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Hazard or habitat: injured and unhealthy trees host most of the tree microhabitats in tropical forests

Bharati Patel
KSCSTE – Kerala Forest Research Institute
Peroth Balakrishnan
baluperoth@gmail.com

KSCSTE – Kerala Forest Research Institute

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Author Names and Affiliations:

Bharati Patel[1,2], Peroth Balakrishnan[1*]

1 KSCSTE – Kerala Forest Research Institute, Peechi-680 653, Thrissur, Kerala, India

2 ICFRE – Institute of Forest Biodiversity, Dulapally-500 100, Hyderabad, Telangana, India

* Corresponding author

Corresponding Author:

Peroth Balakrishnan (Orcid ID: 0000-0002-3697-1322)
Department of Wildlife Biology,
KSCSTE – Kerala Forest Research Institute, Peechi-680 653, Thrissur, Kerala, India.
Email: baluperoth@gmail.com

Present Address:

Dr. Peroth Balakrishnan, Scientist, Kerala Forest Research Institute, Peechi-680 653, Thrissur, Kerala, India.

Bharati Patel, ICFRE – Institute of Forest Biodiversity, Dulapally-500 100, Hyderabad, Telangana, India. (Orcid ID: 0000-0002-2567-906X)

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Author contributions

Bharati Patel and Peroth Balakrishnan conceived the ideas and designed methodology; Bharati Patel and Peroth Balakrishnan collected the data; Bharati Patel and Peroth

Balakrishnan analysed the data; Bharati Patel and Peroth Balakrishnan led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The datasets analyzed for the current study are available from the corresponding author on reasonable request. R codes used for analysis are provided as Supplement B.

Conflict of interest statement

The authors declare no conflict of interest

Declarations

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Research involving human and animal participants

Our study did not involve participants or animals.

Hazard or habitat: injured and unhealthy trees host most of the tree microhabitats in tropical forests

Abstract

Tree microhabitats are essential structural features on trees that support a wide range of forest-dwelling flora and fauna. Their value as indicators of biodiversity and tools for forest management is increasingly recognized by scientists and policymakers. While well-studied in temperate zones, research in tropical forests, despite their exceptional ecological complexity remains limited. This study assessed the influence of habitat and tree characteristics on tree microhabitats in evergreen and deciduous habitats in the Western Ghats, India. Stand-level attributes were examined using ordination analysis, supported by Bray-Curtis dissimilarity measures to uncover patterns in tree microhabitat occurrence and abundance in relation to specific stand parameters. In deciduous forests, tree microhabitat abundance was associated with species evenness and dominance. In evergreen forests, the number of trees, presence of unhealthy trees, species richness and diversity, and the number of tree microhabitat and cavity-hosting trees were critical. Despite structural differences between the two habitats, common patterns emerged. Tree microhabitat abundance was consistently linked to the presence of cavity-host trees, unhealthy live trees, and dead trees in both forest types. Tree vitality (healthy, unhealthy, or dead) and diameter are key predictors of tree microhabitat presence. Specifically, unhealthy trees with diameters greater than 0.34 meters had a higher likelihood of hosting cavities, pointing to the role of fungal rot and injuries in cavity formation. This study advances the understanding of structural diversity in tropical forests by identifying thresholds where tree microhabitat richness increases. Overall, the presence of large healthy trees, alongside an adequate supply of unhealthy and dead trees, appears vital for supporting tree microhabitat diversity and abundance. Forest management must prioritize the preservation of these

structures, recognizing that "unhealthy" trees are not merely hazards but critical biodiversity hotspots.

Keywords

Tree microhabitat, tropical forest, habitat characteristics, tree characteristics, Western Ghats

Introduction

The root of biological diversity lies in the abiotic factors which shape the community composition and structure of the vegetation (Brown, 2014). The heterogeneity in this composition further escalates the complexity in this structure (Leigh et al., 2004). With succession, plants and animals in micro and macro forms evolve, start interacting through positive and negative feedback, making a vegetation forest with high biological diversity (Andersen et al., 2018; Harvey et al., 2020). Some of the key interactions leading to high survival of more living forms through coexistence are mutualism, facilitation and niche partitioning (Zhang, 2003; Bulleri et al., 2016). The biotic components either modify the microclimate or facilitate critical resources for the sustenance of other biotic components. Tree microhabitats or microhabitat structures are such facilities created by the biotic components. Its presence or function serves as habitat resources for other lifeforms and provide services directly or indirectly to the facilitator. For example, epiphytes on large trees serve as a buffer from the direct impact of extreme weather events for the host trees (Stanton et al., 2014). Another example is woodpeckers, which control the pests by foraging wood-boring insects on infected tree species (Mendel et al., 1984). For such reasons, tree microhabitats have gained importance in the community and ecosystem level research as a tool for increasing the biological diversity and initiate measures for its conservation (Lindenmayer et al., 2000; Tews et al., 2004; Oettel and Lapin, 2021; Dutta et al., 2025). But the occurrence and formation of these structures does not depend upon the interaction participants alone. Tropical forest stands

91 are expected to have more density and volume of deadwood, but the higher rate of degradation
92 may be emptying the stock on forest the floor at a faster rate (Griffiths et al., 2019; Seibold et
93 al., 2021; Bhardwaj et al., 2025). This may have a strong impact on the diversity of deadwood-
94 dependent species. Therefore, it is possible that the role of different attributes reported so far
95 for the tree microhabitats may not be generalized. The variation in the forest stands of tropical
96 regions is expected owing to the high species diversity and density, which is also the major
97 source of heterogeneity in these stands (Ricklefs, 1977).

98 The tree and species feature such as basal area, dbh and vitality (live/dead) have significant
99 influence on the abundance of tree microhabitats. Species such as Pine had been identified to
100 have more abundance of tree microhabitats. Even same species in live and dead vital form and
101 larger diameter classes can have varying richness and abundance of tree microhabitats at the
102 individual level (Regnery et al., 2013; Paillet et al., 2019; Kõrkjas et al., 2021; Martin et al.,
103 2021a; Mukardamwala et al. 2025). Trees with large stem diameter can have more deadwood
104 in canopy, more coverage of climbers and potential locations for cavities. Live and dead status
105 of trees also has positive effect on trees microhabitats, with dead hosting more tree
106 microhabitats (especially cavities) compared to the live trees. Non-coniferous tree species tend
107 to be associated with medium sized cavities and fungal fruiting bodies (Regnery et al., 2013).
108 Efforts have been made to estimate the probability of presence and abundance of tree
109 microhabitats based on the abundance of individuals in different diameter classes. It has been
110 observed that, with time the number of tree microhabitats increases significantly on snags, but
111 not in live trees (Larrieu et al., 2014; Paillet et al., 2017). In temperate regions over the time,
112 snags can have more diversity and abundance of tree microhabitats compared to the live trees.
113 On live trees, the abundance of exudates and epiphytes increase significantly due to
114 microclimate effects. However, the incremental effect of tree diameter is not evident for the
115 tree microhabitats such as crown deadwood, broken fork, excavated cavities, natural cavities,

cracks, bark characteristics, outgrowths and epiphytes fungal fruiting bodies in any of the groups (either by diameter or vitality) (Paillet et al., 2017). In abandoned managed landscapes trees may also develop microhabitats over time (Hausmann et al., 2026). Species characteristics such as the development of senescent dead branches with growth favour more abundance of dead branches, rot holes and fungal fruiting bodies (Kõrkjas et al., 2021; Marino et al., 2025). Tree characteristics such as bark features, phyllotaxis and development stage of tree species, compartmentalization (forking) and physiological state of individual tree can be better predictors of tree microhabitats (DeGraaf and Shigo, 1985; Larrieu et al., 2022). An individual tree with even a single microhabitat therefore, has the potential to enrich the habitat with other microhabitats (Winter et al., 2015).

