of their low densities, epiphytes or parasitic shrubs such as *Dendrophthoe* sp. (*Loranthaceae*) were not included in the analysis. All non-climbers were classified into four life-form categories according to the maximum height they can reach under optimal conditions (Table 1): large trees (>25 m), trees (between 8 and 25 m), shrubs (<8 m) and sub-shrubs (lignified herbs). The climbing shrubs, stragglers, twiners, etc. are noted in Table 1, and were simply called climbers. A literature survey (Gamble, 1935; Matthew, 1983; Saldanha, 1984; Pascal, 1988) helped to identify the ecosystems of origin for the different species (Table 1). Late-successional rain forest species were taken from Pascal (1988). The evergreen and semi-evergreen rain forests trees endemic to the Western Ghats have been noted using Ramesh & Pascal (1997). None of the species identified have appeared in the Red Data Book of Indian Plants (Nayar & Sastry, 1990).

The dispersal mode was determined from Ganesh & Davidar (2001), Davidar (unpubl. data) and from literature

**Table 1** Species characteristics

| Species | Family | Life form | Ecosystem EV | SE | MD | DF | SA | Endemic tree | Leaf habit | Spines | Dispersal agent |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Actinodaphne malabarica* Balak | Lauraceae | Tree | * | | | | | X | E | No | Birds |
| *Aglaia barberi* Gamble | Meliaceae | Tree | | X | | | | X | E | No | Monkeys, squirrels |
| *Allophylus serratus* (Roxb.) Kurz | Sapindaceae | Shrub | X | X | X | X | | | E | No | Birds, mammals |
| *Anamirta cocculus* (L.) Wt. & Arn. | Menispermaceae | Liana | | | X | X | | | E | No | Animal |
| *Aporusa lindleyana* (Wt.) Baill. | Euphorbiaceae | Tree | X | X | | | | | E | No | Birds |
| *Archidendron monadelphum* (Roxb.) Nielsen | Fabaceae | Tree | X | | | | | | E | No | Mechanical |
| *Ardisia solanacea* Roxb. | Myrsinaceae | Shrub | X | | | | | | E | No | Birds |
| *Artabotrys zeylanicus* Hook. & Thoms. | Annonaceae | Liana | * | | | | | | E | No | Birds |
| *Artocarpus hirsutus* Lam. | Moraceae | Large tree | * | | | | | X | E | No | Monkeys |
| Asclepiadaceae sp. | Asclepiadaceae | – | – | – | – | – | – | | – | – | – |
| *Asparagus racemosus* Willd. | Liliaceae | Twiner | | X | X | X | | | Cladodes | Spines | Birds |
| *Atalantia wightii* Tanaka | Rutaceae | Tree | * | | | | | | E | Thorns | Animal |
| *Breynia vitis-idaea* (Burm.f.) Fisch. | Euphorbiaceae | Tree | | | | X | | | D | No | Birds |
| *Bridelia crenulata* Roxb. | Euphorbiaceae | Tree | | | | X | | | D | No | Birds |
| *Bridelia scandens* Willd. | Euphorbiaceae | Liana | | | | X | | | D | Thorns | Birds |
| *Butea monosperma* (Lam.) Taub. | Fabaceae | Tree | | | | X | X | | D | No | Mechanical |
| *Calamus gamblei* Becc. | Arecaceae | Liana | X | | | | | | E | Spines | Mammals |
| *Callicarpa tomentosa* (L.) Murr. | Verbenaceae | Tree | X | | | | | | E | No | Birds |
| *Canthium angustifolium* Roxb. | Rubiaceae | Liana | * | | | | | | E | Thorns | Birds |
| *Canthium dicoccum* (Gaertn.) Merr. | Rubiaceae | Tree | * | X | X | X | X | | E | No | Birds |
| *Carallia brachiata* (Lour.) Merr. | Rhizophoraceae | Tree | X | X | | | | | E | No | Birds |
| *Careya arborea* Roxb. | Lecythidaceae | Tree | | | | X | | | D | No | Mammals |
| *Casearia bourdillonii* Mukher | Flacourtiaceae | Tree | X | | | | | | E | No | Birds |
| *Casearia ovata* (Lam.) Willd. | Flacourtiaceae | Tree | * | | | | | | E | No | Birds |
| *Cassine glauca* (Rottb.) Kuntze | Celastraceae | Large tree | X | X | | | | | E | No | Birds |
| *Catunaregam dumetorum* (Retz) Tirvengadam | Rubiaceae | Shrub | | | | X | | | D | Spines | Birds |
| *Cayratia japonica* (Thunb.) Gagn. | Vitaceae | Slender climber | X | | | | | | E | No | Birds |
| *Celastrus paniculatus* Willd. | Celastraceae | Liana | | | | X | | | E | No | Birds |
| *Celtis philippensis* Blanco | Ulmaceae | Tree | X | | | | | | E | No | Birds |
| *Ceropegia elegans* Wall. | Asclepiadaceae | Twiner | | | | | | | E | No | Wind |
| *Chionanthus mala-elengi* (Dennst.) P.S.Green | Oleaceae | Tree | X | X | X | X | | | E | No | Birds |
| *Cinnamomum malabathrum* (Burman) Blume | Lauraceae | Tree | * | X | | | | X | E | No | Birds |
| *Cipadessa baccifera* (Roth) Miq. | Meliaceae | Shrub | | X | X | | | | D | No | Monkeys |
| *Cissus heyneana* (Wight & Arn.) Planchon | Vitaceae | Fleshy climber | | | | X | X | | E | No | Birds |
| *Clausena indica* Oliv. | Rutaceae | Shrub | * | X | | | | | E | No | Animal |
| *Clerodendrum serratum* (L.) Moon. | Verbenaceae | Shrub | | | | X | X | | E | No | Birds |
| *Clerodendrum* sp. | Verbenaceae | – | – | – | – | – | – | | – | – | – |
| *Clerodendrum viscosum* Vent. | Verbenaceae | Shrub | X | X | X | | | | E | No | Birds |
| *Connarus wightii* Hook. f. | Connaraceae | Liana | * | | | | | | E | No | Birds |
| Convolvulaceae sp. | Convolvulaceae | – | – | – | – | – | – | | – | – | – |
| *Corchorus* sp. | Tiliaceae | – | – | – | – | – | – | | – | – | – |
| *Desmodium* sp. | Fabaceae | Subshrub | – | – | – | – | – | | – | – | Mechanical |
| *Desmodium triangulare* (Retz.) Merr. | Fabaceae | Subshrub | | | | X | | | D | No | Mechanical |
| *Desmodium triquetrum* (L.) DC. | Fabaceae | Subshrub | | | | X | | | D | – | Mechanical |
| *Dichapetalum gelonioides* Engl. | Dichapetalaceae | Shrub | * | X | | | | | E | No | Birds |
| *Dillenia pentagyna* Roxb. | Dilleniaceae | Tree | | | X | X | | | D | No | Monkeys |

