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# Plant diversity in sacred forest fragments of Western Ghats: a comparative study of four life forms

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**Abstract** The effect of fragmentation on different life forms within tropical forest plant communities is poorly understood. We studied the effect of degree of fragmentation and surrounding matrix on trees, lianas, shrubs and epiphytes in tropical forest fragments of Kodagu, Western Ghats, India. These fragments exist as sacred groves amidst a highly modified agricultural landscape, and have been preserved by the religious sentiments of local communities. Plants were sampled at two sites in continuous forests and 11 forest fragments. A total of 122 species of trees, 29 species of lianas, 60 species of shrubs and 66 species of epiphytes were recorded. Trees exhibited a significant species–area relationship ($R^2 = 0.74$). Richness estimates after controlling for stem density (rarefaction) revealed that observed species–area relationship was not an artefact of passive sampling. Variation in species richness of the other three groups was explained by stem density and structural diversity. Linear distance from the reserve forest did not explain any variation in species richness. All life forms exhibited significant nested pattern. Trees were nested along the area gradient while nestedness in the other three groups showed evidence in support of habitat nestedness. The four life forms thus responded variably to degree of fragmentation. Our study revealed that 74% of the regional diversity for trees was contributed by diversity among plots, highlighting the importance of inter-patch habitat diversity in maintaining the total regional species pool. We conclude that trees alone cannot serve as good indicator for taking appropriate conservation measures to mitigate species loss resulting from habitat fragmentation.

**Keywords** Species–area · Richness · Nestedness · Tropical forest · Fragmentation · Life form

## Introduction

Traditional conservation practices in the form of nature worship have played an important role in protection and conservation of biodiversity in India

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(Bhagwat and Rutte 2006). In the Kodagu district of Karnataka state (India), local communities have traditionally protected forests patches which are dedicated to the local deity. Such forest patches reserved in the name of God (local deity) are called sacred groves (*Devakad* or *Devarakadus*). Forest fragments in Kodagu which exist in the form of sacred groves contain trees, lianas, epiphytes and understorey plants (mainly shrubs). The proximal surrounding matrix is dominated by relatively recent coffee plantations, many of which have maintained native tree cover within them. This tree covered coffee matrix surrounding the forest fragments in Kodagu have helped in maintaining tree diversity within fragments by providing connectivity to other fragments as well as the reserve forest, thus making the effect of fragmentation less severe (Bhagwat et al. 2005a). They act as a reservoir for local, endemic and endangered tree species and as an important source of propagules and genetic diversity (Elouard 2000; Boraiah et al. 2003; Bhagwat et al. 2005b). Coffee plantations that maintain native tree species support a good diversity of epiphytes. Lianas and understorey plants, however, are completely absent in these plantations. This makes fragments of Kodagu an ideal place to study the influence of the matrix on forest plants and to examine the response of four different plant life forms, namely trees, lianas, shrubs and epiphytes, to degree of fragmentation. Since the previous studies carried out in Kodagu have focused only on trees, there is a need to asses the effect of fragmentation on other groups of plants.

The equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1967) has often been invoked to explain species–area relationship and to predict species loss in habitat fragments (Kilburn 1966; Connor and McCoy 1979; He and Legendre 1996; Wilsey et al. 2005). Since the classical equilibrium theory was proposed for strictly insular biotas such as island archipelagos, its application to habitat fragments have certain shortcomings. ETIB considers the matrix lying in between these patches as inhospitable and assumes that species present within patches are absent from the matrix (Cook et al. 2002). Further, it considers mainland as the only source of immigrants and does not anticipate immigration from surrounding matrix. Increasing number of studies from the tropics have recognised the potential of the matrix surrounding the remnant forest patches in biodiversity conservation. While some of these studies have revealed that population declines within patches can be compensated by immigration from surrounding matrix (Brown and Kodric-Brown 1977; Piessens et al. 2004), consequently alleviating patch level extinctions (Knutson et al. 2004; Silva et al. 2005; Bhagwat et al. 2005a), some have highlighted the importance of the matrix itself in housing substantial biodiversity (Sekercioglu et al. 2007). Since the forest fragments in Kodagu are surrounded predominantly by coffee-based agro-forestry, it provides an ideal situation to test the role of matrix in maintaining biodiversity and its influence on plant diversity within the forest fragments.

The broad objectives of the study were (i) to investigate the effect of fragmentation on plant species diversity in the forest fragments of Kodagu, (ii) to assess the influence of spatial attributes (area and isolation) and landscape variables (surrounding matrix) on plant diversity within these remnant forest fragments and (iii) to assess if the diversity and distribution patterns of species vary across these groups. We expect the surrounding matrix to differentially influence trees and epiphytes diversity in the fragments since these plant groups are also supported by the coffee matrix.

## Materials and methods

### Study area

This study was carried out along the eastern slopes of the Western Ghats in Kodagu district (75°25′–76°14′ E and 12°15′–12°45′ N), Karnataka State, India (Fig. 1). This region has several forest types in a relatively small area due to the sharp altitude and rainfall gradients. This study was restricted to the medium elevation wet evergreen forest (650–1,400 m) represented by *Mesua ferrea–Palaquium ellipticum* forest type (Pascal and Meher-Homji 1986). Coffee plantation is one of the most prominent land uses occupying about 29% of the land area in Kodagu district (Elouard 2000). Initially restricted to the moist deciduous areas of the district, the plantations have extended to the medium elevation wet evergreen forest resulting in major alterations in the landscapes of Kodagu and severe fragmentation of the wet evergreen forest (Elouard 2000). Coffee is a

