FRAGMENTATION CAUSES WOODY PLANT COMPOSITION DECLINE IN SACRED GROVE PATCHES IN THE PUDUCHERRY REGION OF SOUTHEAST INDIA

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Abstract. The fragmentation of tropical forests threatens plant community compositions worldwide. In the present study, we examined the impact of fragmentation on plant community compositions over 30 years in sacred forest grove fragments in southern India. For this study, we randomly selected 30 sacred grove patches (hereafter referred to as fragments) of different sizes to examine the effects of fragment size and historical changes on the plant community compositions. A total of 414 woody plant individuals consisting of 53 species belonging to 45 genera and 20 families were recorded from the 30 sites. The total area of the fragments was not significantly related to the current species richness or diversity, although there were significant negative relationships between the total fragment size and the species composition and between the total fragment size and the species evenness, indicating that fragmentation negatively impacted woody plant compositions. Interestingly, our results showed that the woody tree abundance was significantly and positively related to the total fragment size, suggesting a potential increase in recruitment due to the various forms of ongoing human disturbances. Moreover, the woody plant species compositions may be declining in these venerated forest patches due to the removal of plant resources, potentially resulting in declining fragment sizes.
Keywords: *abundance, Coromandel Coast, disturbance, diversity, species-area relationship*

Introduction

Sacred groves are holy places where local people maintain tropical dry evergreen forest patches (TDEFs) due to the many resident tree species considered to be sacred (Ramanujam and Kadamban, 2001; Kent, 2013; Pradhan et al., 2019). The majority of sacred groves are forest patches of different sizes and shapes created through previous human disturbances and forest fragmentation. Human-induced fragmentation and land use changes significantly alter forest tree species richness and compositions worldwide

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(Haddad et al., 2015; Wilson et al., 2016; Zhao et al., 2019). Fragmentation has been shown to impact species diversity and composition both positively and negatively, although the negative responses are much more prevalent (Urban and Keitt, 2001; Haila, 2002; Ethier and Fahrig, 2011; Smith et al., 2011; Munguía-Rosas and Montiel, 2014; Mohandass et al., 2018). Fragmentation is a multidimensional process because it can influence numerous patch metrics, such as patch area, shape and isolation. A decrease in patch area may result in a decrease in the amount of available habitat (Laurance et al., 2007). Moreover, a decrease in the area of a fragment may result in a decrease in the amount of forest interior relative to the edges, possibly resulting in a loss of species given that forest interiors are more similar to pre-fragmentation conditions than forest edges (Petit et al., 2004). Moreover, human-induced fragmentation may result in both direct and indirect disturbances that may influence the spatial arrangement and habitat quality of forest patches (Honnay et al., 2005; Guirado et al., 2007). Prior and ongoing disturbances of forest habitats may also increase patch isolation (Turner et al., 2001; Farina, 2006). Thus, in general, fragmentation results in negative effects on landscape-level plant diversity (Urban and Keitt, 2001; Haila, 2002), in part due to reductions in the available forest area leading to decreases in species diversity and population sizes (Dixo et al., 2009; Aguirre-Gutiérrez, 2014).

Larger tropical forest fragments support more species than small fragments do (Munguía-Rosas and Montiel, 2014; Aguirre-Gutiérrez, 2014). In addition to the available area, the species abundance per patch may also be influenced by the dispersal capacity of the resident species, which may determine the functional isolation of patches (Hubbell, 2001). The species richness of patches may influence different environmental conditions, species traits and the ecological conditions of the fragments, which can be determined by the quality of the available resources (Petit et al., 2004; Aparicio et al., 2008; Struebig et al., 2011).

On the Coromandel Coast of South India, sacred forest grove patches range across an array of sizes. There have been limited assessments of the impacts of fragmentation and patch size on the woody tree species richness and abundances in sacred groves of the Coromandel Coast of South India. In this study, we assessed the impacts of fragmentation on tree species richness and abundance in relation to the patch area among different sizes of sacred groves around the Puducherry region of South India, including the influence of historical patch sizes. Thus, this study addresses the following hypotheses: (i) the richness, abundance, composition, diversity and evenness of woody species are related to the total fragment size; (ii) the present fragment sizes differ from the past fragment sizes due to the effects of historical human disturbance factors, and these differences subsequently impact the current measurements listed in hypothesis I; and (iii) species compositional patterns differ with fragment size.

Methods

Study area

The study was conducted in recognized sacred groves (forest fragments) of the tropical dry evergreen forest of the Coromandel Coast of the Puducherry region in southeast India. In the study area, we randomly selected 30 sacred groves for analysis, and the locations of the study sites are marked on the map shown in *Figure 1*. The names of the sites and sacred groves are presented in *Table 1*. The weather data were collected in the Ecolake Estate project located 10 km away from the Puducherry seashore. The climate of the

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study area is a maritime tropical climate with an asymmetric rainfall regime. The weather is generally humid and hot; the average annual temperature was 28.68 °C in Puducherry from 2011 to 2015 (*Fig. 2*), and the daily mean temperature difference was 8 °C between summer and winter (Krishnakumar, 2018). The southwest monsoon contributes 20% of the total rainfall across the July–September period, but the retreating northeast monsoon accounts for the majority of the yearly rainfall (61% of the total) during the principal rainy season covering October, November and December. The mean annual rainfall in the Puducherry region was 1373 mm, with a mean of 57.25 rainy days (Ramanujam and Kadamban, 2001; Krishnakumar, 2018). The weather conditions of the Puducherry region consist of a tropical wet and dry season according to the Koppen-Geiger classification (Peel et al., 2007); however, the dry season comprises a prolonged period of the year, from January-September.