Most of the studies related to tree microhabitats focus on cavities as habitat resource for primary users, epiphytes as part of diversity, injuries and growth forms formed due to the site characteristics. The impact of geographical attributes can be recognizable when assessed at large scale, i.e., comparing similar vegetation from multiple sites from geographically distinct locations and with enough replications. This can give crude information about the variation, mainly in the diversity of microhabitats and abundance to some extent. Impact of vegetation attributes can be identified by sampling at a small scale, i.e., comparing the samples from an ecosystem or a landscape. This can give information about the variations in not only the diversity, but also the range for characteristics, abundances, cooccurrences and dynamics. Researchers have been interested in the factors influencing the dynamics in tree microhabitats to draw conclusions that can help in better conservation and management of forests to keep the production and ecological functions sustainable (Larrieu et al., 2014; Martin et al., 2021b). With intensive research in the temperate forests of European region and a few in tropical forests the factors influencing diversity and abundance of tree microhabitats have been identified as tree related characteristics – species, diameter of trees and their vitality (Winter

and Möller, 2008; Michel and Winter, 2009; Vuidot et al., 2011; Larrieu and Cabanettes, 2012; Regnery et al., 2013; Larrieu et al., 2014; Kozak et al., 2018; Asbeck et al., 2019; Paillet et al., 2019; Mukardamwala et al., 2025). Abundance of trees with untreated wounds and injuries tends to have more tree microhabitats (Großmann et al., 2020). This brings our attention again to stand characteristics which should be investigated for utilizing tree microhabitats as the tool.

Availability of a suitable host is an important feature of the stand to qualify for the abundant and sustainable availability of tree microhabitats. Abundance of trees with untreated wounds and injuries tends to have more tree microhabitats (Großmann et al., 2020), irrespective of the type and intensity of management (Santopuoli et al., 2022; Spînu et al., 2023). Suitable host trees in even low diameter classes are also potential host and can be major stakeholders in stands where they are abundant (Großmann et al., 2018; Courbaud et al., 2022). However, large trees which cross the thresholds of production and commercial forestry demands are even more rich in terms of tree microhabitat richness and abundance and often contrast with the conservation targets (Maier and Winkel, 2017; Cosyns et al. 2020). There are no studies made so far in tropical regions where it can be estimated which characteristic features of trees influence the richness and abundance of tree microhabitats for informed decision-making. Through this study an attempt was made to explain the stand and tree-related attributes which influence the presence and abundance of tree microhabitats. The findings of earlier studies from temperate forests were considered as the research hypothesis for this study. It states that ‘stands with high tree density, species richness and diversity indices will have more occurrences of types of tree microhabitats (diversity of tree microhabitats) as they will have more availability of potential host individuals. It was hypothesised that ‘similar to previous research in temperate forests, the diversity and abundance of tree microhabitats might be a factor of tree species, its diameter and vitality of the trees in the evergreen and deciduous habitats of the tropics’.

Materials and methods

Studied habitats

Evergreen and moist deciduous forests from the Kerala region of the southern Western Ghats of India were selected as representative vegetation for the inventory. Sampling was done in the protected forest areas to avoid bias due to anthropogenic activities. The sampling areas selected were evergreen vegetation (evergreen) of Silent Valley National Park (SVNP, 11° 2'N and 11° 13'N and 76° 24'E and 76° 32'E) and Muthikkulam Reserve Forest (MRF, 10°56'N and 10°59'N and 76°41'E and 76°45' E) and moist deciduous vegetation (deciduous) of Peechi Vazhani Wildlife Sanctuary (PVWLS, 10°28'N to 10°38'N and 76°18'E to 76° 28'E) (Figure 1). SVNP has a core zone of 89.52 sq km with a 148 sq km buffer zone making the total area as 237.52 sq km. The elevation of the park ranges from 70 to 2,383 m asl, annual temperature ranges from 9° C to 38° C. The region receives a bulk of both south-west and north-east monsoon showers with an average annual rainfall >5,000 mm. MRF is under the Mannarkkad Forest Division and forms the southern part of the Nilgiri Biosphere Reserve. The reserve has an area of 63.86 sq km with an elevation ranging from 610 to 2,065 m and a temperature ranging from 10° C in winters to 30–32° C in summers and an average annual rainfall of 2,000 to 4,500 mm. It is also identified as an Important Bird Area (BirdLife International 2000). PVWLS has an extent of 125 sq km. The terrain is undulating with elevation varying from 45 to 900 m and annual temperature ranges from 12°C to 39°C. This area receives an average annual rainfall of 3,000 mm. The inventories were made from December 2017 to June 2020.

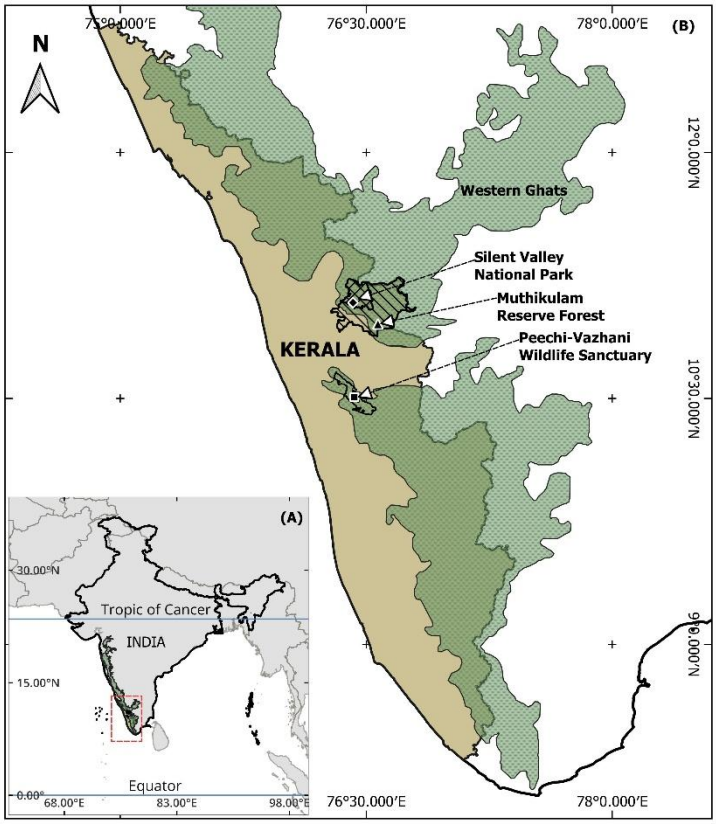


Figure 1: Map of study area: (A) Location of study site in the Western Ghats, India (in inset), (B) Location of studied habitats in the Western Ghats, India

To evaluate the influence of habitat and tree attributes on tree microhabitats, data on habitat and tree characteristics were collected from an 8-ha evergreen forest area and a 6-ha deciduous forest area. In both the habitats, 1000 m × 40 m transect were laid and divided into quadrats, and ten 0.1 ha quadrats per transect were sampled, recording all trees ≥10 cm dbh for species, size, and vitality. Tree microhabitats were recorded by visually inspecting each tree in six vertical zones using binoculars, following a modified typology from Kraus et al. (2016) and Larrieu et al. (2018). Tree microhabitats were classified into 9 categories and 33 sub-categories, with special focus on cavities ≥5 cm deep and wide enough to be suitable for vertebrate use. For detailed descriptions of the study area and locations of sampling plots, sampling method, characterization of tree microhabitats, see Patel et al. (2024). The impact of habitat

200 characteristics was analysed on both categories (n=9) and sub-categories (n=33) of tree
201 microhabitats. The descriptions of 10 habitat characteristics used in this study are provided in
202 Table 1.