**Table 1** *continued*

| Species | Family | Life form | Ecosystem EV | SE | MD | DF | SA | Endemic tree | Leaf habit | Spines | Dispersal agent |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dimocarpus longan* Lour. | Sapindaceae | Tree | * | | | | | | E | No | Monkeys, squirrels |
| *Dioscorea* sp. | Dioscoreaceae | Vine | – | – | – | – | – | | – | – | – |
| *Diospyros angustifolia* (Miq.) Kosterm. | Ebenaceae | Tree | X | | | | | X | E | No | Civets |
| *Diospyros montana* Roxb. | Ebenaceae | Tree | | X | X | X | | | E | Eventual | Birds, civets |
| *Diospyros paniculata* Dalz. | Ebenaceae | Tree | * | | | | | X | E | No | Civets |
| *Diploclisia glaucescens* (Blume) Diels | Menispermaceae | Liana | * | | | | | | E | No | Animal |
| *Elaeagnus kologa* Schldl. | Elaeagnaceae | Liana | X | X | | | | | E | Thorns | Birds |
| *Elaeocarpus serratus* L. | Elaeocarpaceae | Tree | * | | | | | | E | No | Monkeys |
| *Emblica officinalis* Gaertn. | Euphorbiaceae | Shrub | | | | X | X | | D | No | Mammals |
| *Eugenia macrosepala* Duthie | Myrtaceae | Shrub | * | | | | | X | E | No | Birds |
| *Eugenia thwaitesii* Duthie | Myrtaceae | Shrub | X | | | | | | E | No | Birds |
| *Euodia lunu-ankenda* (Gaertn.) Merr. | Rutaceae | Shrub | X | | | | | | E | No | Birds |
| *Ficus religiosa* L. | Moraceae | Tree | | | | | | | D | No | Birds, bats |
| *Ficus tsjahela* Burman | Moraceae | Tree | | X | X | X | | | D | No | Birds, mammals |
| *Flacourtia indica* (Burman) Merr. | Flacourtiaceae | Shrub | | X | X | X | | | E | Spines | Birds |
| *Flacourtia montana* Grah. | Flacourtiaceae | Tree | * | X | | | | X | E | Thorns | Birds |
| *Flemingia macrophylla* (Willd.) Prain ex Merr. | Fabaceae | Shrub | | | X | X | X | | – | – | Mechanical |
| *Garcinia indica* (Thouars) Choisy | Clusiaceae | Tree | * | | | | | X | E | No | Mammals |
| *Garcinia morella* (Gaertner) Desr. | Clusiaceae | Tree | * | X | X | | | | E | No | Mammals |
| *Glochidion malabaricum* Bedd. | Euphorbiaceae | Tree | X | | | | | X | E | No | Mechanical |
| *Glochidion velutinum* Wt. | Euphorbiaceae | Shrub | | | | | X | | D | No | Mechanical |
| *Glycosmis macrocarpa* Wight | Rutaceae | Shrub | X | X | | | | | E | No | Mammals |
| *Gnidia glauca* (Fres.) Gilg. | Thymelaeaceae | Shrub | | | | | X | | D | No | Mechanical |
| *Grewia* sp. | Tiliaceae | Climber | – | – | – | – | – | | – | – | – |
| *Grewia tiliifolia* Vahl. | Tiliaceae | Tree | | X | X | X | | | D | No | Animal |
| *Helicteres isora* L. | Sterculiaceae | Shrub | | X | X | X | | | D | No | Mechanical |
| *Hemidesmus indicus* (L.) R. Br. | Asclepiadaceae | Twiner | | | | | X | | E | No | Wind |
| *Hibiscus aculeatus* Roxb. | Malvaceae | Climber | | X | X | X | | | E | Prickles | Mechanical |
| *Holigarna arnottiana* Hook f. | Anacardiaceae | Large tree | * | | | | | X | E | No | Mammals |
| *Holigarna grahamii* (Wt.) Kurz | Anacardiaceae | Large tree | * | | | | | X | E | No | Mammals |
| *Hopea ponga* (Dennst.) Mabberly | Dipterocarpaceae | Large tree | * | | | | | X | E | No | Wind |
| *Ixora brachiata* Roxb. ex DC. | Rubiaceae | Shrub | * | X | | | | X | E | No | Birds |
| *Ixora nigricans* R. Br. ex Wt. & Arn. | Rubiaceae | Shrub | * | | | | | | E | No | Birds |
| *Jasminum cordifolium* Wall. ex G. Don. | Oleaceae | Liana | | | | X | | | E | No | Birds |
| *Jasminum* sp. | Oleaceae | Liana | – | – | – | – | – | | – | – | Birds |
| *Knema attenuata* (Hook & Thoms.) Warb. | Myristicaceae | Tree | * | | | | | X | E | No | Birds |
| *Kydia calycina* Roxb. | Malvaceae | Tree | | | | X | | | D | No | Mechanical |
| *Lagerstroemia microcarpa* Wt. | Lythraceae | Tree | | | | X | | | D | No | Wind |
| *Leea indica* (Burm. f.) Merr. | Leeaceae | Shrub | X | | | | | | E | No | Birds |
| *Ligustrum perrottetii* DC. | Oleaceae | Tree | X | X | X | X | | | E | No | Birds |
| *Litsea deccanensis* Gamble | Lauraceae | Shrub | * | | | | | | E | No | Birds |
| *Litsea floribunda* (Blume) Gamble | Lauraceae | Tree | X | | | | | X | E | No | Birds |
| *Macaranga peltata* (Roxb.) Muell. | Euphorbiaceae | Tree | X | | | | | | E | No | Birds, mammals |
| *Madhuca neriifolia* (Moon) Lam. | Sapotaceae | Tree | * | | | | | | E | No | Bats |
| *Mallotus philippensis* (Lam.) Mueller | Euphorbiaceae | Tree | X | X | | | | | E | No | Birds |
| *Mangifera indica* L. | Anacardiaceae | Tree | * | | | | | | E | No | Mammals |
| *Maytenus rothiana* (Walp.) Ramam. | Celastraceae | Shrub | * | X | X | X | | X | E | Spinescent | Birds |
| *Memecylon malabaricum* (Clarke) Cogn. | Melastomataceae | Shrub | X | | | | | X | E | No | Birds |