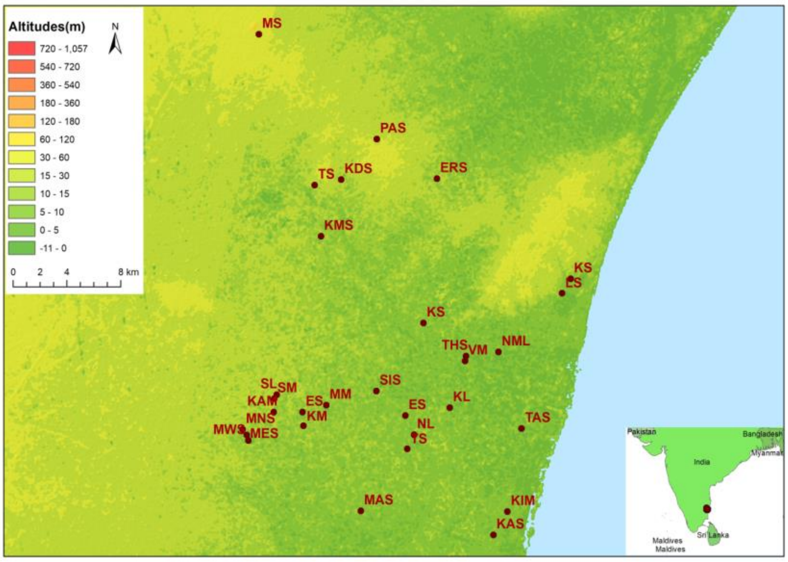

Figure 1. *Map showing the 30 sites of sampled sacred grove forest patches in the inland Puducherry region of southern India*

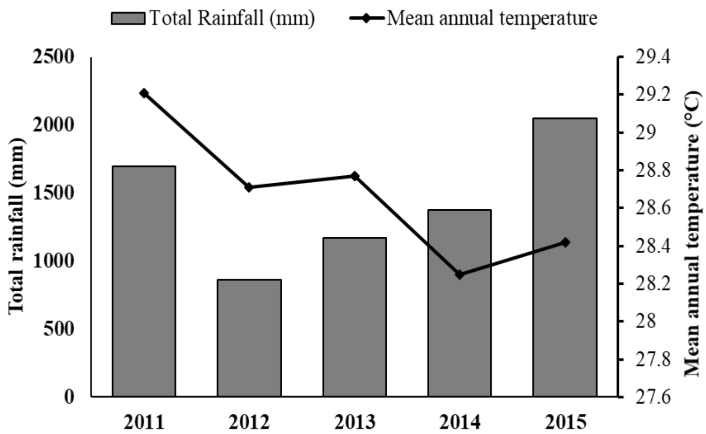

Figure 2. *The patterns of rainfall and temperature in the inland Puducherry region from 2011 to 2015 are shown. The maximum total rainfall was recorded in 2015, and the minimum total rainfall was recorded in 2012. The mean annual temperature reached a maximum in 2011 (29.2 °C), and the minimum rainfall was recorded in 2014 (28.2 °C)*

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Table 1. *Site name, latitude (°N) and longitude (°E), fragment size, total (historical) fragment size (ha), present fragment size (ha), species richness, species abundance, species composition (%), Shannon diversity index, Simpson diversity index and evenness of woody species in the sacred groves of the Puducherry region, South India*

Site number	Site name	Site code	Latitude (N)	Longitude (E)	Fragment size	Total size (ha)	Present fragment size (ha)	Reduction	Species richness	Abundance	Species composition (%)	Shannon	Simpson	Evenness
1	Villianur	VM	11°54’39.82”	79°45’19.42”	Medium	3.2 ± 0.848	0.13	3.07	17	49	34.69	2.33	0.86	0.6
2	Koodapakkam	KS	11°56’09.34”	79°43’40.70”	Small	0.45 ± 0.0617	0.04	0.41	5	8	62.5	1.49	0.75	0.89
3	Lawspet	LS	11°57’19.88”	79°49’10.74”	Small	0.17 ± 0.00667	0.07	0.1	9	12	75	2.1	0.86	0.9
4	Thennapakkam	TS	11°51’12.89”	79°43’01.52”	Small	0.35 ± 0.008	0.04	0.31	5	9	55.56	1.52	0.77	0.92
5	Embalam	ES	11°52’31.42”	79°42’57.55”	Small	0.19 ± 0.013	0.05	0.14	7	13	53.85	1.89	0.84	0.94
6	N. Manaveli	NML	11°55’01.30”	79°46’39.38”	Large	5.40 ± 0.37	0.02	5.38	4	9	44.44	1.27	0.69	0.89
7	Nathamedu	NL	11°51’46.32”	79°43’17.89”	Large	5.6 ± 0.174	0.06	5.54	11	18	61.11	2.25	0.88	0.86
8	Korkadu	KL	11°52’50.08”	79°44’43.22”	Large	6.8 ± 0.326	0.08	6.72	10	31	32.26	1.91	0.81	0.68
9	Kalmandapam	KM	11°52’07.59”	79°38’54.28”	Medium	4.5 ± 0.38	0.04	4.46	6	18	33.33	1.51	0.74	0.76
10	Kariyamanikkam	KAM	11°52’39.77”	79°37’43.27”	Medium	4.6 ± 0.263	0.04	4.56	8	12	66.67	1.98	0.85	0.9
11	Sooramangalam	SL	11°53’20.28”	79°37’50.42”	Large	6.5 ± 0.235	0.04	6.46	7	17	41.18	1.81	0.82	0.87
12	Sooramangalam	SM	11°53’10.94”	79°37’44.77”	Medium	2.8 ± 0.653	0.03	2.77	4	7	57.14	1.28	0.69	0.9
13	Mitta mandagapattu	MM	11°52’56.17”	79°39’48.87”	Medium	1.2 ± 0.133	0.03	1.17	3	5	60	1.06	0.64	0.96
14	Sivaranthagam	SIS	11°53’29.02”	79°41’48.46”	Small	0.9 ± 0.107	0.03	0.87	4	7	57.14	1.35	0.73	0.97
15	Eripakkam	ES	11°52’39.66”	79°38’52.18”	Small	0.5 ± 0.042	0.04	0.46	7	9	77.78	1.89	0.84	0.94
16	Madukarai East	MES	11°51’45.84”	79°36’39.28”	Small	0.11 ± 0.013	0.04	0.07	6	9	66.67	1.58	0.74	0.81
17	Madukarai West	MWS	11°51’32.60”	79°36’43.19”	Small	0.5 ± 0.026	0.02	0.48	5	5	100	1.61	0.8	1
18	Madukarai North	MNS	11°51’58.92	79°36’29.25”	Small	0.6 ± 0.058	0.04	0.56	7	11	63.64	1.77	0.79	0.84
19	Mayalam	MS	12.07’29.78”	79°37’08.11”	Small	0.3 ± 0.06	0.04	0.26	3	8	37.5	0.97	0.59	0.88
20	Manadau	MAS	11°48’46.97”	79°41’11.29”	Small	0.2 ± 0.04	0.03	0.17	4	6	66.67	1.33	0.72	0.94
21	K. Manaveli	KMS	11°59’33.55”	79°39’36.12”	Small	0.73 ± 0.119	0.03	0.7	5	8	62.5	1.56	0.78	0.95
22	Thiruvakkarai	TS	12°01’34.19”	79°39’20.93”	Small	0.83 ± 0.092	0.04	0.79	6	12	50	1.75	0.82	0.96
23	Thirumangalam	THS	11°54’51.55”	79°45’21.85”	Small	0.32 ± 0.054	0.03	0.29	4	7	57.14	1.28	0.69	0.9
24	Karuvadikuppam	KS	11°57’53.58”	79°49’31.69”	Small	0.44 ± 0.0562	0.06	0.38	9	16	56.25	1.99	0.84	0.82
25	Kannikoil	KAS	11°47’50.25”	79°46’27.07”	Small	0.6 ± 0.044	0.06	0.54	10	18	55.56	2.17	0.87	0.87
26	Kirumampakkm	KIM	11°48’45.50”	79°47’00.76”	Medium	1.1 ± 0.163	0.12	0.98	16	33	48.48	2.51	0.9	0.77
27	Thavalakuppam	TAS	11°52’01.08”	79°47’34.52”	Small	0.7 ± 0.076	0.08	0.62	11	18	61.11	2.26	0.88	0.87
28	Parankal	PAS	12°03’22.89”	79°41’49.38”	Small	0.5 ± 0.03	0.06	0.44	6	15	40	1.52	0.72	0.76
29	Erraiyur	ERS	12°01’49.76”	79°44’12.77”	Small	0.9 ± 0.01	0.09	0.81	10	13	76.92	2.25	0.89	0.94
30	Kadakam Pattu	KDS	12°01’47.22”	79°40’24.38”	Small	0.45 ± 0.022	0.04	0.41	7	11	63.64	1.85	0.83	0.91