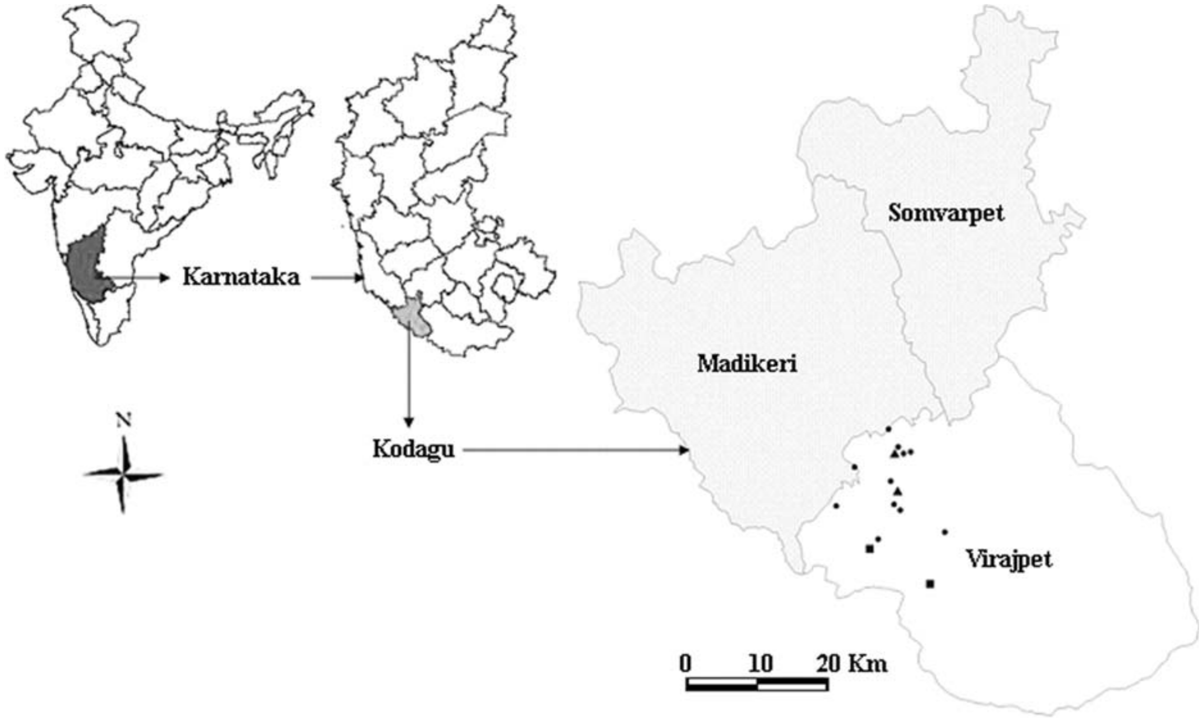


**Fig. 1** Location of the study area in the Virajpet Taluka of Kodagu district in Karnataka State, India. *Dots* represent fragments; *squares* represent the two sampling localities in the reserve forest while *triangles* represent coffee plantations

shade-demanding plant, hence the planters maintain canopy cover in coffee plantations, which may either be constituted exclusively of native forest species or with varying percentage of exotics. Paddy is the next most prominent crop of the study area. A large fraction of the forest fragments in Kodagu (>1200) are sacred groves, (Kalam 1996), making it the district with perhaps the highest density of scared groves in the world (Bhagwat et al. 2005b). Most of the contiguous and undisturbed forest are now found only in the Reserve Forests (RF), which constitute 30% of Kodagu's forest cover. These RFs are contiguous with large protected areas in this region such as the Bramhagiri, Talakaveri and Pushpagiri Wildlife Sanctuaries (Elouard 2000).

## Study design

A total of 11 sacred groves (henceforth 'fragments') ranging in size from 0.94 to 47 ha, two coffee plantations and two sites within the RF, were sampled across 5 months, from December 2006 to April 2007 (Table 1). Fragments were selected such that they represented a size gradient, and chosen such that they had similar topography, altitude and the surrounding landscape type. In addition, two sites in coffee plantations, one which had mostly native shade trees and another which had primarily exotic shade trees (Silver oak, *Grevillea robusta*), were sampled to investigate the epiphyte diversity supported by these plantations. Two sites were also sampled within the reserve forest adjoining Bramhagiri Wildlife Sanctuary as controls. All 11 fragments and the two sites in reserve forest were grouped into five size classes such that each class had 2–4 replicates (Table 1). Stratified random sampling (Mueller-Dombois and Ellenberg 1974) was carried out for woody species in each of the fragments and reserve forest sites. Quadrats of 25 m × 25 m ($n = 57$) were used as the primary sampling unit for trees, lianas and epiphytes. Each fragment was divided into edge, intermediate and interior strata and plots were laid in each of the strata so as to capture the heterogeneity in vegetation structure and composition. Distribution of plots within these strata was arbitrary. Within these plots, we recorded all trees with girth at breast height (GBH; measured at a height of 1.35 m from the ground) exceeding 0.30 m and lianas with GBH exceeding 0.10 m. All epiphytes

