

Species abundance distributions of selected communities in the *Myristica* swamp forests of southern Kerala

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The species abundance distribution (SAD) utilizes all the information gathered in a community and is the most complete mathematical description of the data. *Myristica* swamp forests are an endemic, highly fragmented ecosystem, naturally restricted due to systematic destruction and the special abiotic conditions required for their survival. Species diversity of amphibians, reptiles and trees in the *Myristica* swamp forests of southern Western Ghats in Kerala was documented using standard protocols for two years. Conventional species abundance distribution models could not be fitted into the datasets of this study. Graphical representations of the distribution of the dataset suggest that existence of multiple peaks on a log scale does not reject the universal hollow curve law on the arithmetic scale, but it will reject all SAD models producing unimodal curves. Various studies using SAD as a tool for community and ecosystem studies were reviewed and it was found that the presence of many species of intermediate abundance and decrease in rare species in our datasets could be an indication of natural distributions moving apart under disturbance and enrichment. Deconstruction and identification of resident and transient groups was done. We suggest that the *Myristica* swamps, which are situated in an area with high potential for rare species, may be in a transition due to disturbance and fragmentation. Ground truthing and previous studies already indicate these swamp forests as highly fragmented and disturbed.

Keywords: Amphibians, conservation, *Myristica* swamps, reptiles, species abundance distribution, trees.

THE species abundance distribution (SAD) utilizes all the information excepting trophic interaction or spatio-temporal dynamics gathered in a community¹. Therefore SAD models have been advocated by many as providing the only sound basis for examination of species diversity. Although plotting has been widely used in diversity studies, visual inspection is not a guaranteed method to determine the model that describes the data best.

Goodness-of-fit test should be done mathematically¹. Conventionally, ecologists have used four SAD models – the geometric series, the log series, the truncated lognormal series and the broken stick. Dissatisfaction with these models has led to a plethora of models (more than 40)². But no consensus has been reached as to the efficacy and suitability of these models. Processes such as species turnover, succession and habitat change underpin the accumulation of species over space and time³. An increasing appreciation in the dynamical aspects of ecological communities combined with the need to devise effective conservation policies has reawakened interest in Preston's propositions⁴. SAD may be used to distinguish the occasional and the core species⁵, structure and composition changes linked to succession⁶, or anthropogenic changes⁷.

SAD has thus become the focus of intense research activity around the globe, though in India, it has not been given much attention. SAD performs well in distinguishing terrestrial communities under different influences⁸. Studies show the high potential of SAD models to serve as environmental indicators defined as an easily measured index that is indicative of the state (health) of an ecosystem⁹.

Here, we examine the SADs of selected animal and plant groups in the study area, and the SAD potential as an easily measured index indicative of the state (health) of an ecosystem.

Myristica swamps were first described by Krishna-moorthy¹⁰ and classified in the subgroup of tropical freshwater forests (4c/FS1)¹¹. These freshwater swamp forests are highly fragmented and restricted in distribution due to systematic destruction^{12,13} and special abiotic conditions^{14–17} required for their survival. *Myristica* swamps in India have been reported in the Western Ghats from southern Kerala^{10,17–21} Uttara Kannada in Karnataka^{14–16} and Satari in Goa²². These swamps are characterized by the dominance of two tree species, *Myristica fatua* Houtt. var. *magnifica* (Bedd.) Sinclair and *Gymnacranthera canarica* (Hook. f. & Thomson) Warb. The *Myristica* swamps in Kulathupuzha region constitute less than 0.01% of the total land area of Kerala^{21,23}. These

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swamps show high concentration of endemics in spite of restricted distribution^{24,25}. Since *Myristica* swamps were not reported prior to the 1960s there is no record of the swamps that perished during logging operations, the Grow More Food Campaign of 1950s and due to associated microclimatic changes. The resultant phenomenon of fragmentation leaves the surviving species in the habitat remnants confronted with a modified environment of reduced area, increased isolation and novel ecological boundaries.

In this article, we use data obtained from field work conducted during 2005 March to 2007 February in the *Myristica* swamps of Kulathupuzha region.

Methods

Species abundance data for amphibians, reptiles and trees were collected from 15 randomly selected swamps in Kulathupuzha region. For amphibians and reptiles, transect sampling was carried out in early mornings and late evenings²⁶. The transect size was 100 m (length) × 4 m (width) × 2 m (height) with sampling time of 1 h. For trees, sample plots of 100 × 10 m (0.1 ha) divided into ten 10 × 10 m quadrats were used²⁷. Transects were inclusive of the different microhabitats present in the swamp. For reptiles, *S* the number of species was 55 and *N* the number of individuals was 956. For amphibians *S* was 56 and *N* was 17,869. For trees, *S* was 58 and *N* was 2246.