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Biocultural perspectives

The majority of the examined sacred groves were located away from human habitation, although 5 sacred grove patches were located relatively close in proximity to human settlements, within a distance of 500 meters. At the edge of each sacred grove was an open shrine of Lord Siva under a banyan tree with a granite bull (Nandhi) facing the eastern side. Well-built, modern, concrete temples were located in the center of each grove. The presiding deities include Selliamman, Iyynarappan and other gods and powerful goddesses worshipped by the people, and in some temples were broken terracotta horses (*Fig. 3A*, *B*). The villagers claim that the entire stretch between the temples, including some of the study sites along with the intervening plantations, was a continuous forest until the 1970s, but large tracts were subsequently cleared for raising *Eucalyptus* plantations. However, most of the sacred groves had clear cutting of trees for further construction of god statues, and other temple and building construction developments were established within the temple borders (*Fig. 3C*, *D*). Information on the locations of the sacred groves and the temple complexes was recorded by direct observations during field visits. Traditions, beliefs, taboos, restrictions and folklore pertaining to each temple were recorded from local devotees randomly selected from the community.

Figure 3. *(A) A sacred forest grove patch that was reduced to a patchy forest area due to deity statue construction in the Suramangalam site. (B) The forest patch area was reduced due to ground floor development in the sacred grove of the Lawspet site. (C and D) Sacred forest tree individuals were removed for further temple construction in the Madukarai and Villianur sites of the inland Puducherry region of Southern India*

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Assessment of disturbances

The area of the total (historic) fragment size of each sacred grove was recorded by interviewing elderly locals > 60 years of age who were living near the sacred groves (*Table 2*). The total (historical) fragment size was estimated using their (the interviewed individuals') recollection of the size of the sacred groves in the 1980s (a minimum of 36 years ago), while the existing fragment sizes were measured through direct sampling. The incidence and series of disturbance activities of the sacred groves over the period from 1980-2016 were identified using the aforementioned interviews (*Table 2*). At each site, we interviewed 6-10 respondents, and the average size of the area was used for further data analysis. No accurate area size was available in any of the records. The outcome data of the oral interviews delivered important conservation research findings (Young et al., 2018).

Table 2. *Various disturbance attributes recorded as having occurred over the period from 1980 to 2016 in the examined sacred groves of the Puducherry region, southeast India*

S. No.[#]	Disturbance attributes
1	**Road establishment**
	a. Creation of a bridle path
	b. Vehicle parking
	c. Creation of a cement floor or siting place for devotees
2	**Land encroachment**
	a. Removal of trees in the edge zone of the forest area
	b. Agricultural land expansion and removal of trees
	c. Creation of a cement floor for crop drying
3	**Land use for general uses**
	a. Cooking construction place and cooking inside the forest
	b. Devotees' congregation place for festivals/ceremonies
	c. Trees cut for firewood prior to festival season
4	**Habitat Conversion/Resource removal**
	a. Grass and weed colonization after tree removal
	b. Secondary vegetation establishment
	c. Plantation of edible and ornamental plants
5	**Land use change for personal use**
	a. Encroachment for house construction (temporally)
	c. Creation of roads to access houses
	b. Creation of home gardens

[#]Disturbance number

Plant sampling

We counted the plant individuals and collected plant samples from 30 sites from August 2016 to February 2017 in the inland Puducherry region among different sacred grove patches. In each sacred grove patch, 10 × 10-m quadrats were laid, and all woody species above 3 cm in dbh (Diameter at Breast Height) were sampled in each sacred grove, with the total sampled areas ranging from 0.03 to 0.12 ha in the 30 sacred grove patches. The fragments were placed in size categories based on their existing areas, with those with areas < 0.01 ha considered small, > 0.01 to < 1 ha considered medium-sized, and > 1 ha considered large. Quadrats were laid contiguously as stratified sampling, but

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the continuity was broken to exclude temples and buildings whenever necessary. In particular, we sampled the area of occurrence of woody plant species that were composed of shrubs and trees. We excluded nonwoody species from this study. Species identification was counterchecked with the herbarium collections of the French Institute of Puducherry, India. The nomenclature of each species follows the Flora of Tamil Nadu (Nair and Henry, 1983; Henry et al., 1987, 1989), with the exception of updated species being incorporated from the website www.theplantlist.org. All the sampled herbarium specimens were deposited in the Department of Botany, Tagore Arts College, Puducherry, India.

Species richness, abundance, diversity and evenness

Biotic richness (at the species, genera and family levels) and stem abundance were counted in all 30 examined sacred groves. Species richness was defined as the number of species in each sacred grove, and abundance was defined as the number of individual stems above 3 cm in dbh in each sacred grove (Mohandass et al., 2018). For the floristic analyses, all collected data were pooled at the patch level, and the total number of species and individuals were tallied. Using the pooled data, the overall species richness, genera- and family-level richness, abundance, and diversity were calculated. The dominant species were considered to be those that were the most abundant in the inventory, and the dominant family was represented by the highest number of stems.