**Table 1** *continued*

| Species | Family | Life form | Ecosystem EV | SE | MD | DF | SA | Endemic tree | Leaf habit | Spines | Dispersal agent |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Memecylon talbotianum* Brandis | Melastomataceae | Tree | * | | | | | X | E | No | Birds |
| *Memecylon umbellatum* N. Burman | Melastomataceae | Tree | * | X | | | | | E | No | Birds |
| *Mezoneuron cucullatum* (Roxb.) Wt. & Arn. | Fabaceae | Liana | X | X | | | | | E | Prickles | Mechanical |
| *Microcos paniculata* L. | Tiliaceae | Shrub | | X | X | X | | | E | No | Mechanical |
| *Mimusops elengi* L. | Sapotaceae | Large tree | * | | | | | | E | No | Bats |
| *Neolitsea cassia* (L.) Kosterm. | Lauraceae | Tree | * | | | | | | E | No | Birds |
| *Nothapodytes nimmoniana* (J. Grah.) D.J. Mabberly | Icacinaceae | Tree | * | | | | | | E | No | Birds, bats |
| *Nothopegia racemosa* (Dalz.) Ramam. | Anacardiaceae | Tree | * | | | | | | E | No | Squirrels, birds |
| *Olea dioica* Roxb. | Oleaceae | Tree | X | X | | | | | E | No | Birds, mammals |
| *Osbeckia aspera* (L.) Blume | Melastomataceae | Shrub | | | | | X | | E | No | Mechanical |
| *Osyris quadripartita* Salzm. ex Decne. | Santalaceae | Shrub | | | | X | X | | E | No | Birds |
| *Pavetta indica* L. | Rubiaceae | Shrub | X | | | | | | E | No | Birds |
| *Pavetta tomentosa* Roxb. ex Smith | Rubiaceae | Subshrub | | | X | X | | | D | No | Birds |
| *Persea macrantha* (Nees) Kosterm. | Lauraceae | Tree | * | | | | | | E | No | Birds |
| *Phoenix humilis* Royle | Arecaceae | Shrub | | | | | X | | E | No | Birds |
| *Piper hymenophyllum* Miq. | Piperaceae | Vine | X | | | | | | E | No | Birds |
| *Pittosporum dasycaulon* Miq. | Pittosporaceae | Tree | X | | | | | X | E | No | Birds |
| *Pothos scandens* L. | Araceae | Twiner | * | | | | | | E | No | Birds |
| *Psychotria nigra* (Gaertn.) Alston | Rubiaceae | Shrub | X | | | | | X | E | No | Birds |
| *Pterospermum diversifolium* Blume | Sterculiaceae | Tree | X | | | | | | E | No | Mechanical |
| *Sarcostigma kleinii* Wight & Arn. | Icacinaceae | Liana | X | X | | | | | E | No | Animal |
| *Schefflera venulosa* (Wt. & Arns) Harms | Araliaceae | Liana | * | | | | | | E | No | Birds, monkeys |
| *Securinega leucopyrus* (Willd.) Mueller | Euphorbiaceae | Shrub | | X | | | | | D | Sharp branchlets | Birds, mammals |
| *Smilax perfoliata* Lour. | Smilacaceae | Liana | X | X | X | X | | | E | Prickles | Birds |
| *Smilax* sp. | Smilacaceae | Vine | – | – | – | – | – | | – | – | – |
| *Smilax zeylanica* L. | Smilacaceae | Liana | X | X | X | X | | | E | Armed | Birds |
| *Solanum* sp. | Solanaceae | – | – | – | – | – | – | | – | – | – |
| *Stephania japonica* (Thunb.) Miers | Menispermaceae | Twiner | | | | X | | | E | No | Animal |
| *Sterculia guttata* Roxb. | Sterculiaceae | Tree | | X | X | X | | | D | No | Mechanical |
| *Symplocos racemosa* Roxb. | Symplocaceae | Tree | * | | | | | | E | No | Birds |
| *Syzygium cumini* (L.) Skeels | Myrtaceae | Tree | * | X | | | | | E | No | Birds |
| *Syzygium montanum* Gamble | Myrtaceae | Tree | X | X | | | | | E | No | Birds |
| *Tabernaemontana heyneana* Wall. | Apocynaceae | Tree | X | X | X | X | | | D | No | Birds |
| *Tamilnadia uliginosa* (Retz.) Tir. & Sastre | Rubiaceae | Shrub | | | | X | X | | D | Thorns | Birds |
| *Terminalia alata* Heyne ex Roth. | Combretaceae | Tree | | | | X | | | D | No | Wind |
| *Terminalia bellirica* (Gaertn.) Roxb. | Combretaceae | Tree | | X | X | X | | | D | No | Wind |
| *Terminalia chebula* (Gaertn.) Retz. | Combretaceae | Tree | | | | X | | | D | No | Wind |
| *Terminalia paniculata* Roth. | Combretaceae | Tree | | | | X | | | D | No | Wind |
| *Tetrastigma* sp. | Vitaceae | Vine | | X | | | | | – | – | Birds |
| *Thespesia lampas* (Cav.) Dalz. ex Dalz. & Gibs. | Malvaceae | Shrub | X | X | X | X | | | E | No | Mechanical |
| *Toddalia asiatica* (L.) Lam. | Rutaceae | Liana | * | X | X | X | | | E | Prickles | Birds, mammals |
| *Toona ciliata* Roemer | Meliaceae | Tree | * | | | | | | E | No | Wind |
| *Trichilia connaroides* (Wt. & Arn.) Bent. | Meliaceae | Tree | * | | | | | | E | No | Birds |
| *Turpinia malabarica* Gamble | Staphyleaceae | Tree | * | | | | | X | E | No | Birds |
| *Tylophora indica* (Burm. F.) Merr. | Asclepiadaceae | Twiner | | X | X | | | | E | No | Wind |
| Unidentified 1 | – | – | – | – | – | – | – | | – | – | – |
| Unidentified 2 | – | – | – | – | – | – | – | | – | – | – |
| Unidentified 3 | – | – | – | – | – | – | – | | – | – | – |
| Unidentified 4 | – | – | – | – | – | – | – | | – | – | – |
| *Vepris bilocularis* (Wt. & Arn.) Engler | Rutaceae | Tree | * | | | | | X | E | No | Monkeys, civets |