203 Table 1: Habitat characteristics used to analyse the impact of habitat on diversity and abundance
204 of tree microhabitats

Variable	Type of data	Description	Variable	Type of data	Description
habitat	categorical	Habitats: Evergreen, Deciduous	D	numeric	Diameter of tree at breast height in m
tree	numeric	Number of individuals	H	numeric	Height of tree at breast height in m
tmhtrees	numeric	Number of trees hosting at least one tree microhabitat	richness	numeric	Number of species
livehtree	numeric	Number of live and healthy trees	Shannon	numeric	Shannon's Diversity Index value
liveuhtree	numeric	Number of live unhealthy trees	Simpson	numeric	Simpson's Diversity Index value
cvtree	numeric	Number of trees hosting at least one cavity	inverseSimpson	numeric	Inverse of Simpson's Index value
tmh_occur	numeric	Number of tree microhabitats	Logalpha	numeric	Log series Alpha diversity Index
di_1	numeric	Tree microhabitat diversity index for nine categories	Berger	numeric	Berger-Parker Index of Dominance
di_2	numeric	Tree microhabitat diversity index for 33 sub-categories	Jevenness	numeric	Pielou's J Evenness Index (Shannon's Evenness Index)
G	numeric	Basal area of the tree in sq m	Eevenness	numeric	Shannon's Evenness Index value

205

206 **Data collection**

207 Certain tree microhabitats, such as injuries and fungal decay, can promote the development of
208 other microhabitat types. Because tree microhabitats often occur in a sequential pattern in terms
209 of type and abundance, the presence of at least one microhabitat has been regarded as an
210 indicator of a tree's potential to function as a host. As the analysis aimed to examine and relate
211 tree characteristics to the presence of tree microhabitats, individual trees were treated as the
212 smallest unit of analysis.

213 To identify which tree characteristics make them suitable hosts for tree microhabitats, the
214 following attributes were recorded: habitat type (hbt), species name (sps), family name (fam),

diameter at breast height in meters (dbh), tree height in meters (ht), basal area in square meters (G), tree vitality class (classified as dead, live healthy, or live unhealthy), and unhealthiness cause (classified as the presence of fungal fruiting bodies, termite infestation, or other causes for unhealthy trees; healthy for healthy trees; and dead for dead trees). Other parameters included branchiness (branch), decay class (dcy), crown shape class (cr_shp), categorized by the percentage of canopy damage (1 = 0–25%, 2 = 25–50%, 3 = 50–75%, 4 = 100%), and crown class (cr_cls), categorized as overtopped, intermediate, codominant, dominant, or emergent. Data on the presence and abundance of both tree microhabitats and tree cavities were recorded and calculated for each tree.

Statistical analysis

Assessment of stand characteristics

The abundance data for the categories and sub-categories of tree microhabitats exhibited high variability in minimum and maximum values. Therefore, the data were transformed into relative abundance per tree for each tree microhabitat category and sub-category by dividing the individual values by the total abundance.

Plot level associations of tree microhabitats was analyzed using asymmetric distance measures for quantitative abundance. These asymmetrical coefficients utilize presence data while avoiding the inferential issues associated with double zeros (i.e., joint absence in both sites being compared). Similarity measures were converted into a distance matrix using the formula Dissimilarity (D) = 1 – S, implemented via the vegan package in R (Oksanen et al., 2022) and visualized with gclus package (Hurley, 2019). The Bray-Curtis dissimilarity index was used, as it minimizes distortion of the original data and preserves actual abundance values.

Composition and distribution patterns of tree microhabitats across habitat gradients were assessed through clustering and ordination analysis. The habitat gradients included the stand

characteristics related to trees, their diversity and spatial distribution of potential microhabitat host trees (Table 1). The aim was to uncover patterns in tree microhabitat occurrence and abundance in relation to specific stand parameters. The sampled habitats were considered proxies for distinct microclimatic conditions within each stand.

All variables, except for stand height (H), violated normality assumptions. Therefore, analytical methods capable of accommodating non-linear responses in abundance data were employed. Non-Metric Multidimensional Scaling (NMDS) was deemed most appropriate due to its ability to represent complex relationships in a low-dimensional space with minimal stress (Borcard et al., 2011). Assumption with detailed description of NMDS analysis and calculations are provided in Supplement A. Similarities between composition of categories and sub-categories of tree microhabitats were examined quantitively using Mantel's test (Mantel 1967). The null hypothesis assumes no significant difference tree microhabitat occurrences of the two habitats. Correlation analysis assessed the relative importance of stand related variables for the diversity and abundance of tree microhabitats through pair-wise calculation to compute a scalar product (r) (Guillot and Rousset, 2013) and p-value.

Multivariate ANOVA was performed to test the homogeneity in multivariate dispersions for the abundance of tree microhabitats in the two habitats using *vegan* package. The homogeneity in dispersions using distance measure was applied as the community data was skewed and had many zeros (Gijbels and Omelka, 2013). The most significant factors identified from NMDS were tested with 200 and models were compared using ANOVA.

Assessment of tree characteristics

For the species-level analysis of tree microhabitat host tree species, only those species with a minimum of 10 individuals hosting tree microhabitats were included. Microhabitat host tree species and families were compared with one-way ANOVA followed by Bonferroni test at 95%

confidence interval. No host tree species were common between the two habitats. It was assumed that each species was specific to its respective habitat; hence, a habitat-level comparison based on host tree species was not conducted. Three host tree families were common between deciduous and evergreen habitats, allowing comparison of family-level performance between habitats. Differences in the occurrence of tree microhabitats, types of tree microhabitats, and the presence of tree cavities (both natural and excavated) were compared for each selected species and family.

Tree characteristics associated with the presence of tree microhabitats and cavities were analyzed using random forest multiple regression. In the dataset, the number of tree microhabitat and cavity occurrences was much lower than the number of absences, which reduced the effective sample size. Random forest uses recursive partitioning and is well-suited for small sample sizes and high-dimensional data (Cootes et al., 2012). Therefore, this method was used to improve the probability of tree microhabitat and cavity presence and abundance with respect to various tree characteristics (Chen et al., 2004). Presence or absence of tree microhabitats (tmhtree) was included as one of the predictor variables for predicting tree cavity (cavity) occurrence. Existing literature indicate that trees bearing other microhabitats have a higher probability of developing cavities.

Random forest generates predictions by averaging the results of multiple decision trees trained on bootstrap samples from the dataset (Breiman, 2001; 2002). This ensemble approach helps reduce overfitting and allows for variable importance assessment (Liu et al., 2012). The classification model was used to predict categorical variable presence or absence of tree microhabitat and cavity. Model optimizes the splits yields highest information gain typically measured by Gini index. Gini impurity measures the likelihood of incorrect classification when labels are randomly assigned based on class distribution and prior probabilities (Breiman, 2001; Cutler et al., 2012).

Discriminative analysis was used to train classifiers for estimating the presence or absence of tree microhabitats and cavities, the dependent variable a binary categorical variable (Yes = present, No = absent).