The commonly used SAD models, namely geometric series, log series, truncated log normal and broken stick model were fitted to understand the ecological organization of the herpetofauna and trees in the study area.

Geometric series

$$n_i = NC_k k(1 - k)^{i-1},$$

where *n_i* is the number of individuals in the *i*th species, *N* the total number of individuals, *k* the proportion of resource pre-empted and *C_k* is computed using the formula

$$C_k = [1 - (1 - k)^S]^{-1}.$$

Log series

$$N = \alpha \left[\ln \left(1 + \frac{N}{\alpha} \right) \right],$$

where *α* is an index of diversity and can be obtained from the equation

$$\alpha = \frac{N(1-x)}{x}.$$

Truncated log normal

$$S(R) = S_0 e^{(-a^2 R^2)},$$

where *S(R)* is the number of species in the *R*th octave, *S₀* the number of species in the modal octave and *a* = (2σ²)^{1/2}, which is the inverse width of distribution.

Broken stick model

$$S(n) = [S(S - 1)/N](1 - n/N)^{S-2},$$

where *N* is the total number of individuals, *S* the total number of species and *S(n)* is the number of species in the abundance class *n*.

As these models did not fit into the datasets, the datasets were subjected to further study. Results from other studies were reviewed and interpretations were drawn for the datasets of the study.

Results

Conventional models could not be fitted into the datasets of the present study, except for the reptile abundance data which fit into the lognormal distribution (Table 1). The data when arranged into log octaves show multimodal properties. The peaks are large and therefore cannot be attributed to sampling noise. Graphical representation of the distribution of the dataset shows that existence of multiple peaks on a log scale (Figure 1) does not reject the universal hollow curve law on the arithmetic scale (Figure 2), but statistically rejects all SAD models producing unimodal curves.

Reptiles

The dataset for reptiles shows multimodal properties when arranged in log octaves and does not form the expected bell-shaped curve (with or without skew) as evident from the histogram (Figure 3). But it is closest to the log normal distribution and the goodness-of-fit test indicates that the resemblance is mathematically significant (Table 1). Therefore, deconstruction studies²⁸, where SAD models for two subsets within the same community are compared, were not done for reptiles.

Amphibians

The dataset for amphibians did not follow any of the conventional distributions. Rare species were excluded one by one in ascending order and the modified datasets were compared with conventional distributions. None of the distributions could be fitted with any of the modified datasets.

Table 1. Goodness of fit for common species abundance distribution models

	Geometric	Logistic	Log normal	Broken stick
Amphibians				
Chi-square (observed value)	11,084.673	253.694	60.232	297.655
Chi-square (critical value)	14.067	14.067	14.067	14.067
P-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Alpha	0.05	0.05	0.05	0.05
Reptiles				
Chi-square (observed value)	183.574	132.529	12.994	114.36
Chi-square (critical value)	14.067	14.067	14.067	14.067
P-value	< 0.0001	< 0.0001	0.072*	< 0.0001
Alpha	0.05	0.05	0.05	0.05
Trees				
Chi-square (observed value)	1,343,681.896	345.776	103.159	285.432
Chi-square (critical value)	15.507	14.067	14.067	14.067
P-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Alpha	0.05	0.05	0.05	0.05

*Significant at alpha = 0.05. (The risk to reject the null hypothesis while it is true is 7.22%.)