**Table 1** *continued*

| Species | Family | Life form | Ecosystem EV | SE | MD | DF | SA | Endemic tree | Leaf habit | Spines | Dispersal agent |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Vitaceae sp. | Vitaceae | Climber | – | – | – | – | – | | – | – | Birds |
| *Vitex altissima* L. f. | Verbenaceae | Tree | X | X | X | X | | | E | No | Birds |
| *Wendlandia thyrsoidea* (Roem. & Schult.) Steud. | Rubiaceae | Shrub | | | | | X | | D | No | Birds |
| *Xantolis tomentosa* (Roxb.) Raf. | Sapotaceae | Tree | * | X | | | | | E | Thorns | Birds, bats |
| *Zanthoxylum ovalifolium* Wt. | Rutaceae | Liana | X | X | X | | | | E | Prickles | Birds |
| *Zanthoxylum rhetsa* (Roxb.) DC. | Rutaceae | Tree | * | | | | | | E | No | Birds |
| *Ziziphus glaberima* Heyne ex Roth. | Rhamnaceae | Tree | | | | X | X | | D | No | Birds |
| *Ziziphus nummularia* (Burm. f.) Wt. & Arn. | Rhamnaceae | Shrub | | | | | X | | D | Thorns and prickles | Birds, mammals |
| *Ziziphus rugosa* Lam. | Rhamnaceae | Liana | | | | X | X | | D | Thorns and prickles | Birds |
| *Ziziphus xylopyrus* Willd. | Rhamnaceae | Tree | | | | X | X | | D | Thorns | Birds, mammals |

EV, evergreen rain forest; SE, semi-evergreen rain forest; MD, moist deciduous forest; DF, deciduous forest; SA, savanna; E, evergreen species; D, deciduous species. *Late successional species.

survey. We distinguished four categories of dispersal agents: birds, mammals, wind and mechanical means. The category 'dispersed by mammals' is highly variable because it contains species dispersed by bats, monkeys, civets and squirrels, etc. but excludes birds.

## Succession

The proportion of evergreen plants was studied in two height classes: ≤2 m and >2 m. Those below 2 m in height were considered to be regenerating saplings. The climbers were not included because it was difficult to estimate their height. The proportion of evergreen plants in each height category was plotted against the thickets' area. Data on proportions were arcsine transformed to improve normality (Sokal & Rohlf, 1981). The population structures (relative to size) of the two most abundant species among the five tallest trees in every thicket were examined. To synthesize the structure of the species assemblage in each thicket, we used the non-symmetric correspondence analysis (NSCA). Correspondence analysis (CA) (Hill, 1973) orders sites according to their species composition (species frequencies). The symmetry between species and sites in the calculation introduces a bias when the sampling of vegetation has not been carried out in standardized relevés (Gimaret-Carpentier *et al.*, 1998). Moreover, CA gives prominence to rare species, which is a problem when early succession is concerned, because regular patterns in species composition are to be distinguished. The NSCA (Lauro & D'Ambra, 1984), by contrast, separates sites according to their species profiles and is much less sensitive to the presence of rare species (Gimaret-Carpentier *et al.*, 1998).

Following Gaston (1994), species were considered rare if they fell below the first quartile of the frequency distribution of abundance. Above the first quartile of the frequency distribution, species were considered abundant. We compared the abundant and rare species for a few characteristics: the proportions of (1) species belonging strictly to the rain forest, (2) deciduous species, (3) bird dispersed, (4) mammal dispersed, (5) wind dispersed, and (6) mechanically dispersed species.

As some species were dispersed by both birds and civets, the sum of the proportions for dispersal is not equal to 1. Our classification among abundant and rare species was relative as in Gaston (1994). The abundant and rare species did not belong to independent statistical populations. No statistical test was available to test the significance of differences between proportions of rare and abundant species within the categories cited above.

## Nestedness

Nestedness of species among thickets was measured using the index $T$ developed by Atmar & Patterson (1993, 1995). Nestedness occurs when the species recorded in a smaller thicket is from subset of species found in a larger thicket. It is analysed as a presence–absence matrix: species are organized in columns in descending order from those occurring in most thickets to those occurring in the least number of thickets; thickets are organized in rows from the largest to the smallest. The summary of the procedure is given in Wright *et al.* (1998). The index $T$ provides a standardized measure of matrix disorder by assessing the deviation of an ordered matrix from one of the same rank and fill that is perfectly nested. $T$ ranges from 0 for a perfectly nested matrix to 100 for one that is completely disordered. The $T$ value of the observed matrix was compared with matrices generated randomly by Monte Carlo simulations.