The model used for predicting the probability of a tree hosting a tree microhabitat was:

tmhtree ~ hbt + dbh + ht + G + vital + dcy + cr_shp + cr_cls + branch

The model used for predicting the presence of tree cavities was:

cavity ~ hbt + dbh + ht + G + vital + dcy + cr_shp + cr_cls + branch + tmhtree

Presence of tree cavities was in significantly low number. Thus, the model was trained for imbalanced data. For this analysis, 70% of the data was used for training and 30% for validation. Within the training data, the binary classes were imbalanced at 91% "No" and 9% "Yes", with 65% of the training samples belonging to the "No" class and 34% to the "Yes" class. Predictor variables were randomly selected by the algorithm from the full set of input variables. The best-performing split was then used to form decision nodes. Prediction of the binary variable follows 'Classification Model':

$$\text{Predictor variable (m)} = \sqrt[2]{Total\ number\ of\ all\ predictors\ for\ classification}$$

The number of predictor variables (m) remains constant throughout the random forest. The best split is used for developing the standard tree. The model uses the remaining data (30 % of the data) to validate the standard forest and to calculate the misclassification rate as Out Of Bag error rate (OOB). The OOB error is the average of all the errors calculated from the dataset which was not included in bootstrapping. In this analysis the standard tree was selected out of *ntry* = 2000 bootstrapped trees (Liaw and Wiener 2002; Breiman and Cutler 2022). The hierarchical decision tree was developed. For model evaluation precision and recall metrices were calculated using the confusion matrix. Decision trees were developed using significant

311 variables. The numbers in parentheses refer to the number of observations/occurrences unless
312 specifically mentioned.

313 The proportion of positives (cavity presence) was very low in the dataset i.e., 0.09%. Therefore,
314 performance of classification models was evaluated using Precision (proportion of positive
315 predictions actually true) and Recall (proportion of actual positive cases identified by the
316 model) metrices (Sokolova et al. 2006). F1 score was calculated to estimate model accuracy
317 using harmonic mean of precision and recall metrices of the models.

318 F1 = 2 * ((Precision * Recall) / (Precision + Recall))

319 The cavity presence was highly skewed due to very low proportion of presence data. Therefore,
320 the model was evaluated with gain matrices to predict presence of cavity gain metrices (Flach
321 and Kull 2015):

322 $$\text{Precision Gain} = 1 - \frac{\pi}{1-\pi}\frac{\text{False Positive}}{\text{True Positive}}$$

323 $$\text{Recall Gain} = 1 - \frac{\pi}{1-\pi}\frac{\text{False Negative}}{\text{True Positive}}$$

324 where, π = proportion of positives

325 $$\text{F1 Gain} = Precision\ Gain + Recall\ Gain/2$$

326

327 # Results

328 **Habitat characteristics associated with tree microhabitats**

329 Total 6363 trees were sampled in the evergreen habitats out of which nearly 42.8% of the
330 individuals had no microhabitats, 31.1% individuals had at least one tree microhabitat and only
331 18.3% had three tree microhabitats (hereafter microhabitats). In the deciduous habitat 1,545

trees were sampled; nearly 28.3% individuals had no microhabitat, 26.2% individuals had at least one tree microhabitat, and 23% individuals had three tree microhabitats. The frequencies of microhabitats were thus skewed towards y-axis (Figure 2).

Evergreen habitat had 12.4 ± 4.9 microhabitats per tree and 942.8 ± 341.4 per ha. Deciduous habitat had 20.4±7.2 microhabitats per tree and 493.7±133.3 microhabitats per ha. Among the nine categories of tree microhabitats, both the habitats had approximately 1±1 (range: 0-6) microhabitat per tree. However, they differed in the occurrences and diversity of microhabitats. In evergreen habitat five to nine categories of tree microhabitats were observed in the transects while in deciduous it was four to eight. The tree microhabitat category *Crematogaster* ant nests (m9) was absent in the deciduous habitats. Among the 33 sub-categories, 13 to 28 sub-categories were observed per ha in evergreen while in deciduous 8 to 26 were observed per ha.

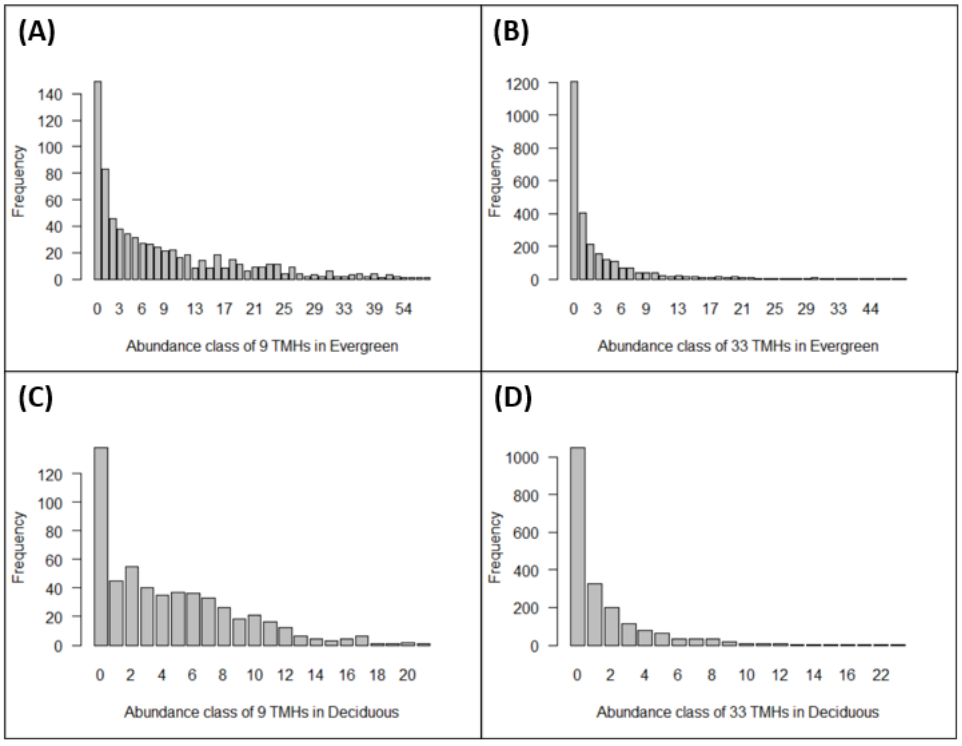


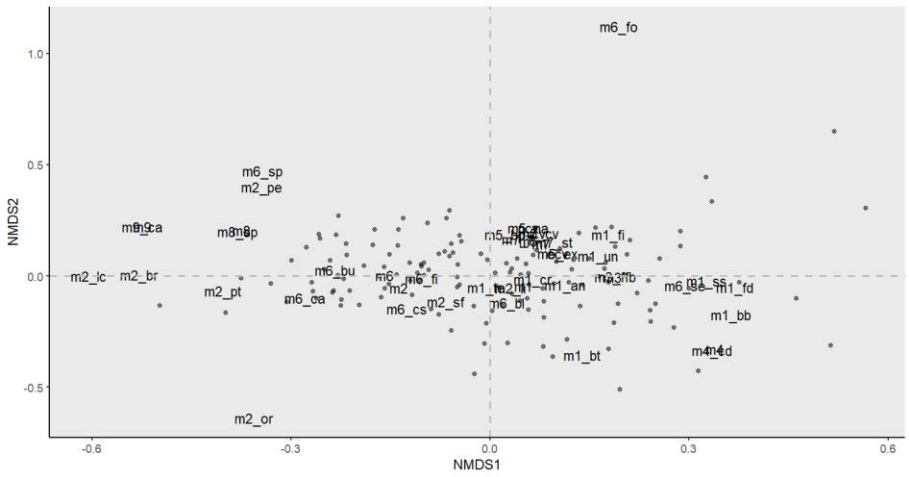
Figure 2: Abundance classes of tree microhabitats in the studied habitats