We calculated two diversity indices: the Shannon–Wiener index (H’) was calculated using the following formula:

$$H' = -SP_i \ln P_i$$

where $P_i = ni/N$, n_i is the number of individuals of a species, and N is the total number of identified plants in a sacred grove.

Species evenness (E) was calculated as follows:

$$E = H'/H'_{max}$$

where H’ is the Shannon–Wiener index and H'_{max} is In*S* (Magurran, 2004).

Data analyses

All the data were logarithmically transformed to allow for analytical assumptions of normality for each forest patch, including for fragment sizes and other floristic variables. The total fragment area size and existing fragment area size were analyzed by paired t-tests to compare the averages before and after the changes in fragment size. Principal component analysis was applied to test the correlations between the total fragment sizes and among different vegetation parameters, such as species richness, abundance, species composition, and the Shannon, Simpson and evenness indices. PCA was also applied to test the relationship between each species distribution among the 30 fragment sites based on presence/abundance data to determine whether there was significant positive or negative correlations in relation to fragment area. Regression analysis was used to test the effect of the existing fragment size on each species response. All statistical analyses were performed using the software Past version 3.01.

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Results

Plant communities

A total of 414 individuals from 53 species belonging to 50 genera and 30 families were recorded from the 30 examined sacred groves (*Table A1*). Of these, 51 woody trees and 2 shrubs were counted, with occasional nonwoody species also recorded (*Table A1*). Among all examined patches, the species richness ranged from 3 to 17, the abundance ranged from 5 to 49, the species composition ranged from 32.26 to 100%, the Shannon index ranged from 0.97 to 2.51, the Simpson index ranged from 0.59 to 0.90, the evenness ranged from 0.60 to 1.00 (*Table 1*), and the number of plant families ranged from 3 to 15. The means of these variables among the patches was: species richness, 7.20 ± 0.63; mean abundance, 13.80 ± 1.72; species composition, 57.37 ± 2.72; Shannon index, 1.73 ± 0.07; Simpson index, 0.79 ± 0.01; evenness, 0.87 ± 0.02; and number of plant families, 6.27 ± 0.56 (*Table 1*).

The species richness and abundance of all woody species ≥ 3 cm in dbh were recorded from 30 sacred groves. The frequency of occurrence of individuals varied among the number of species: species that showed < 6 stems had a high frequency of 38%, while species with 6 < stems < 12 had a 6% frequency of occurrence. In addition, species with 12 < stems < 18 had a 4% frequency of occurrence. In addition, the individuals with between 48 and 54 stems represented 1% of the total frequency (*Fig. 4*).

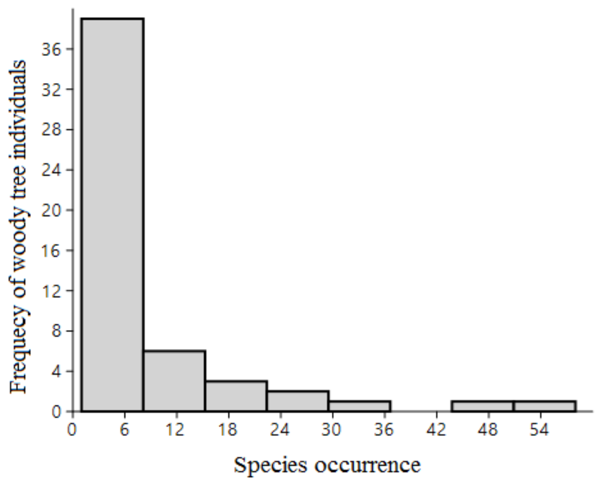

Figure 4. *Frequency of woody tree individuals based on species occurrence among 30 sacred groves in the inland Puducherry region of southern India*

The rank of the relative abundance curve is shown on the Y axis, and the abundance rank is shown on the X-axis of *Figure 5*. On the X-axis, the most abundant species was ranked 1, the second most abundant was ranked 2, the species with common abundances were ranked 10-15, the species with uncommon abundance were ranked 25-35, and rare species were ranked 45-54 (*Fig. 5*). The Y-axis shows the number of individuals, which is a measure of species abundance.

The examined sacred groves were dominated by *Azadirachta indica* A. Juss. (14%) and *Cocos nucifera* L. (12%), both of which are large trees, followed by *Ficus benghalensis* L. (8%), *Tectonia grandis* L.f. and *Borassus flabellifer* L. (6%), *Mangifera indica* (5%), *Musa paradisiaca* L. and *Tamarindus indica* L. (4%), then

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Couroupita guianensis Aubl., *Aegle marmelos* (L.) Correa., *Ficus racemosa* L., *Ficus religiosa* L., *Lepisanthes tetraphylla* Radlk. and *Sapindus emarginatus* Vahl (3%). Some rare species were *Naringi crenulata* (Roxb.) D.H. Nicolson, *Neolamarckia cadamba* (Roxb.) Bosser., *Nerium odorum* Sol, *Phoenix sylvestris* (L.) Roxb., *Sterculia foetida* L. and *Thespesia populnea* (L.) Sol. ex Corrêa. Only two genera comprised 5 species, and the other recorded genera comprised single species. *Albizia* had 2 species, and *Ficus* had 3 species recorded in the 30 sacred groves. Thus, *Ficus* was the dominant family, followed by *Albizia*.

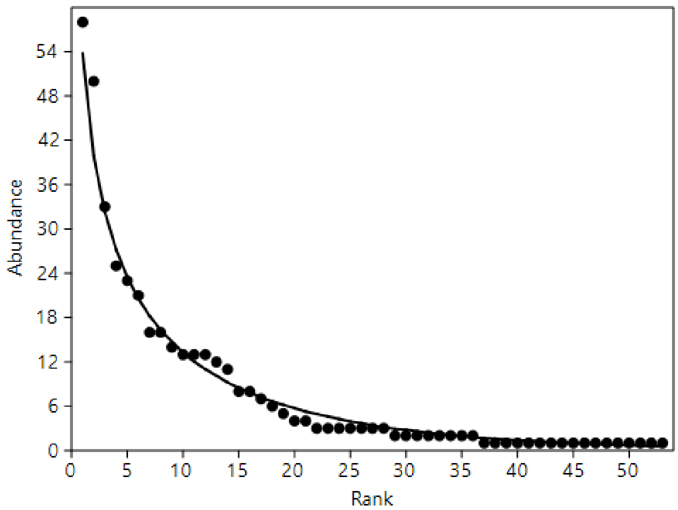

Figure 5. *Species ranked based on their tree abundances in 30 sacred groves in the Puducherry region of southern India*

Overall, abundance decreased with an increasing number of species among the 30 sacred groves. The abundance size class frequency distribution of the sacred grove stands exhibited a tendency towards a reverse J-shaped distribution (*Fig. 6*), indicating that the population was skewed towards species with fewer individuals and that species with greater numbers of individuals were disproportionally represented in the abundance of woody trees.