# RESULTS

## Floristics

In a total sampled area of 2100 $m^2$, 154 species (2558 individuals) were recorded in thirty thickets. The species belonged to fifty-six families and 115 genera. The most common families were *Euphorbiaceae* (ten species), *Rubiaceae* (ten), *Rutaceae* (eight), *Fabaceae* (seven), *Lauraceae* (six), *Oleaceae* (six) and *Verbenaceae* (five). Four species could not be identified, not even to the family level. Three species were identified to family level only, and nine to generic level (Table 1). The most abundant species was *Aporosa lindleyana*, an evergreen tree of the evergreen and semi-evergreen rain forest, followed by *Leea indica* (an evergreen shrub), *Catunaregam dumetorum* (a deciduous shrub), *Allophylus serratus* (an evergreen shrub with large ecological amplitude) and *Olea dioica* (an evergreen tree). Among the set of 150 largest trees (five trees in each thicket), *Aporosa lindleyana* was the most abundant with thirty-two individuals followed by *C. dumetorum* (thirty individuals). Of the species identified, eighty-seven occur under natural conditions in rain forest, forty-seven in semi-evergreen rain forest, thirty in moist-deciduous forests, forty-nine in deciduous forests and eighteen in savannas (Table 1). A total of forty-seven species (30% of the taxa represented) were late-successional rain forest species of narrow ecological amplitude. Among these, *Artocarpus hirsutus*, *Holigarna arnottiana*, *H. grahamii*, *Hopea ponga* and *Mimusops elengi* are dominant in the rain forest type present in this region. Only seven savanna species were found: *Emblica officinalis*, *Glochidion velutinum*, *Hemidesmus indicus*, *Osbeckia aspera*, *Phoenix humilis*, *Wendlandia thyrsoidea* and *Ziziphus nummularia* (Table 1). As many as twenty-three tree species (15%) were endemic to the Western Ghats of India, the majority being late-successional rain forest species. Nearly 100% of the rain forest species found in the thickets were evergreen (Fig. 2). The proportion of evergreen species diminished from the rain forest to savanna species. The proportion of armed species (species with spiny anti-herbivore defence) was low among the rain forest species and maximum for the moist deciduous forest species (Fig. 2). The proportion of armed savanna species was intermediate. A highly significant linear relationship was observed between (1) the log-area of the undisturbed thickets and the log-number of species ($n = 13$, $P < 0.0002$) (Fig. 3) and (2) the log-area of the disturbed thickets and the number of species ($n = 17$, $P < 0.004$). There was also a significant positive relationship between log-number of individuals and the log-number of species in the undisturbed thickets ($n = 13$, $P < 0.0001$) and disturbed thickets ($n = 17$, $P < 0.001$). Species abundance and occurrence in different thickets was highly correlated ($r_s = 0.19$, $P < 0.0001$).

## Dispersal mode

Among the 143 species for which dispersal mode was known, seventy-four (51%) were dispersed by birds,

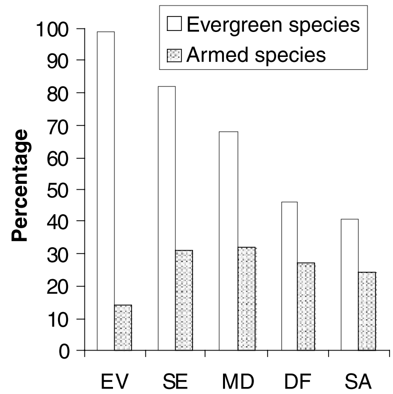


**Figure 2** Percentage of evergreen and armed species among the plant assemblages from the evergreen rain forest (EV), semi-evergreen rain forest (SE), moist-deciduous forest (MD), deciduous forest (DF) and savanna (SA).

forty-one (29%) by mammals, ten (7%) by wind and eighteen (13%) by mechanical means (Table 1). Dispersal by animals (birds and vertebrates) was more common among rain forest species than savanna species. Conversely, the percentage of species with mechanical dispersal increased from rain forest species to savanna species. Wind dispersal was the least represented dispersal mode. Half of the wind-dispersed species originated from deciduous forests.

## Succession

No significant relationship existed between the proportion of evergreen plants >2 m high and thicket area. The proportion of evergreen plants ≤2 m in height varied widely among small thickets. When thickets larger than 10 $m^2$ were removed, the proportion of evergreen plants ≤2 m in height was significantly related to the thicket area (Fig. 4a). The number of tall individuals >4 m in the undisturbed thickets increased linearly with log-area ($r^2 = 0.56$, $n = 13$, $P < 0.005$). As the height of the trees is related to their age, larger thickets are also older thickets. No such relationship existed for disturbed thickets. There was a significant linear relationship between the number of climbers and log-area of undisturbed thickets ($r^2 = 0.48$, $n = 13$, $P < 0.01$). The mean number of climbers was 1.8 plants per disturbed thicket and there was no relationship between the number of climbers and the area of disturbed thickets. The number of armed plants decreased with log-area of thickets (Fig. 4b), but the linear relationship was not significant by a small margin. The population structure of the two most abundant species among the dominant thicket trees were markedly different (Fig. 5). *Aporosa lindleyana* could regenerate successfully in the thickets whereas *C. dumetorum* had fewer representatives in the smaller size classes.