Table 1 Description of study sites in Kodagu district, Karnataka State, India

| Name | Status | Location | | Area[a] (ha) | Size class | No. of plots | Observed species richness | | | | Tree rarefied richness | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Latitude | Longitude | | | | Trees | Lianas | Shrubs | Epiphytes | Mean[c] | 95% CI |
| Devangere-1 | Sacred grove | 12.25556 | 75.79844 | 0.95 | 1 | 3 | 17 | 5 | 14 | 6 | 17 | 0.00 |
| Mytadi-1 | Sacred grove | 12.28567 | 75.77744 | 4 | 1 | 3 | 19 | 5 | 22 | 17 | 13 | 3.25 |
| Mytadi-2 | Sacred grove | 12.26350 | 75.79103 | 4 | 1 | 3 | 22 | 6 | 21 | 14 | 17 | 3.20 |
| Devangere-2 | Sacred grove | 12.25819 | 75.80747 | 8.26 | 2 | 3 | 24 | 5 | 16 | 22 | 19 | 2.41 |
| Arji | Sacred grove | 12.18286 | 75.79744 | 8.51 | 2 | 4 | 26 | 8 | 16 | 20 | 17 | 3.59 |
| Kadanoor | Sacred grove | 12.21925 | 75.78356 | 9.07 | 2 | 4 | 30 | 4 | 19 | 31 | 16 | 4.22 |
| Bettoli | Sacred grove | 12.18986 | 75.78883 | 9.72 | 2 | 5 | 22 | 2 | 21 | 22 | 17 | 3.38 |
| Rudraguppe | Sacred grove | 12.15725 | 75.85583 | 13 | 3 | 4 | 37 | 12 | 14 | 30 | 19 | 3.97 |
| Arapattu | Sacred grove | 12.23536 | 75.73592 | 19.27 | 3 | 4 | 26 | 5 | 19 | 23 | 15 | 3.83 |
| Heggala-1 | Sacred grove | 12.14481 | 75.77039 | 42.05 | 4 | 6 | 51 | 7 | 27 | 9 | 22 | 4.24 |
| Palangala | Sacred grove | 12.18456 | 75.71458 | 46.43 | 4 | 6 | 45 | 10 | 16 | 30 | 19 | 4.21 |
| Heggala-2 | Reserve forest | 12.13233 | 75.76061 | >1000 | 5 | 6 | 50 | 12 | 25 | 4 | 20 | 3.93 |
| Kokka | Reserve forest | 12.09075 | 75.84008 | >1000 | 5 | 6 | 46 | 10 | 14 | 10 | 18 | 4.33 |
| Mytadi | Coffee plantation | 12.25569 | 75.78692 | 12 | – | 1[b] | 17 | – | – | 25 | – | – |
| Chikpet | Coffee plantation | 12.20781 | 75.79297 | 15 | – | 1[b] | 29 | – | – | 10 | – | – |

[a] Source for area—Details of Devarakadus of Virajpet Forest Division of Kodagu circle, Karnataka, Survey of India

[b] Belt transect of 20 m × 100 m

[c] Values represent mean tree species richness at 32 individuals for all fragments

within these plots were noted using a pair of binoculars and we occasionally had to climb trees to confirm their taxonomic identity. Nested plots of 5 m × 5 m ($n = 90$) were laid in corners of the plot for sampling shrubs. All life forms were identified to species level with the help of local and regional floras. Voucher specimens were deposited at the Herbarium department of Wildlife Institute of India, Dehradun, India.

### Data analysis

Species accumulation curves were generated after 1,000 randomizations using the program EstimateS (Colwell 1997). The non-parametric estimator Jackknife-1 was used to estimate species richness in each fragment (Heltshe and Forrester 1983). Jackknife-1 gives an estimate of absolute number of species in an assemblage based on number of rare species (species that occur only in one sample; Magurran 2004). Linear form of Arrhenius' (1921) power function ($\log S = \log k + z \log A$) was used for estimating '$z$' values resulting from species–area relationship. The slope values were estimated using linear regression equation with the help of program SPSS 14 (SPSS Inc. 2005). Both area and stem density were used to explain the variation in plant species richness using Pearson's correlation test. Rarefied species richness was used to make valid comparisons across different fragments and to test for passive sampling (Simberloff 1978). Randomisations of individuals were done using program EcoSim700 (Gotelli and Entsminger 2001). We calculated beta diversity using Whittaker's $\beta$ as a measure of species turnover because of its advantages over other indices (Wilson and Shmida 1984). However, Whittaker's $\beta$ performs poorly in case of changing alpha diversity across a gradient (Harrison et al. 1992), hence we also calculated Cody's index (1993) as an additional measure of beta diversity. The additive partitioning model of Lande (1996) was used to calculate overall beta diversity. Effect of fragmentation on relative species abundance of plants was assessed based on dominance diversity curves generated using program BioDiversity ProVer.2 (McAleece et al. 1996). Differences in species abundance with respect to patch size were tested using Wilcoxon's paired sample test.

Program Nestedness (Ulrich 2006) was used to quantify nestedness of species by site matrix. The program provides nestedness scores in form of 'temperature-$T$', the values of which range between 0 (perfect order) and 100 (perfect disorder). The significance of the observed temperature was judged from the 95% CI after 1,000 randomisations. Mantel's test was used to test the correlation between dissimilarity distance matrices (McCune and Grace 2002). We used Mantel's test to detect the effect of geographical distance between patches on (i) absolute differences in residual values resulting from species–area regression, (ii) species compositional similarity, and (iii) patch temperature. Geographical distance between patches (from the center) was calculated using ArcView GIS (ESRI 1998) software. Area was correlated with rank order of fragments in maximally nested matrix using rank correlation analysis to test the influence of area on patch temperature, i.e. to test whether fragments were nested along an area gradient.