Arecaceae was the dominant family (19.08%) among the 30 sacred groves, followed by Moraceae (14.7%), Meliaceae (13.8%), Verbenaceae (6%), Sapindaceae (5.8%), Anacardiaceae (5.56%), Caesalpiniaceae (5.3%), and Fabaceae (4.83%). Five and seven families shared two and one species from each family, respectively (*Table A1*).

Fragment size reduced over time

All fragment size classes (small, medium and large) decreased significantly in size (small: $t = 8.327$, $N = 20$, $P = 0.0001$; medium: $t = 4.503$, $N = 6$, $P = 0.006$; large: $t = 18.14$, $N = 4$, $P = 0.0001$) over the examined time period (*Table 3*).

Impact of the total fragment size on the resident plant communities

Species richness did not show a significant relationship with total (historical) fragment size, whereas abundance showed a significant positive relationship with total fragment size. In contrast, species composition showed a significant negative

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relationship with total fragment size. The Shannon and Simpson indices were not significantly related to total fragment size, while evenness showed a significant negative relationship with total fragment size (*Table 4*).

The PCA of the fragment size and plant community composition showed a significant correlation (*Table 5*). The cumulative percentage variance of the plant community data showed that the first two PCA axes explained 95.2% of the variability among different fragment sizes. Of these, axes 1 and 2 explained 74% and 21.2% of the variance in fragment size in relation to the plant community, respectively (*Fig. 7*).

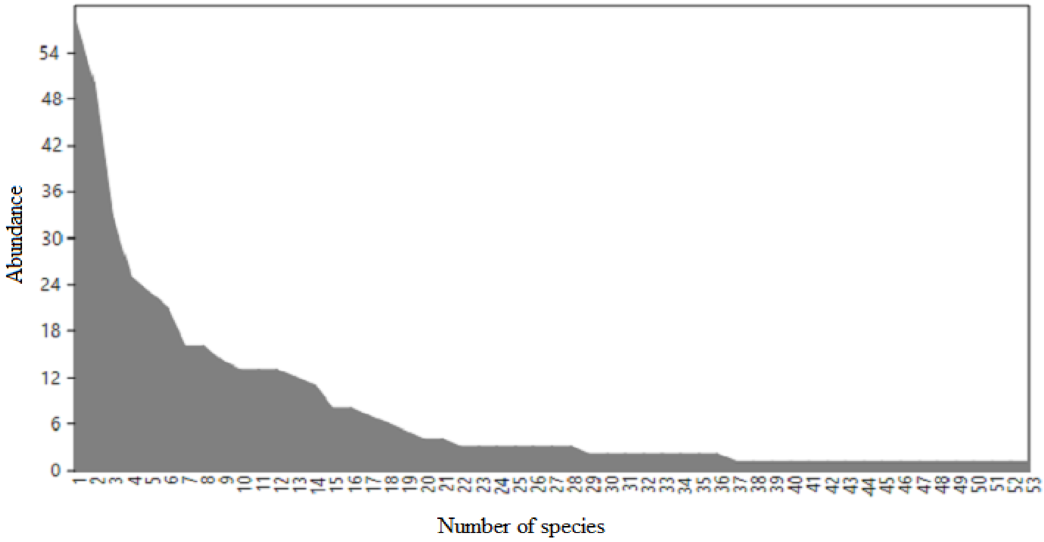

Figure 6. *Species richness and abundance patterns showed a reverse J-shaped curve from 30 sacred groves examined in the Puducherry region of southern India*

Table 3. *Average differences between past and present fragment size in the examined sacred groves of the Puducherry region, South India*

Fragment class	Fragment size (mean ha)			P-value
	Total fragment size (30 years ago)	Existing fragment size	Paired t-test	
Small fragments	0.49	0.05	8.327	0.0001
Medium fragments	2.90	0.07	4.503	0.006
Large fragments	6.08	0.05	18.142	0.0001

Table 4. *Effects of total fragment sizes on different floristic variables among the examined sacred groves of the Puducherry region, South India*

Floristic variable	Mean	Std. dev.	*r*	*P*
Species richness	7.20	3.45	0.20	0.142
Abundance	13.80	9.40	0.39	0.017
Species composition	57.37	14.88	-0.47	0.004
Shannon index	1.73	0.40	0.12	0.257
Simpson index	0.79	0.08	0.08	0.332
Evenness	0.87	0.09	-0.40	0.013

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Table 5. *Effects of total fragment size on different floristic variables according to principal component analysis (PCA) among sacred groves of different sizes in the Puducherry region, South India*