The NSCA (Fig. 6a,b) isolated a few species with high absolute contributions to factor 1 (20% of the total inertia): *Aporosa lindleyana* (21%), *Olea dioica* (21%) and *Thespesia lampas* (14%). This factor opposes species

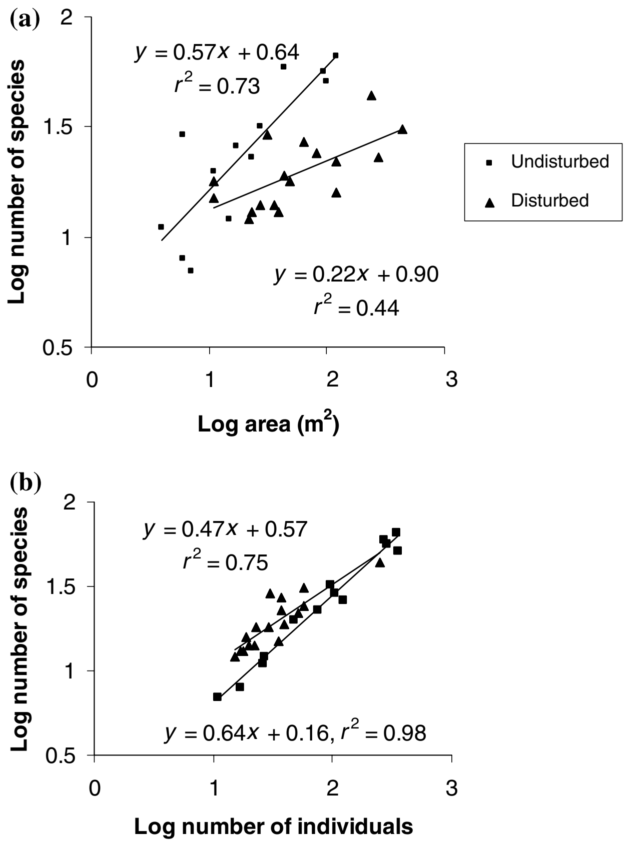


**Figure 3** Relationship between the log-number of species and (a) log-area of the thicket, and (b) the log-number of individual plants.

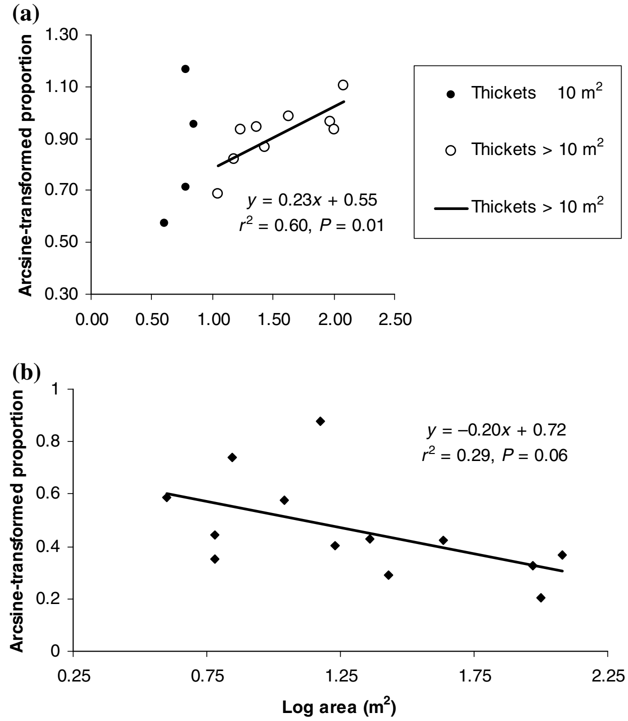


**Figure 4** (a) Arcsine-transformed proportion of evergreen individuals and species (below 2 m in height) in relation to the log-area of thickets. (b) Arcsine-transformed proportion of armed individuals and species in relation to the log-area of thickets.

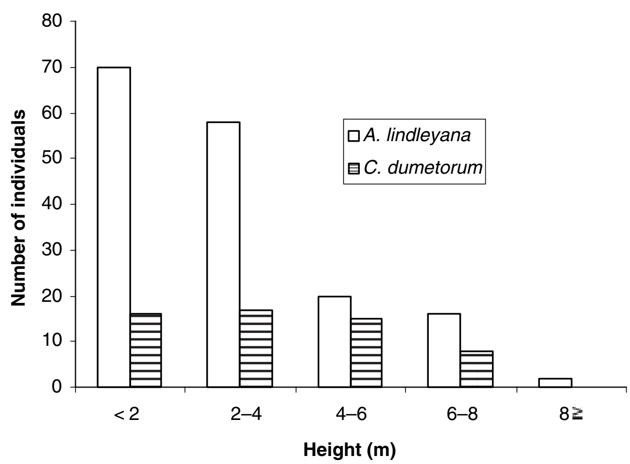


**Figure 5** Size structure of the populations of *Catunaregam dumetorum* and *Aporosa lindleyana*.

with different dispersal modes. *Aporosa lindleyana* and *Olea dioica* are bird-dispersed and very abundant in ecotones. *Thespesia lampas* is mechanically dispersed. The species with highest absolute contributions to factor 2 (17% of the total inertia) was *C. dumetorum* (54% of total contribution), a grassland tree. The disturbed thickets appear on the right upper quadrant of the figure, i.e. characterized by species with high dispersal ability and a higher frequency of *C. dumetorum*. The largest undisturbed thickets (thickets 18, 19, 22, 25 and 27) appear to be grouped mostly with negative ordinates and are close to the origin. The small, undisturbed thickets (20, 21, 23, 24, 26, 28, 29 and 30) with small areas are more patchily distributed. The dispersion of the small thickets seems to be related to their species composition which is a random subset of available species in the nearby rain forest.

There were 121 rare species that fell below the first quartile of the frequency distribution. Rare species have a high proportion strictly limited to the evergreen rain forest compared with the abundant species (Fig. 7). Deciduous species were less represented. Rare species were proportionally more mammal-dispersed and less bird-dispersed or mechanically dispersed than abundant species. The proportion of wind-dispersed species did not vary.