## Results

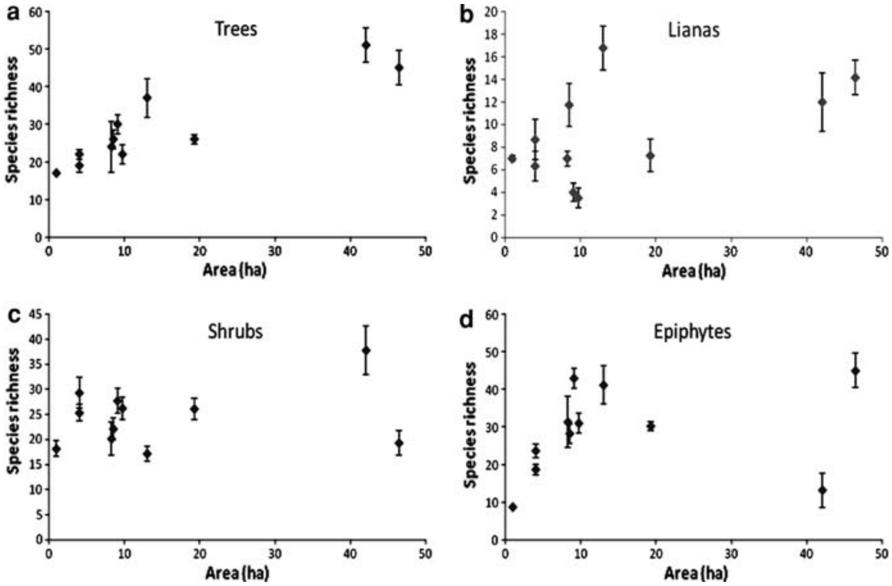
### Species richness

A total of 122 species of trees, 29 species of lianas, 60 species of shrubs and 66 species of epiphytes were recorded in 11 fragments and two sites in reserve forests. Of these, 47 species of trees, 12 species of lianas, 29 species of shrubs and 55 species of epiphytes were recorded exclusively in the fragments, while 19 species of trees, 6 species of lianas and 8 species of shrubs were recorded only in the reserve forest. No species of epiphyte was unique to the reserve forest. We recorded 41 species of native trees apart from two exotics (*Grevillea robusta* and *Erythrina* sp.) and 28 species of epiphytes in two coffee plantations. We did not observe any epiphytes growing on the exotic tree species within the coffee plantation.

Tree species richness increased consistently with area (Table 1, Fig. 2a). Shrub and liana species richness did not show any particular trend with area while epiphytes species richness peaked at intermediate sized fragments (Fig. 2b–d).

Stem density of trees was also correlated with area ($R = 0.66$, $P = 0.01$). This resulted in a significant correlation of tree species richness with both area and stem density. Increase in stem density of trees with area was because of increase in proportion of tree

**Fig. 2** Scatter plot of estimated species richness (±1 SD) plotted against area for four plant life forms



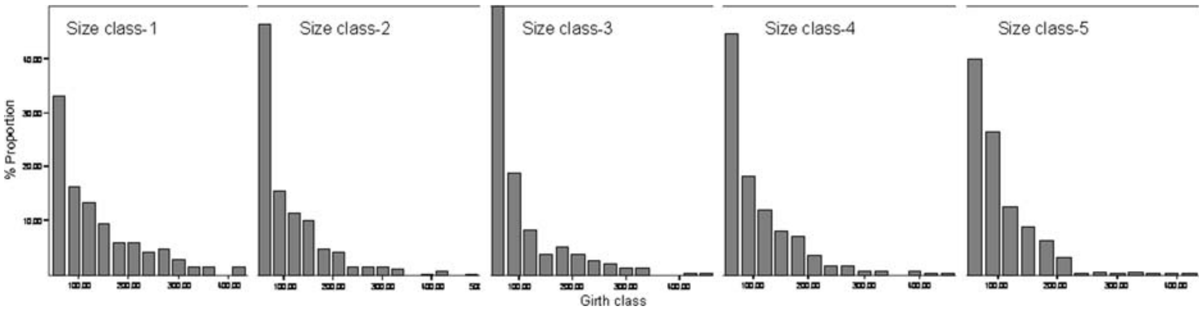


**Fig. 3** Girth class distribution for trees across five size classes. GBH of trees was divided into 15 girth classes with a class interval of 0.3 m, shown on the *x*-axis, while *y*-axis represents proportion of stems in each girth class

individuals in smaller girth classes (Fig. 3). Species richness when controlled for stem density (rarefied richness) did not show a significant difference between any of the size classes.

## Dominance and diversity

The dominance diversity curves of trees for all five size classes exhibit similar shape but differ in their slope, degree of dominance of the community by common species and number of rare species in each (Fig. 4a). Size class 1 shows the steepest slope (Fig. 5), indicating high dominance. The species distribution in this size class is least equitable, showing high abundance of common species and absence of rare species. Larger size classes successively showed higher number of rare species with reserve forest having the highest proportion of rare species and also exhibiting the lowest slope (Fig. 5). Certain species such as *Xanthophyllum flavescens*, *Nothopegia racemosa* and two species of *Holigarna* were the most abundant in the forest fragments but were recorded in very low abundance in reserve forest (Fig. 4a). On the other hand, species like *Elaeocarpus tuberculatus* and *Olea dioica* were most abundant in reserve forest but were encountered rarely in forest fragments. *Dimocarpus longan* was the only species that remained the most dominant species in both forest fragments and reserve forest.