NMDS ordination identified 2 dimensions with a stress value 0.1563, stress type 1 with weak ties. It gave the best solution after iterations through scaling method '*centring*' (Figure 3). The

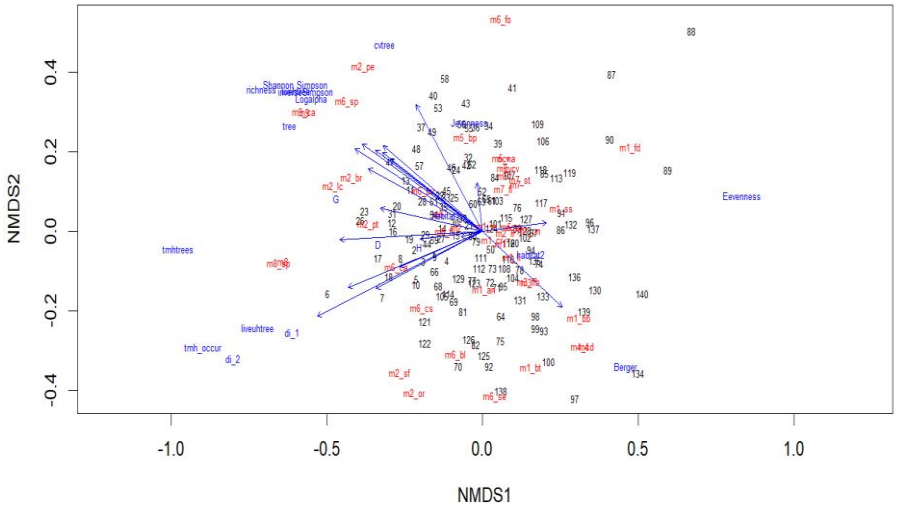
347 microhabitats show clustering of the following sub-categories of cavities (natural cavities and
348 excavated cavities), deadwood (snags and logs), and injuries in the form of fissures and
349 unidentified cause of decay (Figure 3A). The occurrences of these structures are highly
350 correlated and influenced by similar gradients of habitat characteristics as indicated by close
351 clustering in NMDS. The microhabitat structure - forked stems were also correlated with cavity
352 abundance, indicating tree growth forms as an important factor for occurrence of natural
353 cavities (Nußer et al., 2024). Quadrats sampled in the evergreen and deciduous habitats are
354 clustered in the ordination environment, such as quadrats 12 and 76 of evergreen habitat and
355 quadrats 101, 115 and 127 of deciduous habitat are clustered along the evenness of tree
356 community in the stands (Figure 3B). The abundance of microhabitats in the deciduous habitat
357 is following the habitat characteristics Berger-Parker dominance index and evenness probably
358 because the tree microhabitat host range in deciduous habitat is narrow compared to the
359 evergreen habitat. Due to high number of individuals, species richness and diversity of species,
360 the tree microhabitat host range is wide and quadrats of only evergreen habitats are dispersed
361 along these environmental gradients. Live unhealthy trees probably have high impact on the
362 diversity as well as abundance of microhabitats. The convex hull around the habitats shows
363 significant overlap in the sampled quadrats (Figure 3C). Also, nearly 20 microhabitat structures
364 can be observed in the overlapping region. The similarities in these quadrats may be due to
365 similar abundance of host trees of tree microhabitats and cavities, abundance of unhealthy and
366 dead trees. This indicates that in any habitat, it is the abundance of suitable hosts which mainly
367 influence the abundance of tree microhabitats, especially for cavities.

368 Out of the twenty stand characteristics used in ordination, only 12 showed to have significant
369 effect on the microhabitat abundance in evergreen habitats. These include – number of trees in
370 the stand (trees), number of microhabitat categories present, diversity of tree microhabitat
371 categories and sub-categories, stand basal area, Shannon diversity index and Simpson's

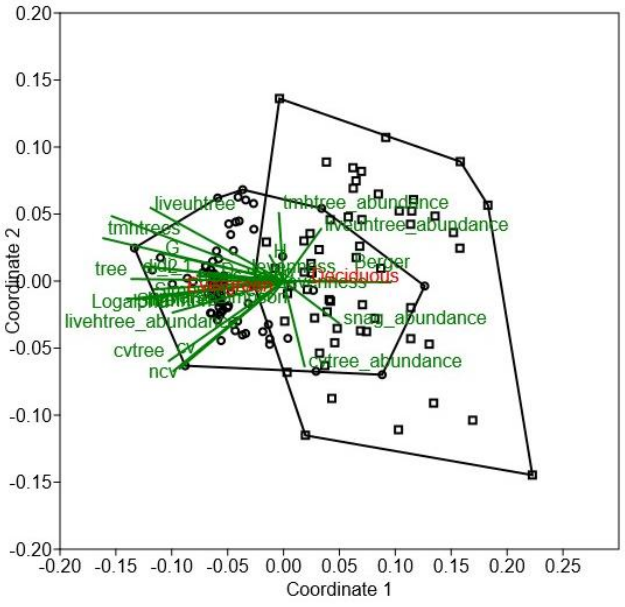
372 diversity index of the stand, Alpha diversity, Pielou's *J* or Shannon's equitability index (Table
373 2). Various diversity indices were estimated to understand if diversity in the stand is related to
374 high diversity and abundance of microhabitats. In deciduous habitats, only two stand
375 characteristics were identified to have significant effect – Berger-Parker index of dominance
376 and Shannon's equitability index.



377 (A)



378 (B)



379 (C)

380 Figure 3: Stand characteristics influencing the occurrences of tree microhabitats: (A) Dispersion of
381 samples in the ordination bubbles represent quadrats sampled and tree microhabitats represented with
382 codes; (B) numbers represent the quadrats (quadrats 1 to 80 represent evergreen habitat, 81 to 140
383 represent deciduous habitats) tree microhabitat categories indicated as codes, stand parameters fit with
384 samples, direction of arrow represents significant correlation and it direction represent direction of the
385 gradient, length of the arrow is proportional to correlation; (C) Convex hulls of the habitats evergreen
386 (circles) and deciduous (squares) showing overlap due to similarities in stand characteristics of some of
387 the quadrats [variable descriptions: Number of individuals (tree), Number of microhabitat host trees
388 (tmhttrees), Number of live healthy trees (livehtree), Number of live unhealthy trees (liveuhtree), Number of
389 cavity trees (cvtree), Number of microhabitats (tmh_occur), Diversity index of microhabitat categories (di_1),
390 Diversity index of microhabitat sub-categories (di_2), Stand basal area ha^{-1} (G), Stand density ha^{-1} (D), Stand
391 height ha^{-1} (H), Tree species richness (richness), Shannon diversity index (Shannon), Simpson diversity index
392 (Simpson), Inverse Simpson index (Inverse Simpson), Alpha diversity index (Logalpha), Berger-Parker index of
393 dominance (Berger), Pielou's evenness index (*J*evenness), Evenness index (*E*evenness)]
394