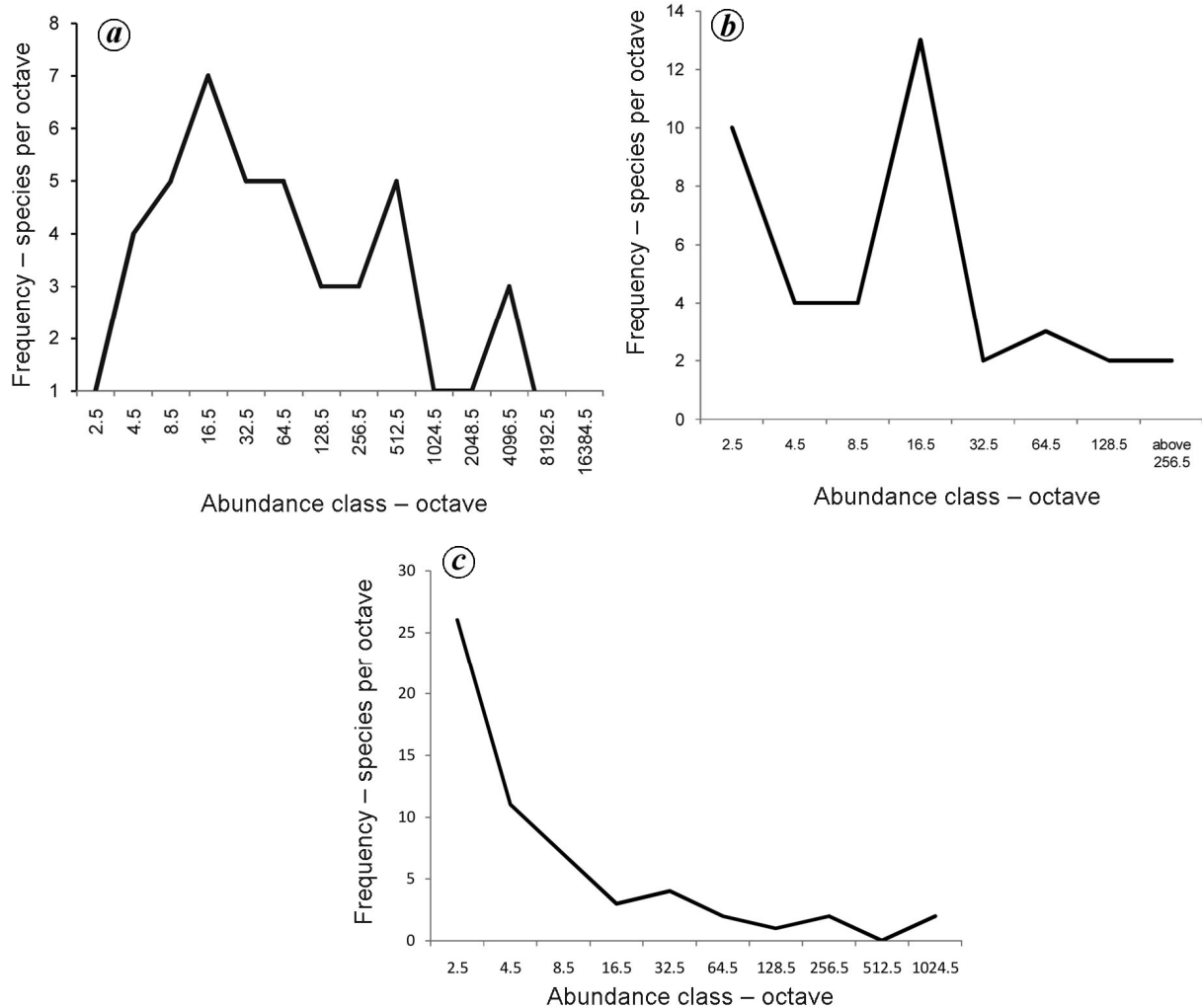


Figure 1. Rank abundance plot (log scale) for (a) amphibians, (b) reptiles and (c) trees (data in log 2 octaves).