General trends for shrub species abundance were similar to those of trees (Fig. 4b). The relative abundance of *Coffea canephora*, an exotic grown

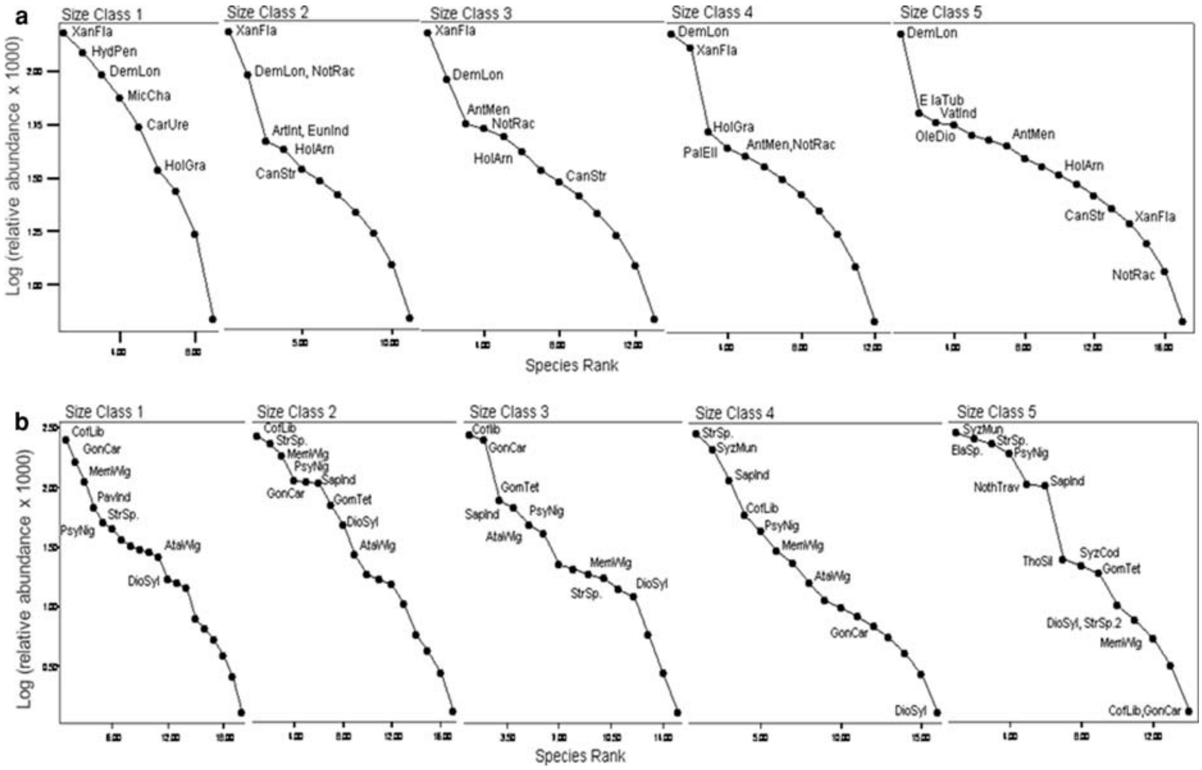


**Fig. 4** Rank abundance curve for trees and shrubs across five size classes for trees (**a**) and shrubs (**b**) in Kodagu district, Western Ghats. The *x*-axis represents species rank, with the most abundant species ranked 1 and species with successively lower abundances are assigned higher ranks. The *y*-axis represents log of abundance of a species relative to that of other species. Only species showing a change in abundance across size classes are shown on the curve by their abbreviations. The abbreviations of the plant names are as follows. Trees: *Xanthophyllum flavescens* (XanFla), *Hydnocarpus pentadra* (HydPen), *Dimocarpus longan* (DemLon), *Michelia champaka* (MicCha), *Caryota urens* (CarUre), *Holigarna grahmii* (HolGra), *Nothopegia racemosa* (NotRac), *Artocarpus integrifolius* (ArtInt), *Euonymus indicus* (EunInd), *Holigarna arnottiana* (HolArn), *Canarium strictum* (CanStr), *Pallaquium ellipticum* (PalEll), *Antidesma menasu* (AntMen), *Elaeocarpus tuberculatus* (ElaTub), *Vateria indica* (VatInd), *Olea dioica* (OleDio). Shrubs: *Coffea canephora* (CofLib), *Goniothalamus cardiopetalus* (GonCar), *Memecylon wightii* (MemWig), *Pavetta indica* (PavInd), *Strobilanthus sp* (StrSp)., *Psychotria nigra* (PsyNig), *Atalantia wightii* (AtaWig), *Diospyros sylvatica* (DioSyl), *Saprosma indica* (SapInd), *Gomphandra tetrandra* (GomTet), *Syzygium munronii* (SyzMun), *Elatostema sp.* (ElaSp), *Nothopegia travancorica* (NotTra), *Thottea siliquosa* (ThoSil), *Syzygium codyensis* (SyzCod), *Strobilanthus sp.* (StrSp2)

extensively in the coffee matrix, declined with increase in fragment area. Coffee abundance was least in the reserve forest. Although shrub species composition did not change among fragment size classes, there were distinct differences between reserve forests and fragments (Fig. 4b). Species dominant in the fragments such as *Memecylon wightii*, *Diospyros sylvatica* and *Goniothalamus cardiopetalus* were very rare in reserve forests.

Epiphytes species composition was strongly influenced by structural heterogeneity, with a strong positive correlation between standard deviation in stem density and epiphytes richness ($r = 0.66$, $P = 0.02$).

## Species–area relationship

Among the plant life forms, only trees exhibited a significant species–area relationship (Table 2), with 74% variation in tree species richness explained by area. Fragment area was also significantly correlated with both rarefied estimates of tree species richness (Pearson's $r = 0.67$, $P = 0.02$) and Fisher's $\alpha$ (Pearson's $r = 0.68$, $P = 0.02$). Area and density together