S. No.	Name of the sacred grove site	Site code	Fragment category	Existing fragment size (ha)	Total fragment size (ha)	Species richness	Abundance	Species composition	Shannon	Simpson	Evenness
1	Villianur	VM	Medium	0.13	3.2	0.610	0.696	0.590	0.575	0.571	0.576
2	Koodapakkam	KS	Small	0.04	0.45	-0.291	-0.312	-0.285	-0.283	-0.281	-0.281
3	Lawspet	LS	Small	0.07	0.17	-0.686	-0.684	-0.714	-0.701	-0.704	-0.704
4	Thennapakkam	TS	Small	0.04	0.35	-0.400	-0.407	-0.388	-0.392	-0.390	-0.391
5	Embalam	ES	Small	0.05	0.19	-0.649	-0.629	-0.650	-0.654	-0.655	-0.656
6	N. Manaveli	NML	Large	0.02	5.4	0.773	0.751	0.804	0.794	0.797	0.797
7	Nathamedu	NL	Large	0.06	5.6	0.833	0.834	0.804	0.817	0.814	0.813
8	Korkadu	KL	Large	0.08	6.8	0.912	0.970	0.919	0.899	0.898	0.901
9	Kalmandapam	KM	Medium	0.04	4.5	0.712	0.742	0.739	0.717	0.719	0.720
10	Kariyamanikkam	KAM	Medium	0.04	4.6	0.734	0.711	0.715	0.730	0.729	0.727
11	Sooramangalam I	SL	Large	0.04	6.5	0.877	0.892	0.887	0.879	0.879	0.878
12	Sooramangalam II	SM	Medium	0.03	2.8	0.489	0.448	0.508	0.509	0.512	0.512
13	Mitta mandagapattu	MM	Medium	0.03	1.2	0.110	0.057	0.140	0.138	0.144	0.143
14	Sivaranthagam	SIS	Small	0.03	0.9	-0.002	-0.032	0.018	0.017	0.020	0.018
15	Eripakkam	ES	Small	0.04	0.5	-0.231	-0.256	-0.250	-0.234	-0.235	-0.237
16	Madukarai East	MES	Small	0.04	0.11	-0.892	-0.896	-0.896	-0.893	-0.893	-0.891
17	Madukarai West	MWS	Small	0.02	0.5	-0.246	-0.314	-0.262	-0.236	-0.235	-0.237
18	Madukarai North	MNS	Small	0.04	0.6	-0.152	-0.159	-0.162	-0.156	-0.156	-0.156
19	Mayalam	MS	Small	0.04	0.3	-0.489	-0.483	-0.436	-0.465	-0.458	-0.457
20	Manapet	MAS	Small	0.03	0.2	-0.652	-0.683	-0.638	-0.636	-0.634	-0.634
21	K. Manaveli	KMS	Small	0.03	0.73	-0.082	-0.107	-0.076	-0.072	-0.071	-0.072
22	Thiruvakkarai	TS	Small	0.04	0.83	-0.019	-0.013	-0.010	-0.015	-0.015	-0.017
23	Thirumangalam	THS	Small	0.03	0.32	-0.448	-0.469	-0.428	-0.433	-0.430	-0.429
24	Karuvadikuppam	KS	Small	0.06	0.44	-0.275	-0.253	-0.290	-0.289	-0.291	-0.290
25	Kannikoil	KAS	Small	0.06	0.6	-0.137	-0.110	-0.155	-0.153	-0.156	-0.156
26	Kirumampakkam	KIM	Medium	0.12	1.1	0.146	0.206	0.113	0.112	0.108	0.109
27	Thavalakuppam	TAS	Small	0.08	0.7	-0.066	-0.045	-0.093	-0.085	-0.089	-0.089
28	Parankal	PAS	Small	0.06	0.5	-0.238	-0.205	-0.218	-0.237	-0.236	-0.233
29	Erraiyur	ERS	Small	0.09	0.9	0.038	0.029	0.004	0.024	0.020	0.019
30	Kadakampattu	KDS	Small	0.04	0.45	-0.277	-0.280	-0.286	-0.280	-0.281	-0.282

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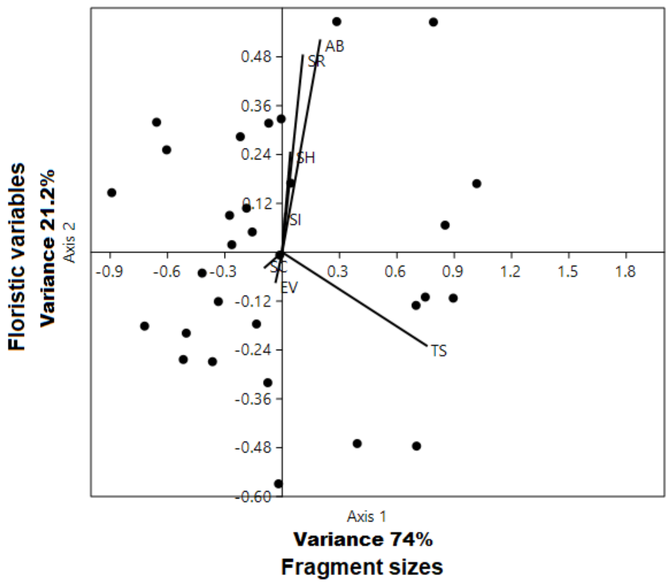

Figure 7. *Principal component analysis showed the relationships between different fragment sizes and floristic variables in Axis 1 (variance = 74%) and Axis 2 (variance 21.2%) from the examined sacred grove patches of the Puducherry region of South India*

Effect of existing fragment size on species distributions

Most species responded significantly to the existing patch size, although the direction of their response was not always consistent since a few species did not show any significant response (*Table A1*). PCA showed the species composition of the pooled data, with axis 1 describing 36.37% of the variance and axis 2 describing 17.64% based on the species presence/absence occurrence from each of the 30 sacred grove patches (*Fig. 8*).

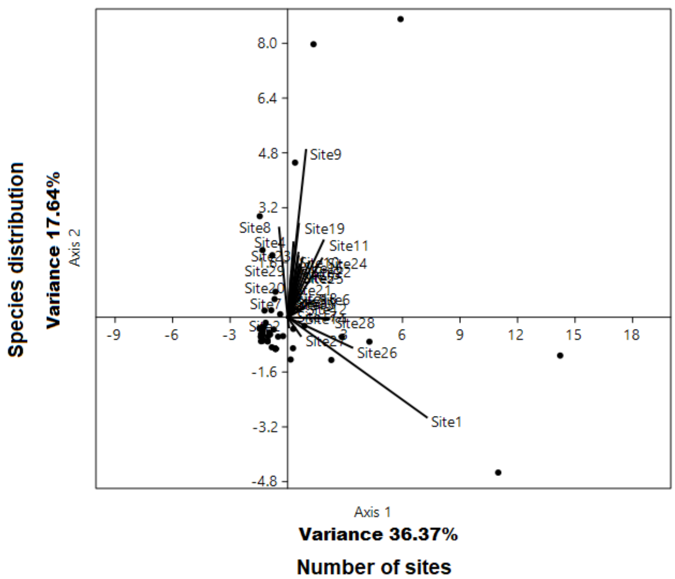

Figure 8. *Principal component analysis showed the relationships between site distribution and each species based on presence/absence data. X-axis 1 shows a variance of 36.37%, and Y-axis 2 shows a variance of 17.64% in relation to fragmented sites and to the species distributions of the sacred groves in the Puducherry region of South India*

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Species compositional patterns

The species composition pattern did not differ significantly among different fragment sizes. The overall mean rank value of different fragment sizes was 234.9 ($R = 0.159$; $P = 0.0766$). Of these, species composition also did not differ between large and medium fragments (Mean Rank Value = 25.23; $R = 0.212$; $P = 0.101$), between medium and small fragments (Mean Rank Value = 173.6; $R = 0.1034$; $P = 0.192$) or between large and small fragments (Mean Rank Value = 158.6; $R = 0.205$; $P = 0.106$).