## Nestedness

The nestedness index $T$ is 20° for all thickets as well as for the undisturbed thickets, which indicates that species composition of the thickets is fairly nested. The plant species

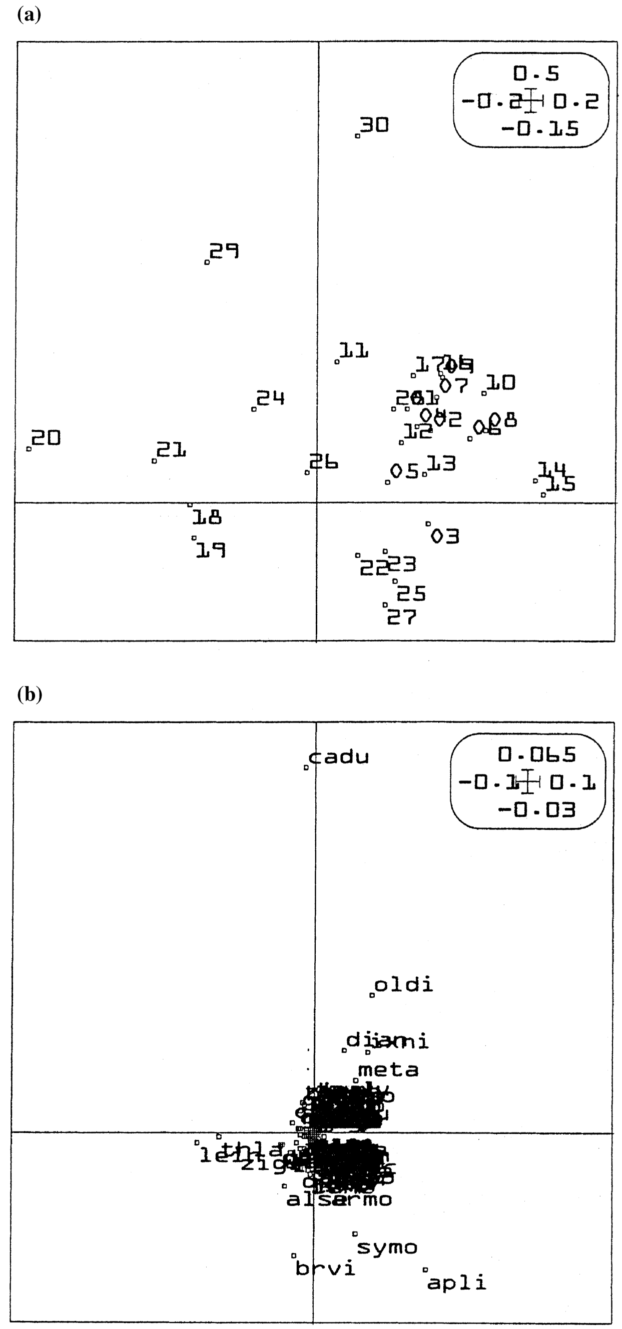

Figure 6 Ordination of thickets (a) and species (b) by non-symmetric correspondence analysis.

occurring in small thickets can be considered a subset of those in the larger thickets. The probability that a randomly ordered matrix is the same as that of the observed matrix is practically nil [$P(T < 20°) = 1.41 \times 10^{-22}$]. That $T$ increases to 29° indicates that disturbance brings about disorder in the species arrangement. The matrix is still significantly nested [$P(T < 29°) = 5.16 \times 10^{-15}$].

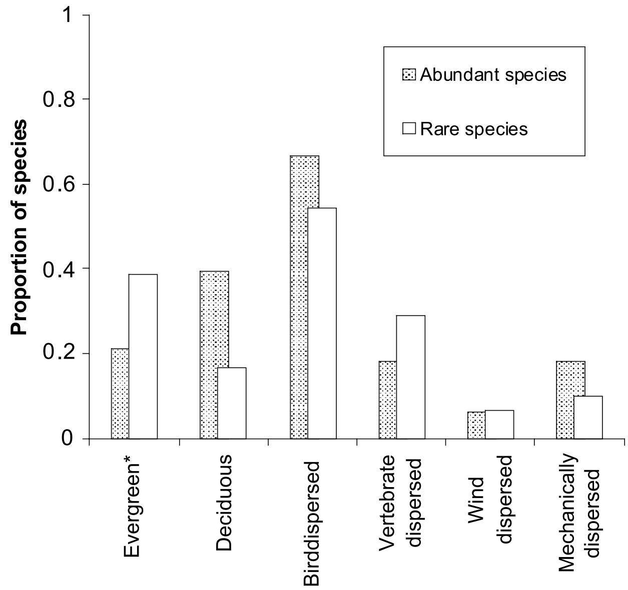


**Figure 7** Proportion of individuals within abundant and rare categories of species. *Evergreen indicates species recorded exclusively from the evergreen rain forest. The other legends are self-explanatory.

## DISCUSSION

### Forest expansion in grasslands

When human-related disturbance is low in the ecotone of the Central Western Ghats rain forest, evergreen species expand into grasslands (Mariotti & Peterschmitt, 1994; Puyravaud *et al.*, 1994). The present study supports these findings, suggesting that the formation of thickets could be a major process by which rain forest vegetation can colonize a hostile environment. A series of changes associated with increasing undisturbed thicket area confirmed rain forest succession: (1) the proportion of evergreen rain forest species rose with increasing thicket area; (2) small thickets were dominated by deciduous species whereas large thickets were dominated by evergreen species; (3) the regeneration of evergreen species was more pronounced than the regeneration of deciduous species; and (4) the proportion of armed species seemed to diminish with succession.

In Belize, Kellman & Miyanishi (1982) reported that thickets, an early colonization stage of forest succession, contained few seedlings of forest species. By contrast, in this study, we observed that the forest flora was overwhelmingly represented in thickets. Grassland thickets included 154 species among the 2558 stems recorded, in a total area of 2100 m$^2$. In a 3.12-ha plot of undisturbed rain forest of the Central Western Ghats, Pascal & Pélissier (1996) found ninety-one tree species for 1981 stems >30 cm girth at breast height (GBH) and in a 50-ha plot of tropical deciduous forest of the same region, Sukumar *et al.* (1992) recorded seventy-one woody species for 25,929 stems >1 cm DBH. On a per individual basis, thicket species richness matched rain forest species richness. Most of the individual plants in thickets were small and had not reached the reproductive stage. The high species richness of thickets was partly the result of the seed rain from the forest. Thickets also covered a fairly large area and thus included many different microhabitats, which in turn increased species richness further. The commonest families (Euphorbiaceae, Fabaceae, Lauraceae and Rubiaceae) are among the most dominant rain forest families world-wide (Morley, 2000). As much as 15% of the late-successional species recorded were endemic to the evergreen and semi-evergreen forests of the Western Ghats.