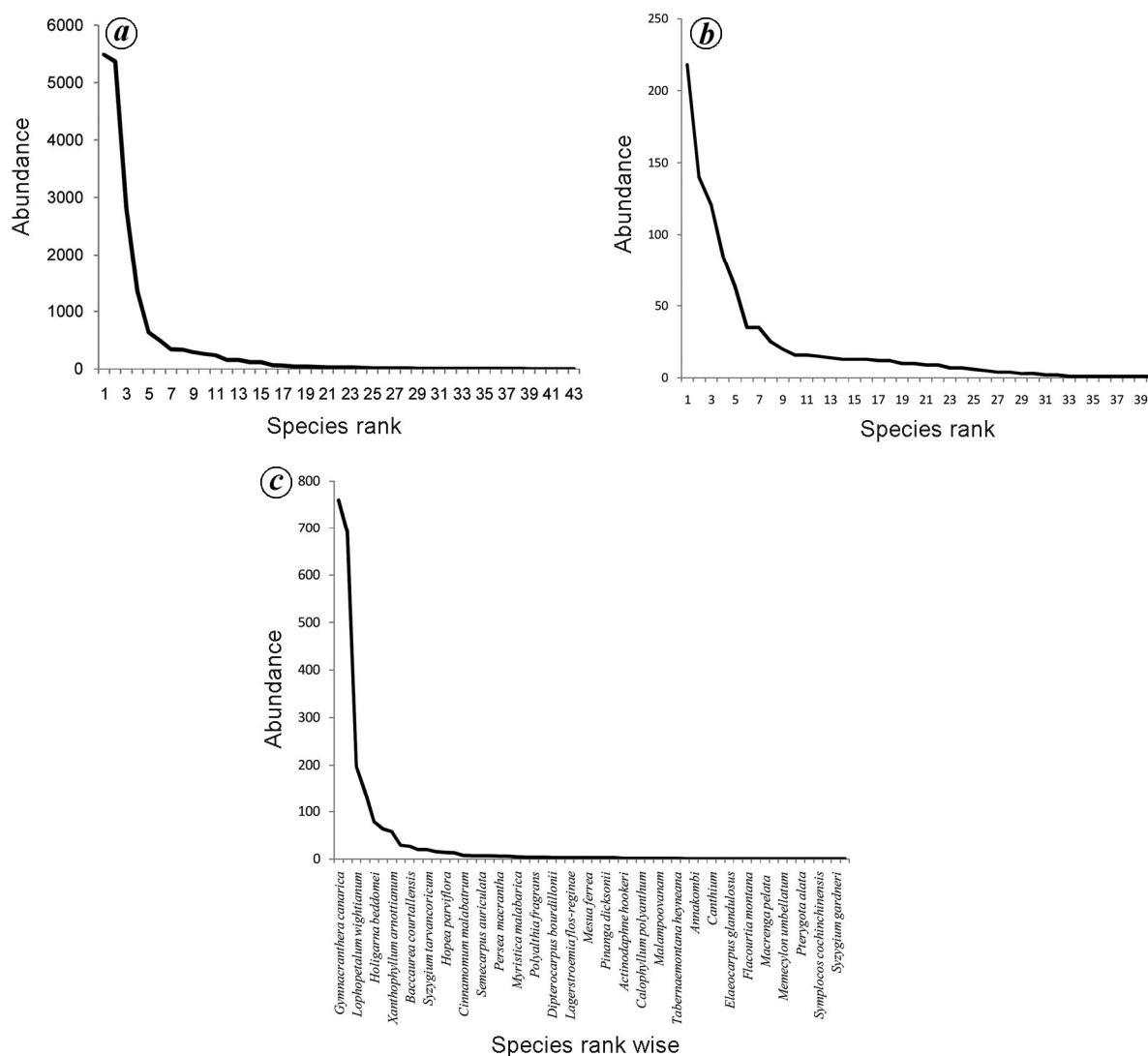


Figure 2. Rank abundance plot (arithmetic scale) for (a) amphibians, (b) reptiles and (c) trees showing the typical hollow J curve.

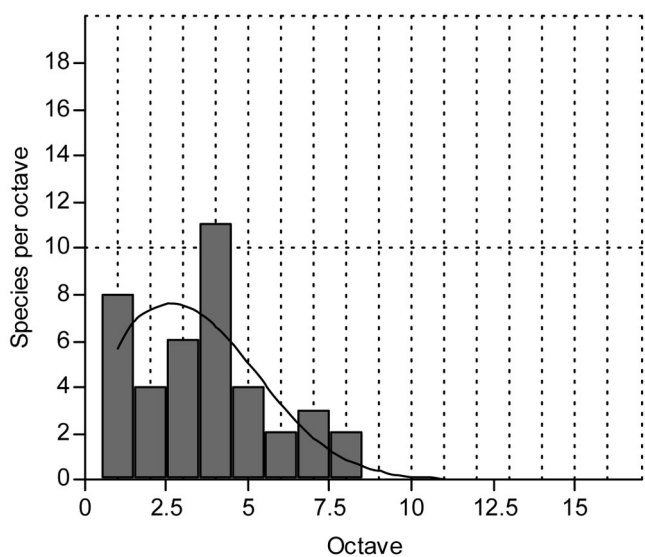


Figure 3. Log normal distribution model fitted into the dataset for reptiles.