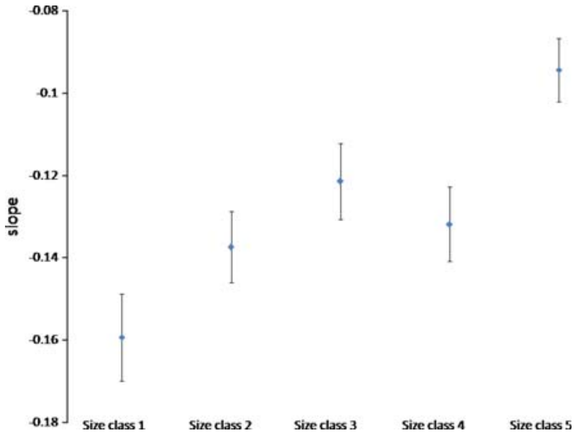


**Fig. 5** Slope values of the rank abundance curve with 95% CI for each of the five size classes

**Table 3** Mantel's summary statistics for correlation between geographical distance and species compositional similarity

| | Mantel's test statistic (*r*) | *t* value | Significance value |
|---|---|---|---|
| Trees | 0.5286 | 3.0901 | $P < 0.05$ |
| Lianas | 0.0649 | 0.4147 | $P > 0.05$ |
| Shrubs | 0.1620 | 0.9777 | $P > 0.05$ |
| Epiphytes | 0.0649 | 0.4147 | $P > 0.05$ |

**Table 4** Comparison of values of beta diversity for trees between fragments and reserve forest with number of sites indicated in parenthesis

| | Fragments (11) | SD | Reserve forest (2) | SD |
|---|---|---|---|---|
| Mean alpha | 28.81 | 10.13 | 48 | 2.82 |
| Gamma | 101 | | 75 | |
| Cody's beta | 0.54 | 0.07 | 0.56 | |
| Whittaker's beta | 4.70 | 1.40 | 2.54 | 0.15 |

accounted for most of the variation in liana and epiphyte species richness ($R^2 = 0.57$, $P = 0.03$ and $R^2 = 0.53$, $P = 0.04$ for lianas and epiphytes, respectively). However, neither area nor density could explain the variation in shrub species richness. Isolation did not explain the residual variation after accounting for area, since inter-patch distance was not correlated with residuals resulting from species–area regression, as revealed by Mantel's test. A significant positive correlation was observed between geographical distance and species compositional dissimilarity for trees (Table 3). This indicates that only trees showed significant spatial autocorrelation in species composition, implying that fragments closer to each other are more similar in species composition than ones that are further away.

## Beta diversity

Using the additive partitioning model of Lande, the average $\alpha$ diversity was 26.03% while average $\beta$ diversity was 73.97%. This shows that most of $\gamma$ richness is contributed by $\beta$ richness. Although the mean $\alpha$ and $\gamma$ richness was much higher in continuous (reserve) forest than the fragments, Whittaker's $\beta$ richness was found to be slightly higher among fragments than among continuous forest (Table 4). Higher values for beta diversity between fragments, in spite of lower gamma and alpha diversity compared to Reserve Forest, partially reflect inter-patch habitat heterogeneity resulting in higher species turnover.

## Nestedness

All the four plant groups exhibited moderate levels of nestedness (Table 5). Epiphytes were found to be the most ordered followed by lianas and trees. Ordering the matrix according to temperature resulted in lower overall matrix temperature. The matrix temperature when ordered by this method was $T = 20.61$, 18.76,

**Table 2** Parameters of species–area relationship for 11 fragments derived from linearised form of power function

| | $R^2$ | $F$ | Sig. | Parameter Estimates | | |
|---|---|---|---|---|---|---|
| | | | | $c \pm$ SE | $z$ | 95% CI for z |
| Trees | 0.74 | 26.15 | 0.00 | 1.297 ± 0.06 | 0.29 | 0.16 to 0.42 |
| Lianas | 0.18 | 2.06 | 0.18 | 0.701 ± 0.18 | 0.19 | 0 to 0.89 |
| Shrubs | 0.07 | 0.74 | 0.41 | 1.324 ± 0.07 | 0.06 | 0 to 0.22 |
| Epiphytes | 0.27 | 3.37 | 0.09 | 1.173 ± 0.14 | 0.24 | 0 to 0.54 |

**Table 5** Nestedness and matrix temperature (when packed according to species richness)

| | Matrix temp. | Simulated temp. | SD | *Z*-score | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|
| Trees | 26.34 | 55.91 | 2.71 | −10.9 | 50.62 | 61.04 |
| Lianas | 24.63 | 47.84 | 5.27 | −4.4 | 38.08 | 58.82 |
| Shrubs | 31.95 | 56.65 | 3.8 | −6.5 | 49.09 | 64.26 |
| Epiphytes | 21.62 | 55.01 | 3.74 | −8.93 | 47.59 | 62.09 |

26.68 and 18.58 for trees, lianas, shrubs and epiphytes, respectively.

Fragment area was significantly correlated with matrix temperature (Spearman's coefficient = 0.86, $P = 0.001$) for trees species only showing that only trees were nested along the area gradient. From correlation of geographical distance matrix with absolute differences in patch temperature for each pair of fragments, we found that isolation could not explain the species nestedness pattern in any of the plant groups.

## Discussion

### Species richness

### *Effect of area and isolation*

A positive species–area relationship, as observed for trees indicates that species richness was a function of patch area, highlighting once again the importance of area as one of the most important determinants of species richness in fragmented habitats. The rate at which species accumulate with area or the z value for trees ($z = 0.29$) and for epiphytes ($z = 0.24$, but with wider confidence intervals) in the present study lies within the canonical range proposed by Preston (1962) and MacArthur and Wilson (1967). Rarefied estimates of species richness indicate that passive sampling was not responsible in generating significant positive correlation between area and tree species richness, as area was significantly correlated with tree species richness even after controlling for sample size and abundance. Thus, increasing trees species richness was not because of larger patches containing larger samples and effectively more species, as proposed by the passive sampling hypothesis (Connor and McCoy 1979).