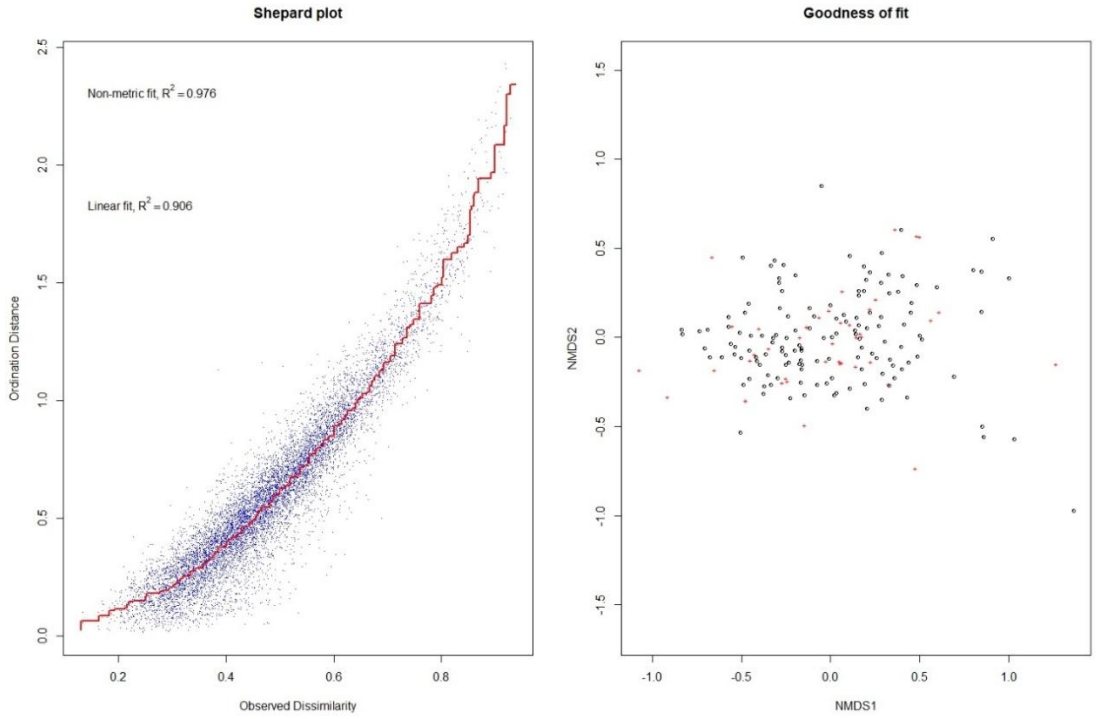
395 Table 2: Stand characteristics identified to have significant effect on the abundance of tree
396 microhabitats

Variable	NMDS1	NMDS2	R^2	Significance
Number of individuals (tree)	-0.97005	-0.24292	0.4940	0.001***
Number of microhabitat host trees (tmhttrees)	-0.99447	0.10499	0.7843	0.001***
Number of live healthy trees (livehtree)	-0.87864	-0.47748	0.4142	0.001***
Number of live unhealthy trees (liveuhtree)	-0.81191	0.58378	0.5120	0.001***
Number of cavity trees (cvtree)	-0.83239	-0.55419	0.2313	0.001***
Number of microhabitats (tmh_occur)	-0.93469	0.35546	0.7937	0.001***
Diversity index of microhabitat categories (di_1)	-0.97464	0.22378	0.1095	0.004**
Diversity index of microhabitat sub-categories (di_2)	-0.99731	0.11027	0.3935	0.001***
Stand basal area ha^{-1} (G)	-0.99731	0.07334	0.2896	0.001***
Stand density ha^{-1} (D)	-0.96945	-0.24529	0.0245	0.187^{NS}
Stand height ha^{-1} (H)	-0.02566	0.99967	0.0153	0.360^{NS}
Tree species richness (richness)	-0.90756	-0.41992	0.5619	0.001***
Shannon diversity index (Shannon)	-0.88952	-0.45690	0.5032	0.001***
Simpson diversity index (Simpson)	-0.90954	-0.41562	0.3799	0.001***
Inverse Simpson index (Inverse Simpson)	-0.89366	-0.44875	0.3850	0.001***
Alpha diversity index (Logalpha)	-0.83263	-0.55383	0.3203	0.001***
Berger-Parker index of dominance (Berger)	0.92312	0.38452	0.2611	0.001***
Pielou's evenness index (*J*evenness)	-0.66561	-0.74630	0.0085	0.557^{NS}
Evenness index (*E*evenness)	0.97143	0.23731	0.0985	0.002**

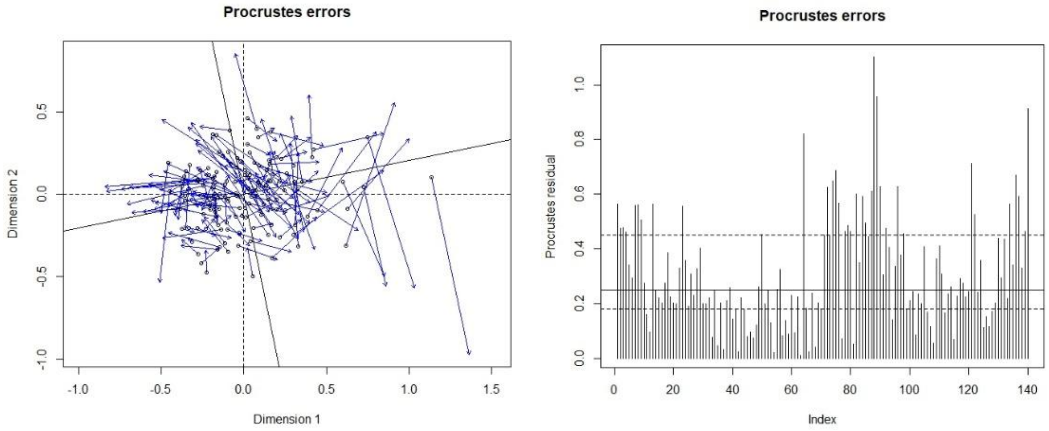
NS = Not significant, ** Significant at 0.05 level, *** Significant at 0.01 level

The two ordinations (metaNMDS and isoNMDS) were compared using Procrustes rotation and model difference was 19.65, indicating good improvement. The stress in monoMDS was 0.000128, which is close to zero and therefore a good fit. 'Shepard plot' and plot for 'Goodness of fit' test showed highly significant correlation of tree microhabitat abundance with habitat characteristics ($r^2 = 0.448$, $p = 0.001$**) and quadrats (Figure 4A). Similar steps were followed to apply NMDS ordination for 33 subcategories of tree microhabitats. The abundance related data was then attached to the stand characteristics (applied fit with 999 permutations). Highly significant relationship was obtained between the stand parameters, except occurrences, abundance and *E*venness which were significant, and stand basal area, diameter at breast height, height and *J*evenness were not significance. Thus, rather than the diameter and density of trees, it is the diversity of species in stand which influences tree microhabitat occurrences in the tropical forests. The *z* values were always high indicating associations among the microhabitats. Differences were observed in the abundance of microhabitat as an effect of habitat characteristics.

The test for homogeneity of multivariate dispersion showed significant difference in the dispersion pattern of tree microhabitats in the two habitats (Figure 5A). The fit of these models was tested using standard ANOVA (F = 2.783, p = 0.0975*), and variance plot was plotted applying 999 permutations (F = 2.783, p = 0.09*) (Figure 5B). The pairwise analysis using Tukey's test for post-hoc analysis estimated the difference in the mean distance to centroid as -0.02 ($Adj.p$ = 0.975, lower confidence level = -0.044, upper confidence level = 0.004). The results indicate that the models were a good fit.