Discussion

Current species richness was not significantly related to past fragment size or total fragment size in the forest groves of Puducherry, likely because the effective areas of the patches have often been reduced due to human disruption and encroachment. Moreover, fragment size had a larger influence on species richness than did total (historical) patch size, thus indicating that many species may have been extirpated by the identified patch size reductions. Sacred grove fragment size was also found to decline significantly in the region due to long-term human disturbance through tree harvesting at patch edges and encroachment for agricultural practices. Our results also suggest that the reduction in total fragment size has resulted in a concurrent decline in species population sizes and an increase in the number of fragments in the smaller size category. The decrease in fragment size is likely to result in degradation of the microenvironmental features in the fragments, leading to further declines in species richness (Campbell and Ortíz, 2011; Kettle and Pin Koh, 2014).

Species composition showed a significant negative relationship with total (historical) patch size. This finding is likely due to the ongoing human disturbance (such as logging and encroachment) of the forest patches. Moreover, declines in the plant community composition over time due to habitat fragmentation may have resulted from cascading effects on ecosystem properties (Tabarelli et al., 2012). In addition, the negative relationship between species composition and fragment area may also be due to factors such as matrix quality and historical legacies of human land uses in the areas surrounding the sacred groves (Driscoll et al., 2013; Ewers et al., 2013; Mesquita et al., 2015). Within the patches, however, the species composition may be influenced over time due to the colonization of disturbance-tolerant species (Mckinney and Lockwood, 1999; Tabarelli et al., 2012). Thus, the species composition of the patches may be concurrently influenced by colonization and extinction over time among the sacred groves (Jackson and Sax, 2010; Dornelas et al., 2014) in addition to gradual degradation due to ongoing human disturbances.

There was a significant impact of patch size on species composition in the examined forest fragments. Most of the examined small fragments displayed negative responses to fragment area, while medium and large fragments displayed positive responses. This finding indicates that fragment colonization may be driving compositional changes over time among the sacred grove fragments and that historical land uses may have also influenced the current plant community compositional changes. For instance, large trees (from successional climax species) may go extinct in patches after several decades due to a lack of recruitment in disturbed environments or through harvesting by locals. This, in turn, results in the creation of large gaps in the patches, leading to the further recruitment of disturbance-adapted species. Concurrently, small trees may also go locally extinct due to overharvesting for firewood, again creating more gaps that change

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the forest grove structures, leading to the patches remaining in an early successional stage. Moreover, the mentioned impacts may also lead to small fragments (as identified) that are increasingly isolated; both small fragment size and isolation contribute to depauperate resident tree communities (Laurance et al., 2018).

The identified ongoing reduction in fragment size in the study area is likely to result in a decline in the ecological functioning of the patches, such as seed dispersal, regeneration and tree stand replacement, which in turn may lead to the local extinction of species among sacred groves (Auffret et al., 2015; Berhanu et al., 2017). In the sacred grove patches, forest edges are exposed to intense and ongoing anthropogenic disturbances through practices such as agriculture and road development, which may also affect species recruitment. As a consequence, ongoing disturbances may prevent the recruitment of new seedlings to forest patches and edges or may result in increased levels of mortality due to habitat and microclimatic alterations (Comargo and Kapos, 1995; Turner and Corlett, 1996).

We used interviews to collect information of historical patch sizes and changes from local people and elucidate that long-term human intervention has highly influenced both the fragment sizes and ongoing disturbances of the examined forest grove patches (*Table 1*). Our findings suggest that the area of the examined fragments was significantly reduced, leading to negative impacts on species richness, species composition, species diversity (Shannon and Simpson indices) and evenness. However, the species abundance of the examined patches appears to have been positively influenced by disturbances, possibly due to the intervention of locals attempting to maintain woody sacred trees for religious purposes in larger fragments. Moreover, larger fragments are likely to maintain the abundance and diversity of woody species due to their fragment size (Laurance, 2008).

The sacred groves decreased in size across the period of time analyzed. In fact, the land area of sacred groves decreased by approximately 97% from the 1980s compared to that in 2016. Nevertheless, in the present study, large fragments maintained their species richness and abundances of woody species positively and consistently among sacred groves due to the slow process by which fragment areas decrease due to agricultural expansion and settlements. Even large or small fragments maintain few sacred trees due to cultural and ritualistic beliefs that species such as *Aegle marmelos* (L.) Corrêa, *Calophyllum inophyllum* L. *Couroupita guianensis* Aubl., and *Drypetes sepiaria* (Wight & Arn.) Pax & K. Hoffm. The same species found in larger fragments are also found in smaller fragments, thus indicating that the fragmentation process also maintains species specificity due to anthropogenic cultural perspectives. This suggests that changes in sacred grove landscape structure and functions across patch mosaics are influenced by human landscape alterations (Berhanu et al., 2017). In addition, losses of habitats affect interior and edge zones among patches, which influence native trees and are highly invisible as a result of human land use. Under these extreme conditions, sacred grove fragments cause small, isolated remnants of varying sizes to develop from the native original patch, which influences all margins and borders through conversion into other new landscapes by the consequences of building construction, cement floors, road establishment, agricultural expansion, and construction of temples and god statues. Similarly, an earlier study also reported that fragmentation influenced several small isolated remnant patches, which led native forests to become fragments of different small sizes due to agriculture, grazing land and human settlements (Laurance et al., 1998; Laurance, 2008).

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Conclusion

The present study represents the first investigation of the relationship between woody species richness and patch area in the sacred groves of Puducherry regions and thus shows that the species richness and diversity of woody trees are not related to fragment area. However, the abundance showed a significant positive response to fragment area due to the slow process of extinction caused by large natural fragment area sizes. Moreover, the species composition and evenness showed significant negative relationships with the total fragment size due to matrix effects. This indicates that long-term direct and indirect human intervention and disturbance might affect woody species composition, especially synanthropic species. Conventionally, the empirical evidence suggests that patch fragmentation is largely a matter of tree harvesting and thus influences habitat degradation at the edges and interiors of patches. In the studied sacred groves, human disturbances influence the spatial and temporal aspects of fragmentation that may reflect reductions in patch size. Traditionally, it is theorized that reductions in edge effects may affect patch sizes and site scales. We suggest that controlling reductions in patch size may be applicable by reducing human contact with sacred groves through closing unpaved roads and by letting woody growth close the forest edges. However, future studies are needed to examine the reproductive biology and regeneration of forest fragments. These studies may reveal the forest growth structure in relation to fragment size. Most of the fragment areas were encroached by human activities, and it may not be possible to extend these forest areas; thus, studies of seed dispersal and regeneration may facilitate sustained forest density within the existing areas of the fragments. This study concept may be conducive to understanding the enhancement of biodiversity in a narrow range of sacred groves.