Animal dispersal is widespread among rain forest trees (Howe, 1984). We found that 81% of the species for which the dispersal mode was known, were dispersed by animals. Holl (1999) suggested that the most important limitation for rain forest expansion into pastures is the lack of seed dispersal, because many tropical forest birds and mammals rarely venture into open areas (Cardoso Da Silva *et al.*, 1996). The bird community of the Western Ghats rain forest is not species rich (Daniels *et al.*, 1992), but birds appear to be generalists and capable of thriving in a variety of habitats (Daniels, 1989). Thus, in comparison with Neotropical situations, it is possible that local disperser characteristics may allow more efficient seed dispersal in the pastures. This hypothesis could explain the abundance of many rain forest tree species in thickets.

### Forest succession within thickets

In a Texan savanna ecosystem, Archer (1990) observed that *Prosopis glandulosa* was the most abundant grassland tree and was facilitating the establishment of other woody species otherwise restricted to more humid habitats. In the Western Ghats, the same process of thicket establishment around grassland trees seems to be valid. The NSCA indicated that small undisturbed thickets have a variety of dominant species, the most abundant being *C. dumetorum*, a deciduous tree common both in savannas and deciduous forests of southern India (Champion & Seth, 1968). Undisturbed thickets of intermediate size have a higher proportion of ecotone and bird-dispersed species, whereas the largest thickets include a smaller number of ecotone species. *Aporosa lindleyana* contributed the most to the set of dominant trees. As an ecotone species, it can tolerate the microclimatic conditions of the thickets. The number of plant species was dependent on the area of the thickets and on the number of stems. These relationships were less strong with disturbance. On average, locally abundant species were more widespread in different thickets than rare species were, and large undisturbed thickets had markedly different species composition among the rare species. These differences probably were a consequence of high variability both in seed dispersal among rain forest tree species (Holl, 1999) as well as in the distance to mother trees. Despite these differences in species composition, the species assemblage of thickets of different sizes was nested. Nestedness in land-bridge archipelagos and 'virtual' islands is brought about by different factors: selective extinction (Patterson & Atmar, 1986), selective colonization (Cook & Quinn, 1995), habitat nestedness (Davidar *et al.*, 2002) and speciation (Goode, 1974). No study is available at present to differentiate the influence of these various factors. However, the organization of species occurrence patterns underlines the high determinism of the successional process.

### The effect of disturbance

Wood and NTFP harvesting is the primary cause of thicket destruction. Harvesting lowered plant species richness, disrupted the species–area relationship, and affected the vertical structure of thickets. Disturbance led to the invasion of species with large ecological amplitude. Undisturbed thickets had higher species richness and more rare species than disturbed thickets of the same area. Thickets were destroyed by humans cutting pathways to collect NTFPs and not by cattle grazing or fire.

The abundance and ecological characteristics of climbers can be used to distinguish different intensities of disturbance in the rain forest (Garrigues, 1999). In undisturbed thickets, the number of climbers increased with the area of undisturbed thickets, but climbers were poorly represented in disturbed thickets. Contrary to the rain forest, an increasing number of climbers was related to decreasing thicket disturbance. This effect may be the result of the selective destruction of climbers that block the entry of harvesters into thickets.

### Consequences for management

The main immediate threat to the rain forest ecotone is the policy of the Forest Department to destroy thickets with the objective of 'restoring the degraded land'. As a consequence, a species-rich vegetation with an abundant soil fauna and fertile soil (Basu *et al.*, 1996) is replaced by mono-cultural plantations that decrease soil fertility and stop rain forest expansion. Establishing exotic tree plantations for industrial purposes in a rain forest area is questionable for other reasons as well. Contrary to the village woodlots of the social forestry programmes, industrial plantations generally do not benefit farmers (Gadgil, 1992; Sharma, 1993), nor do they provide NTFPs. When industrial plantations are installed at the expense of useful vegetation, the farmers shift to the rain forest to meet their needs. Policies based on such vague concepts as 'restoration of degraded land' do not help to identify clear environmental objectives. Its flawed logic is ironic because restoring a degraded land literally means putting it back to its original degraded condition. The term 'restoration' should refer to an ecosystem (or to a soil). It is never achieved with plantations. Plantations of exotic trees can help to start a succession (Janzen, 2000; Feyera *et al.*, 2002), but it remains to be checked whether the use of local fast growing trees to form thicket would not be a quicker method for restoration in this region.

Indeed, the strategy of re-growing rain forest from vegetation thickets may be a useful one in places. Thickets are resilient to disturbance and they protect rain forest seedlings against a variety of threats. Contrary to plantations that are fragile and need strict cattle control, thickets are not directly affected by cattle. Moreover, cattle are useful in early succession because they consume the grass layer, a potential fuel for fire (Janzen, 2000). The main causes of thicket disturbance are wood collection and cutting to provide shelter for cattle. Without these human disturbances, the thickets will coalesce and in time will form a secondary rain forest. The structure and species composition of thickets provide clues on how to restore the barren grasslands of this region inexpensively. *Catunaregam dumetorum* and a few other deciduous species, function as primers for thicket formation. Such trees can be planted if necessary when they are not locally abundant. Under their shade, seeds of early successional species of various life-forms (tree, shrub, sub-shrub and climbers) will be introduced as long as the bird community is preserved. These initial steps will recreate thickets with complex vertical structure and high diversity. Simplified thickets can also be formed using the abundant species cited here (Table 1). Thickets result from degradation over natural forest ecosystems and could be used as efficient tools to restore the rain forest.

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