(A) 'Shepard plot' and Goodness of fit test for tree microhabitats in the studied habitats



421

422 (B) Improving the ordination as metaMDS (C) Plot showing difference due to

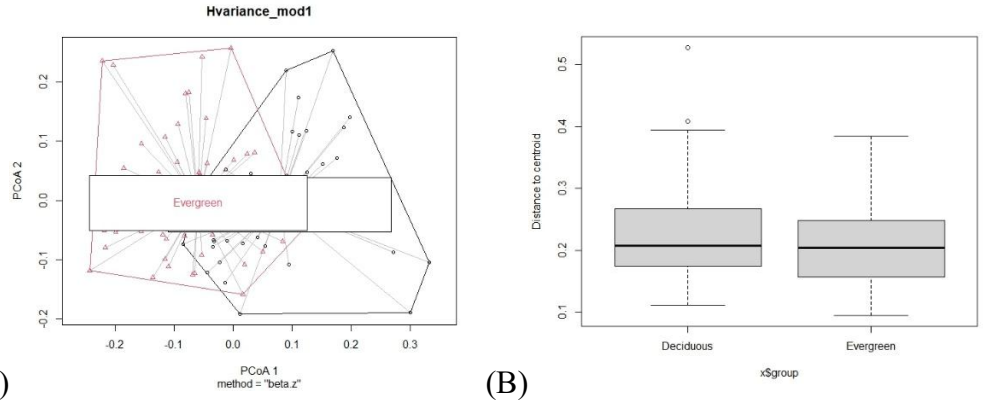
423 through shift in the location of quadrat variations in the quadrats

424 Figure 4: Results of the Goodness of fit test for the NMDS ordination applied to the stand

425 attributes with reference to the abundance of tree microhabitats in evergreen and deciduous

426 habitats

427



428 (A) (B)

429 Figure 5: Results of test for homogeneity of dispersion: (A) Dispersion observed in respective

430 habitats (red triangles represent evergreen habitat, black circles represent deciduous habitat;

431 (B) Comparison of variance observed from multivariate ANOVA for homogeneity of dispersion

432 Despite overlap in the dispersion of quadrats sampled in the evergreen and deciduous habitats,

433 there was significant difference in the habitat characteristics. This influences the overall

diversity and abundance of tree microhabitats in the habitat. It is especially significant for some of the sub-categories of tree microhabitats such as *Crematogaster* ant nest, spiral and twisted tree trunks, other epiphytes which are correlated with the species richness and diversity of trees in the habitat. Cankers and sapruns which act as entry points for decay agents are associated with specific host species and vigour of trees.

Major host tree species and families

In the evergreen habitat, 29 families had at least 10 host individuals, while in the deciduous habitat, 15 families met this criterion (Table S1). A total of 56 species hosted tree microhabitats in the evergreen habitat, compared to 16 tree species in the deciduous habitat (Table S2). Lauraceae was the most represented family for both microhabitats and cavity hosts in the evergreen habitat. Meliaceae, Anacardiaceae, Clusiaceae, Euphorbiaceae, and Phyllanthaceae were well represented as microhabitat hosts, with a greater number of species, but were not major cavity hosts (Table S3 and S4). Lauraceae, Phyllanthaceae, Annonaceae, Elaeocarpaceae, Euphorbiaceae, and Myristicaceae were the most species-rich families among cavity hosts (Figure 6).

In the deciduous habitat, Fabaceae was most species-rich family hosting both microhabitats and cavities. Other notable families that included multiple species acting as hosts for both microhabitats and cavities were Malvaceae, Phyllanthaceae, Rubiaceae, and Combretaceae. While Fabaceae showed high potential as a host for both microhabitats and cavities in the deciduous habitat, it had low host potential in the evergreen habitat and was not observed as a cavity host.

Among the tree species hosting microhabitats, majority were healthy individuals (n = 4855), followed by unhealthy (n = 1818) and dead (n = 125) individuals. In both habitats, most species hosted a greater number of microhabitats when unhealthy. Species such as *Cullenia exarillata*

458 A.Robyns*, Dimocarpus longan* Lour.*, Grewia tiliifolia* Vahl*,* and *Tectona grandis* L.f., served
459 as microhabitat hosts across all vitality classes—healthy, unhealthy, and dead. Notably
460 *Cullenia exarillata, Terminalia paniculata* B.Heyne ex Roth*, Dimocarpus longan, Drypetes*
461 *venusta* (Wight) Pax & K.Hoffm.*, Dysoxylum sp., Garcinia sp., Dillenia pentagyna* Roxb.*,*
462 *Litsea sp., Ligustrum robustum subsp. perrottetii* (A.DC.) de Juana*, Mesua ferrea* L., and
463 *Myristica malabarica* Lam. contributed significantly to the total number of hosts, both in
464 healthy and unhealthy categories (see Table S2 and S4). There was a highly significant
465 difference in the number of microhabitats among host species across different vitality classes
466 ($F = 2.5489$, $p < 0.001$***). Post-hoc test results indicated significant variation in microhabitat
467 abundance among species within each habitat.

468 At family level, in evergreen habitat, microhabitat abundance was highest in trees belonging to
469 Malvaceae (n = 1305), followed by Lauraceae (1043), Myristicaceae (931), Sapotaceae (831),
470 Sapindaceae (721), Putranjivaceae (617), and Calophyllaceae (582). In deciduous habitat, the
471 microhabitat abundances were highest in Fabaceae (n = 1157), Combretaceae (827), Malvaceae
472 (358), Dilleniaceae (334), Euphorbiaceae (274), Lamiaceae (255), and Lythraceae (197) (Table
473 S2). However, the abundance of microhabitats per tree varied across families indicating that
474 size, vitality, and/or health of the tree might be influencing host suitability. In the evergreen
475 habitat, the highest per-tree microhabitat abundance was observed in Malvaceae (maximum =
476 54), followed by Oleaceae (34), Calophyllaceae (31), Myristicaceae (28), and Elaeocarpaceae
477 (21). In the deciduous habitat, it was highest in Combretaceae (22), followed by Euphorbiaceae
478 (17), Dilleniaceae (14), Malvaceae (13), and Apocynaceae (13). There was a highly significant
479 difference in microhabitat abundance among individuals of different host families in both
480 habitats ($F = 6.5673$, $p < 0.001$). Pairwise comparisons showed that in the evergreen habitat,
481 microhabitat abundance was significantly higher in hosts from Dipterocarpaceae and
482 Achariaceae compared to Calophyllaceae, Phyllanthaceae, and Sapindaceae. Similarly,

microhabitat abundance in Dipterocarpaceae and Malvaceae was higher than in Elaeocarpaceae, likely due to the lower presence of epiphytes such as bryophytes and pteridophytes on the latter. In the deciduous habitat, microhabitat abundance differed significantly among families, with particularly high values in Combretaceae, Verbenaceae, Dilleniaceae, and Mimosaceae.