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APPENDIX

Table A1. *Species names, families, habits, and abundances of woody trees in the sacred groves of Puducherry region, South India. Species responses were positive[a], negative[b] or neutral[c] to patch size alterations by human disturbances over time*

S. No.	Species	Family	Habit	Abundance	Intercept	Estimate
1	*Acacia cineraria* (L.) Willd.	Leguminosae	Tree	2	0.03[c]	-0.03
2	*Aegle marmelos* (L.) Corrêa	Rutaceae	Tree	13	-0.25[b]	7.57
3	*Albizia lebbeck* (L.) Benth.	Leguminosae	Tree	3	0.19[a]	0.29
4	*Albizia saman* (Jacq.) Merr.	Leguminosae	Tree	7	-0.88[b]	50.35
5	*Annona squamosa* L.	Annonaceae	Tree	1	-0.16[c]	3.82
6	*Areca catechu* L.	Arecaceae	Tree	2	0.12[c]	-1.03
7	*Artocarpus heterophyllus* Lam.	Moraceae	Tree	3	0.03[c]	1.35
8	*Artabotrys hexapetalus* (L.f.) Bhandari	Annonaceae	Tree	2	0.03[c]	7.31
9	*Azadirachta indica* A. Juss	Meliaceae	Tree	58	-0.03[c]	1.86
10	*Bauhinia tomentosa* L.	Leguminosae	Tree	4	0.01[c]	0.45
11	*Borassus flabellifer* L.	Arecaceae	Tree	23	-0.01[c]	0.93
12	*Butea monosperma* (Lam.) Taub.	Leguminosae	Tree	1	-0.04[c]	1.41
13	*Calophyllum inophyllum* L.	Clusiaceae	Tree	1	-0.14[c]	3.34
14	*Carica papaya* L.	Caricaceae	Tree	1	0.02[c]	0.90
15	*Cassia fistula* L.	Leguminosae	Tree	4	-0.04[c]	1.41
16	*Citrus aurantium* L.	Rutaceae	Tree	3	-0.14[c]	3.34
17	*Cocos nucifera* L.	Arecaceae	Tree	50	-0.59[b]	20.27
18	*Couroupita guianensis* Aubl.	Lecythidaceae	Tree	14	2.25[a]	-6.19
19	*Crateva adansonii* DC.	Capparaceae	Tree	3	1.62[a]	-10.20
20	*Crescentia cujete* L.	Bignoniaceae	Tree	1	0.06[c]	-0.51
21	*Dalbergia sissoo* DC.	Leguminosae	Tree	1	-0.31[b]	11.29
22	*Delonix regia* (Hook.) Raf.	Leguminosae	Tree	6	-0.41[b]	17.35
23	*Drypetes sepiaria* (Wight & Arn.) Pax & K. Hoffm.	Putranjivaceae	Tree	3	-0.62[b]	20.75
24	*Enterolobium cyclocarpum* (Jacq.) Griseb.	Leguminosae	Tree	1	0.18[a]	-1.54
25	*Ficus benghalensis* L.	Moraceae	Tree	33	-0.24[b]	6.64
26	*Ficus racemosa* L.	Moraceae	Tree	13	0.71[a]	1.19
27	*Ficus religiosa* L.	Moraceae	Tree	13	-0.16[b]	3.82
28	*Kigelia africana* (Lam.) Benth.	Bignoniaceae	Tree	1	0.18[a]	-1.54
29	*Kleinhovia hospita* L.	Malvaceae	Tree	1	-0.20[b]	5.23
30	*Lannea coromandelica* (Houtt.) Merr.	Anacardiaceae	Tree	2	-0.16[b]	3.82
31	*Lepisanthes tetraphylla* Radlk.	Sapindaceae	Tree	12	0.01[c]	0.45
32	*Madhuca longifolia* (J.Koenig ex L.) J.F.Macbr	Sapotaceae	Tree	1	0.00[c]	3.21
33	*Mangifera indica* L.	Anacardiaceae	Tree	21	0.07[c]	-0.06
34	*Mitragyna parvifolia* (Roxb.) Korth.	Rubiaceae	Tree	1	-0.32[b]	13.60
35	*Moringa pterygosperma* Gaertn.	Moringaceae	Tree	2	-1.00[b]	33.48
36	*Musa paradisiaca* L.	Musaceae	Large shrub	16	-0.14[c]	4.71
37	*Naringi crenulata* (Roxb.) Nicolson	Rutaceae	Tree	1	-0.14[c]	3.34
38	*Neolamarckia cadamba* (Roxb.) Bosser	Rubiaceae	Tree	1	-0.33[b]	11.77
39	*Nerium oleander* L.	Apocynaceae	Shrub	1	-0.07[c]	11.99
40	*Nyctanthes arbor-tristis* L.	Oleaceae	Tree	2	-0.16[b]	3.82
41	*Phoenix sylvestris* (L.) Roxb.	Arecaceae	Tree	1	-2.42[b]	64.14

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42	*Phyllanthus emblica* L.	Phyllanthaceae	Tree	8	0.02[c]	2.28
43	*Plumeria rubra* L.	Apocynaceae	Tree	3	0.43[a]	0.06
44	*Polyalthia longifolia* (Sonn.) Thwaites	Annonaceae	Tree	3	-0.04[c]	1.41
45	*Prosopis cineraria* (L.) Druce	Leguminosae	Tree	2	0.02[c]	0.90
46	*Prunus amygdalus* Stokes	Rosaceae	Tree	5	0.32[a]	-4.43
47	*Sapindus emarginatus* Vahl.	Sapindaceae	Tree	11	0.01[c]	0.45
48	*Sterculia foetida* L.	Malvaceae	Tree	1	-0.32[b]	7.63
49	*Syzygium cumini* (L.) Skeels	Myrtaceae	Tree	8	0.18[a]	-1.54
50	*Tamarindus indica* L.	Leguminosae	Tree	16	-0.10[c]	3.30
51	*Tectona grandis* L.f.	Lamiaceae	Tree	25	0.39[a]	-3.11
52	*Terminalia arjuna* (Roxb.ex DC.) Wight & Arn.	Combretaceae	Tree	2	0.68[a]	-2.92
53	*Thespesia populnea* (L.) Sol. ex Corrêa	Malvaceae	Tree	1	0.06[c]	-0.51

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