Next, the amphibian population was broken into smaller groups based on (a) ‘family’ (b) ‘genera or similar genera’ and (c) ‘any other’. Different distribution models were fitted into each group. Distribution models did not fit into amphibian groups based on family; they were fitted based on ‘genera or similar genera’. Two groups of amphibians with relatively limited species turnover, namely the genus *Nyctibatrachus* (Jaccard index = 0.33) and Bush frogs (frogs once classified under the genera *Philautus*, but now under *Raorchestes*; Jaccard index = 0.45), showed unimodal distribution. *Nyctibatrachus* followed exponential distribution and Bush frogs collectively followed log normal distribution (Table 2). Other rhacophorids (genera *Polypedates* and *Rhacophorus*), which had a high species turnover (Jaccard index = 1), formed the third guild and followed exponential distribution. While Bush frogs had many rarely sighted species and few species of intermediate abundance *Nyctibatrachus* and other rhacophorids were dominated by one

Table 2. Distribution models fitted into three amphibian genera

Group	Chi-square (observed value)	Chi-square (critical value)	P-value	Alpha	Distribution	Characteristic of group
Other rhacophorids	13.479	15.507	0.096	0.05	Exponential	Dominated by <i>Polypedates pseudocruciger</i>
Bush frogs	10.575	14.067	0.158	0.05	Log-normal	Many rare species
<i>Nyctibatrachus</i>	15.372	15.507	0.052	0.05	Exponential	Dominated by <i>Nyctibatrachus major</i>
Others					None	Diverse groups, cosmopolitan distribution, many habitats

species only (*Nyctibatrachus major* and *Polypedates pseudocruciger* respectively). All other species showed high turnover (Jaccard index = 0.82) and did not fit into conventional distribution models even when groups were made on the basis of genera, observed and/or known habitat preference.

Trees

In the case of trees the rare species were excluded one by one in ascending order and when 52 tree species out of the total 58 were excluded, log normal distribution could be fitted into the modified dataset (chi-square: observed value = 13.927; critical value = 14.067; *P*-value = 0.052; alpha = 0.05). The trees included were *Gymnacranthera canarica* (Hook. f. & Thomson) Warb (760), *Myristica fatua* Houtt. var. *magnifica* (Bedd.) Sinclair (691), *Lophopetalum wightianum* Arn. (197), *Vateria indica* L. (144), *Holigarna beddomei* Hook. f. (79) and *Hydnocarpus pentandra* (Buch.-Ham.) Oken (64). If one more tree, namely *Hydnocarpus pentandra* (Buch.-Ham.) Oken was excluded, log normal distribution failed to fit into the dataset (chi-square: observed value = 14.496; critical value = 14.067; *P*-value = 0.043; alpha = 0.05). This result concurred with ground truthing and field experience as only these six trees were found in all swamps irrespective of size, inundation levels and other variables. Other trees were more concentrated in the peripheral areas of the swamps that were contiguous to other forest types.

Discussion

A geometric series distribution is often found in species poor, often harsh environments, where a few species dominate in the community. A community following a geometric distribution is defined as one where a dominant species pre-empts a proportion *k* of a limiting resource, with the second most dominant species pre-empting the same proportion of *k* of the remainder and so on down the order of dominance¹. In the present datasets, the abundance patterns for amphibians, reptiles and trees show that though very few species have accounted for a very large number of individuals, many species have intermediate and/or rare abundance. The presence of semi co-dominants (5488, 5371, 2826 in amphibians; 218, 140,

121 in reptiles; 760, 691 in trees)^{20,21} precludes the possibility of geometric distribution.

A log series pattern occurs in ecological communities where the arrival of species is random (in geometric series, species arrival is regular)¹. The log series predicts a small number of abundant species and many rare species. In the truncated log normal distribution, a normal bell-shaped curve is followed. In this study the presence of species with intermediate abundance (lesser than expected in the log normal or log series) and many rare species (more than as expected in the log normal) and absence of equal distribution of abundance (broken stick) negates a fit into the log normal, log series or broken stick model for amphibians. The three dominant species for both amphibians and reptiles are habitat generalists that have been found in every microhabitat observed, in all seasons and all plots. The rare species on the other hand, lie at the other end of this spectrum and consist of Red-listed species, range extensions, etc. some of which could be even new to science. The long left skew/tail caused by so many 'rare' reptiles can be explained by the fact that reptiles are much more mobile when compared to amphibians and since the swamps are contiguous with the adjacent forests, there is no control over the resident status of these animals.

For trees, the two most dominant species are exclusive to the swamps and are endemic not only to the Western Ghats, but also to swamps with visible adaptations (knee roots and stilt roots). The other species with relatively higher number of individuals though not visibly adapted to swamps can survive in inundated conditions.