Isolation plays an important role in colonization processes and is one of the important predictors of species diversity in fragmented biotas (MacArthur and Wilson 1967; Simberloff 1972). In the present study, however, there was little evidence suggesting the influence of isolation on plant species richness. However, species compositional data provides evidence in support of inter-patch immigration which is revealed by a significant spatial autocorrelation for trees. It has been predicted that 'reciprocal colonisation' or immigration from neighbouring patches should result in spatial autocorrelation with respect to species composition (Preston 1962). Spatial autocorrelation of trees species observed in our study could be either because of persistence of species in a once contiguous landscape or because of influx of species from the surrounding patches (Hanski 1999).

### *Effect of density*

For trees and lianas, both species density and species richness were lower in smaller fragments than larger fragments and continuous reserve forest. This was partly because smaller fragments had lower stem density, and density increased with an increase in fragment area. Many studies dealing with species–area relationship do not consider correlation between density and area (Preston 1962; MacArthur and Wilson 1967). However, this correlation between area and density has been documented by a few other studies, particularly those carried out in anthropogenic habitat fragments. A similar pattern was observed in a study carried out in forest fragments of Southern Western Ghats, where stem density was correlated with patch area and negatively correlated with the disturbance score (Muthuramkumar et al. 2006). In the present study, the reduced density in smaller fragments was largely attributed to a low proportion of young trees belonging to smaller girth classes. The lower tree density could be a result of higher edge to area ratio and a subsequent increase in exposure to the physical environment. This makes smaller patches prone to large number of gaps that eventually affect tree regeneration and recruitment (Lovejoy et al. 1986; Turner 1996; Laurence et al. 1998).

## Nestedness

Our results clearly indicate that the four plant life forms in fragmented landscapes of Kodagu show an ordered species composition. Nestedness temperature in the present study was higher than values observed for plants in other matrix types such as heathland relicts, isolated mountaintops and fragments in agricultural matrix (Piessens et al. 2004; Bruun and Moen 2003; Butaye et al. 2001). This could be because of the nature of the surrounding matrix that has helped in maintaining similarity in species composition between fragments and reserve forest (Bhagwat et al. 2005a) by facilitating sufficient movement of propagules and pollen flow through the landscape and thus keeping patch extinction low (Piessens et al. 2004; Watling and Donnelly 2006). This effect, often referred to as rescue-effect, was first predicted and then observed for arthropods on isolated thistle plants (Brown and Kodric-Brown 1977), and subsequently many other ecosystems, for e.g. plants in heathland fragments (Piessens et al. 2004). The comparatively low degree of nestedness observed for the plant groups in our study is also consistent with the hypothesis that extinction within patches that originally contained the same set of species, like the forest fragments in the study, should result in irregular and less nested patterns (Darlington 1957).

## Life history and factors influencing nestedness

### *Area*

Area dependent patch extinction has been widely found to be the most important process influencing nestedness (Wright and Reeves 1992; Atmar and Patterson 1993; Watling and Donnelly 2006). However, a similar study dealing with core forest plant species found contrasting results, where patch area did not determine nestedness in forest plants although a significant species–log (area) correlation was observed (Honnay et al. 1999). Trees were the only life form in which the nested pattern was influenced by area and the only group to exhibit a significant species–area relationship. This study therefore provides substantiation in support of patch area as a predictor of nestedness when species richness is significantly correlated with area. Principal processes like area dependent extinction and isolation dependent colonisation, however, did not show any influence on nestedness in lianas, shrubs and epiphytes. In fragmented communities, isolation dependent colonisation is a less likely process as such communities often undergo species relaxation post fragmentation, unlike the colonisation-dominated biotas of island archipelagos (Patterson 1987; Patterson 1990; Wright and Reeves 1992). Area showed a strong influence only on tree species. This is because among the studied life forms, trees probably experience the greatest space constraint and thus are directly influenced by patch area. In addition, the diversity and species composition of trees is relatively independent of other life forms.

### *Habitat diversity*

In the case of epiphytes, most species recorded in smaller fragments were light demanding species which grew abundantly along forest edges, tree fall gaps and in coffee plantations where canopy is mostly open. Smaller fragments favoured the growth of such epiphytes since they had lower canopy cover and stem density. However, relative density of few epiphytic species that require high shade and moisture (such as *Loxoma straminea*, *Phalaenopsis mysorensis* and *Gastrochilus acaulis*) were higher in the interiors of larger fragments. Our findings are consistent with the earlier finding of De Walt et al. (2000) and Padmawathe et al. (2004) that diversity and species composition of lianas, shrubs and epiphytes was dependent on tree structural diversity. Additionally, as epiphytes are highly vagile they can disperse across very large distances. High species richness of epiphytes in medium-sized fragments (Size class-3) was because of high structural diversity. Fragments in this size class had both a prominent edge and a relatively undisturbed interior zone, unlike Size class-1 in which fragments were too small to have a well-defined interior. Medium-sized fragments therefore captured maximum structural heterogeneity and consequently had high habitat diversity allowing for the coexistence of many species. This finding is further supported by the fact that about 85% of total epiphytic species were recorded in Size class-2 and 3. Reserve forests on the other hand, were structurally homogenous on account of their high tree density and unbroken canopy cover. As a consequence they could only support a few epiphytes such as shade loving *Asplenium nidus*.

Observed patterns for lianas and shrubs can be explained similarly. We however, detected that reserve forest had a different set of shrub and liana that were absent in fragments, a trend not observed for epiphytes. These shrubs and lianas could be the species sensitive to fragmentation or those that have specialised requirements. The absence of these species from the fragments may be due to lack of suitable microhabitat or species relaxation due to deterioration in habitat after fragmentation, rather than area dependent extinction. Spatial turnover could also be responsible for the observed change in species composition (Gentry 1988; Benitez-Malvido and Martinez-Ramos 2003). The scale of the present study, however, was too small for spatial turnover to exert a strong influence on the changes in species composition. The influence of light, structural diversity and other habitat variables causes us to suspect that, rather than colonisation or extinction processes, nested distribution of habitats (Honnay et al. 1999; Patterson and Atmar 2000) is the most likely cause for nestedness in epiphytes, shrubs and lianas.

### *Dispersal ability*

Studies that have examined the effect of dispersal ability have highlighted its strong influence on distribution patterns of forest plants (Matlac 1994; Bossuyt et al. 1999). Species with poor dispersal ability are the most nested, while wind and bird dispersed plants are the most ubiquitous (Kadmon 1995; and for exceptions see Schoener and Schoener 1983; Ryti and Gilpin 1987). Our findings were, however, contrary to the above mentioned studies. We noted that about 33% of epiphytes were found to be adapted for bird dispersal while pteridophytes and orchids, which constituted 56% of epiphytes, were dispersed through microspores and are likely to be carried over extremely long distances by wind. Epiphytes were therefore most vagile among the four life forms, and while we expected this group to exhibit high degree of disorder, it was found to be the most nested. Our findings agree with those of Crowe (1979) who found that pioneer weed species with high dispersal ability exhibited colonisation driven nestedness pattern in recently vacated plots.

Shrubs differ greatly from epiphytes in dispersal methods. Shrubs fail to disperse themselves over long distances because most species are autochorus and occupy the forest understorey in which wind is an ineffective agent for seed dispersal (Honnay et al. 1999). Because of these factors, shrubs can be expected to exhibit maximum nestedness. Our results, however, reveal that shrub communities were the most disordered among the four plant life forms, and the observed patterns may be because of two reasons. First, the forest fragments in the present study represent remnants of once contiguous forest (unlike islands). Hence it is apparent that most, if not all of the species present in these patches were also present prior to fragmentation (except epiphytes which may have colonised the fragments post fragmentation). It is therefore unlikely that the species assemblages have been primarily shaped by colonisation of species dispersing from surrounding areas (Wright and Reeves 1992). Second, very static species like the shrubs of the forest understorey are unable to colonise to other habitats and therefore are insensitive to patch isolation (Honnay et al. 1999). In conclusion, the patterns we observe and report for epiphytes, shrubs and lianas present no evidence in favour of selective dispersal affecting nestedness of different plant groups.

## Conclusions

Our study underscores the importance of comparing data across different plant groups in examining the response of plant communities to habitat fragmentation. While large contiguous forests maintain a much larger proportion of regional species on account of their larger area, they do not adequately represent the landscape and habitat heterogeneity within the region. This is partly because, the forest fragments in the region are more spatially separated, and as a consequence they collectively support more diverse life forms than larger continuous forests. Second, higher structural heterogeneity exhibited by the fragments suggests that, unlike continuous reserve

**Table 6** Number of species recorded in the fragments and reserve forest of Kodagu district that are endemic to Western Ghats, India

| Life form | Forest fragments ($n = 11$) | Reserve forest ($n = 2$) |
|---|---|---|
| Trees | 33 (8) | 29 (4) |
| Lianas | 7 (2) | 6 (1) |
| Epiphytes | 15 (15) | 0 |
| Understorey plants | 14 (5) | 10 (2) |
| Total | 69 (30) | 45 (7) |

Numbers in parentheses indicate exclusive species

Ahmedullah and Nayar 1987; Ramesh and Pascal 1997; Gopalan and Henry 2000

forests, these fragments offer more intra patch habitat diversity to life forms such as epiphytes, shrubs and lianas. Hence, intra patch habitat diversity and inter patch landscape heterogeneity are very effective in maintaining the total pool of regional species diversity, as has been pointed out by previous studies (Honnay et al. 1999; Bhagwat et al. 2005a; Muthuramkumar et al. 2006). Maintaining large tracts of forest alone would effectively help preserve only a part of regional plant diversity (Tscharntke et al. 2002). This deficiency of reserve forests has very well been compensated for by locally protected forest fragments in the Kodagu landscape, which is borne out by several observations. First, in comparison to the reserve forests, all the fragments studied collectively house a greater number of plants endemic to the Western Ghats—Sri Lanka biodiversity hotspot (Table 6). Secondly, our study determined that these fragments are particularly important for epiphytes since the only other land use type which harbour comparable levels of epiphyte diversity of epiphytes are the privately owned coffee plantations which maintain native tree cover. These findings have also been supported by some recent fragmentation studies from neotropics where small fragments were extremely valuable for maintaining regional plant diversity since they comprise of diverse native plant communities including endangered and economically important species (Arroyo-Rodrı́guez et al. 2008).

Existing sacred forest fragments and native tree friendly coffee plantations (Anand et al. 2008) therefore, provide a fine example of “reconciliation ecology” (Rosenzweig 2003). These traditional conservation and agricultural practices within the human-modified landscape of Kodagu jointly sustain a wider variety of plants than forest areas that are formally preserved and protected. The high diversity of shrubs and epiphytes recorded in sacred groves and plantations, respectively, suggests that these practices are compatible with the habitat requirements of certain life forms such as epiphytes. Williams et al. (2006) suggested that quality of surrounding landscape matrix is more important for persistence of plants within the forest remnants than the spatial attributes. Therefore, in the present scenario, safeguarding the native tree cover within the coffee plantations is crucial considering its role in maintaining plant diversity in forest remnants.

Our results indicate that the four life forms respond differentially to the degree of fragmentation. We therefore suggest prudence in using any one of these as a surrogate for others. Trees alone may not serve as good indicators to assess the effect of fragmentation and any conservation measures taken to mitigate species loss may not be effective unless different life forms within and across taxonomic groups are taken into consideration.

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