The datasets of this study which are not unimodal do not follow other conventional models as these cater to unimodal data. Many communities have shown patterns which are multimodal². In the present datasets many species of intermediate and rare abundance are present as suggested by previous studies²⁹, where the distributions are said to move apart under disturbance and enrichment in opposition to a single distribution pattern in an undisturbed assemblage. Mc Gill *et al.*² have referred to studies using SAD as an indicator to investigate anthropogenically disturbed environments that found a decrease in rare species and increase in species of intermediate abundance. Another possibility is the inappropriate lumping together of distinct guilds that, if true, can use deconstruction analysis for appropriate separations⁵,

which we could use successfully for three groups of amphibians.

There are many factors which affect the shape of the SAD. Empirical data have been fitted to the neutral theory and more left skew was found in cases where greater immigration was expected³⁰. In this study, both reptiles (Jaccard measure = 0.65, Sorenson's measure = 0.787, Morista-Horn measure = 0.866725) and amphibians (Jaccard measure = 0.577778, Sorenson's, measure = 0.73294, Morista-Horn measure = 0.8932209) showed high species turnover with the adjacent non-swamp regions.

As the sampling duration increases, the mode of distribution moves to the right to become log normal in character^{31,32}. The shape of the abundance distributions tends to change with the sampling duration. This could explain the different distributions followed by the reptile and amphibian population in the study area. Amphibians are highly susceptible to changes in the environment. Different guilds have different niche requirements and the levels of inundation in the swamp may become a limiting factor. Many species may utilize the swamp only during the dry season and move to other areas in the rainy season. Frog species which prefer the swamps to the adjacent areas may have microhabitat preferences (stagnant pools, shallow flowing water, sandy, gravelly or loamy substrate, knee and stilt roots, etc.). Therefore, amphibian sampling may not yet be complete when the assemblage is deconstructed. But for reptiles, which are more resistant to environmental fluctuations, a fixed population may be expected.

In the case of trees, when rare species (tree species not common to all swamp patches and/or existing in the periphery) are removed, a log normal distribution is unveiled. This conforms to other studies where the division of species as transient and resident shows distinct differences in the shape of the SAD^{5,33} and the left skew on a log scale in large country-sized assemblages of birds disappears when species arguably not part of the community are removed³⁴.

Permanently resident species were shown to be log normal and transient species were log series⁵. It is difficult to determine the truly core and truly occasional species for the swamp because of microhabitat heterogeneity, which is thought to influence the shape of species occupancy distributions along with spatial scale³⁵.

Rather, one may have to divide the entire assemblage based on their microhabitat preferences or apply generalized species abundance distributions (GSAD) encompassing several abundance measures, such as numerical abundance, biomass and resource use³⁶.

Conclusion

The following conclusions may be drawn for the three different groups studied in the *Myristica* swamps.

1. Reptiles being more resistant to environmental fluctuations and relatively more mobile do not treat the swamps as a fixed residence. The reptilian population in the swamps is contiguous with the adjacent forests, therefore, a more stable population may be expected.
2. Amphibians are less mobile and more susceptible to environmental fluctuations and habitat heterogeneity. They may be divided into three groups¹³:

A type – species spending most of the time in the swamp and rarely going out.

B type – species spending most of the time outside the swamp, but foraging inside only during dry seasons.

C type – species which are so cosmopolitan in their needs that they can habituate the swamp or adjacent forests with equal ease, though with a preference to swamps.

Using deconstruction we successfully segregated three guilds, i.e. *Nyctibatrachus* (A type), Bush frogs (B type) and other rhacophorids (C type). We were unable to segregate other species.

3. When rare tree species (not true swamp residents) were removed a log normal distribution was obtained, indicating the transient and resident trees (six species) of the *Myristica* swamps.
4. The swamps show a characteristic of anthropogenically disturbed, fragmented environments, i.e. a decrease in rare species and increase in species of intermediate abundance.

The swamps which are situated in an area with high potential for rare species may be in a transition due to disturbance and fragmentation³⁷. The multimodal SAD models obtained here could be due to habitat disturbance, edge effects, microhabitat heterogeneity, high species turnover or a combination of all or some of these. Ground truthing and previous studies^{12,13,17,20,21,23} indicate these swamp forests as highly fragmented and disturbed. Further studies concentrating on the use of simple statistical tools as a diagnostic measure in predicting cryptic disturbances to an ecosystem are needed.

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