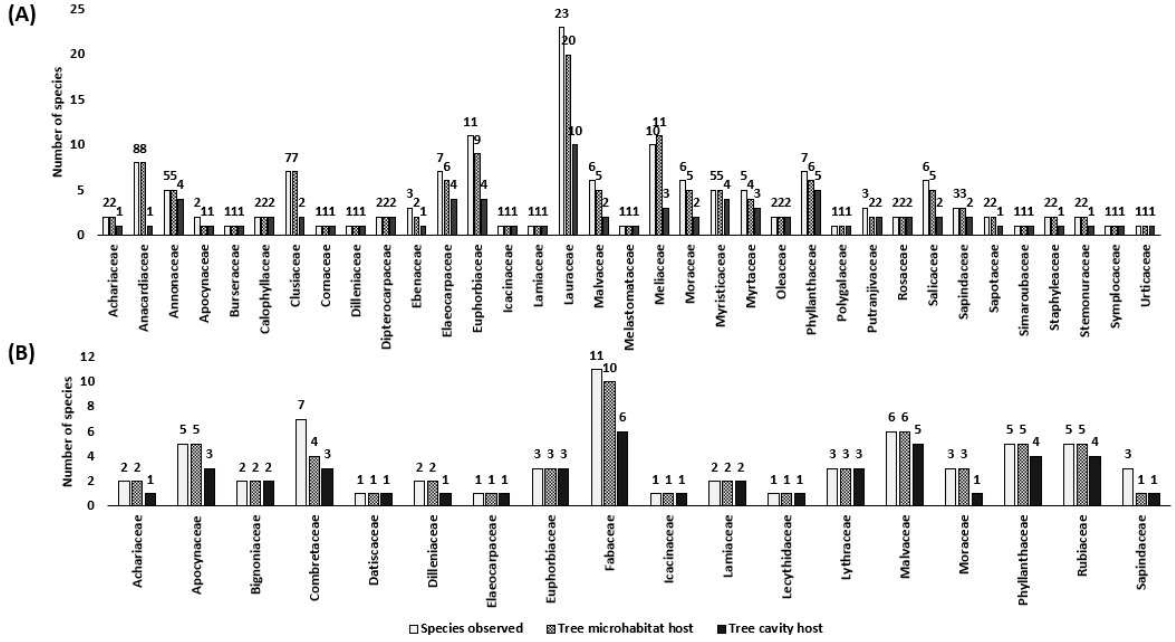


Figure 6: Number of species in the tree families hosting both tree microhabitat and tree cavities

Most individual trees hosted at least one type of microhabitat, with the maximum number of microhabitat types recorded on a single tree being six. There was a significant difference in microhabitat type richness across species ($F = 15.2852$, $p < 0.001$) and families ($F = 4.5628$, $p = 0.001$) between the two habitats. The mean microhabitat richness was 1.0425±1.1037) per tree. Majority of the trees did not host cavities. The highest number of cavities recorded on a single tree was ten. In the evergreen habitat, 49 out of 50 families hosted at least one tree microhabitat, and 35 families hosted at least one cavity. In the deciduous habitat, 29 out of 30 families hosted tree microhabitats, and 19 families had at least one cavity (Figure 6). In

evergreen habitat, most cavity-hosting individuals belonged to the families Myristicaceae, Malvaceae, Lauraceae, Calophyllaceae, and Elaeocarpaceae (Table S2). In the deciduous habitat, the majority of cavity-hosting individuals were from Fabaceae, Combretaceae, Dilleniaceae, and Euphorbiaceae. The tree species with the highest number of cavities in evergreen stands included *Dimocarpus longan, Palaquium ellipticum* (Dalzell) Baill.*, Cullenia exarillata, Myristica malabarica*, and *Drypetes venusta*. In deciduous forests, cavity-rich species included *Xylia xylocarpa* (Roxb.) W.Theob.*, Terminalia paniculata*, and *Macaranga peltate* (Roxb.) Müll.Arg. (Table 6). Among the cavity-hosting trees, there were highly significant differences in both species ($F = 5.1641$, $p < 0.001$) and families ($F = 6.0709$, $p < 0.001$).

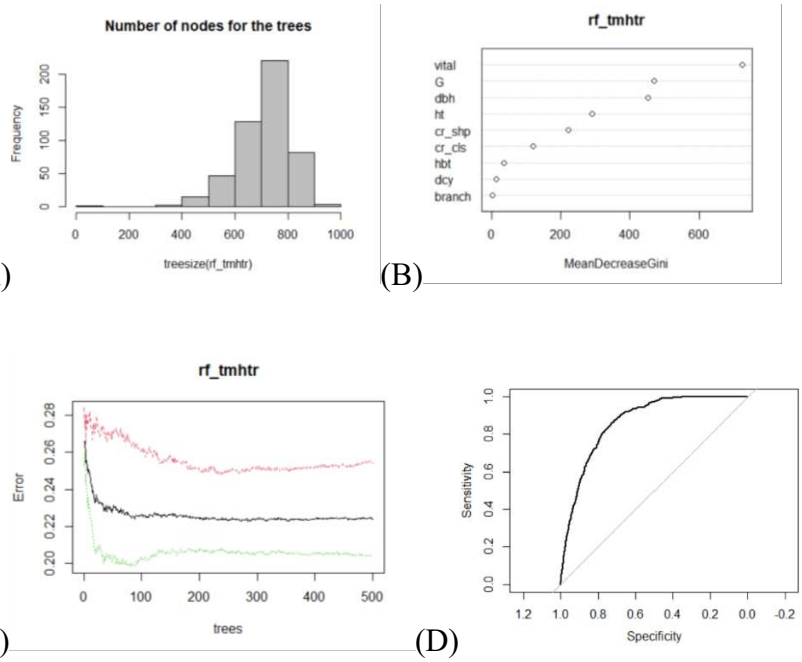
Tree characteristics related to presence/absence of tree microhabitats

In both the habitats, among the live trees more than 90% unhealthy and more than 40% healthy individuals hosted at least one microhabitat (Figure S1). In this study, all the snags were considered as microhabitat hosts as they are potential habitat resources for numerous saprophytic fungi, invertebrates and vertebrates such as cavity excavators, if not at present, then in future.

The presence of microhabitats was 59% and 41% individuals did not host any microhabitat. The model could predict the presence of microhabitats with 84.9% Accuracy (p<0.001***; lower confidence level = 0.8405, upper confidence level = 0.8565). The p value for Mcnemar's test was ≤0.001***, sensitivity 85.4 %, specificity 84.0 %, detection rate was 51.3 %. Nine variables were important for the presence of microhabitats, most important being the dbh of trees, followed by vitality of trees, height of tree, crown shape, crown class, habitat, decay stage, branchiness (Figure 7B). The ROC curve (Figure 7D) showed that approximately 85 %

of the data lies below the curve which validates the model. Precision was 88.9%, recall matrix was 85.4%, and overall accuracy with F1 score was 87.1%.

The decision tree showed vitality of trees was most important factor and mother node to group the host trees placing all the healthy in one group and unhealthy and dead in other (Figure 8). The next node was dbh, trees in small diameter class (up to 0.207 m dbh and the probability even becomes more than 90% if the host was dead. Unhealthy trees with dbh >0.207 m had high probability of hosting microhabitats. Healthy trees in lower diameter class (≤0.143 m) and low basal area (≤0.01 sq m) were less likely to host microhabitat. However, large, healthy trees (diameter at breast height > 0.21) had a high probability of hosting a microhabitat.



(A) (B)

(C) (D)

Figure 7: Variables identified to be important for increasing the probability of presence of tree microhabitats: (A) number of nodes in the trees generated from model; (B) plot showing Mean Decrease Gini (MDG) of variables; (C) error plot; (D) AOC for the final model (area under curve = 0.8466)

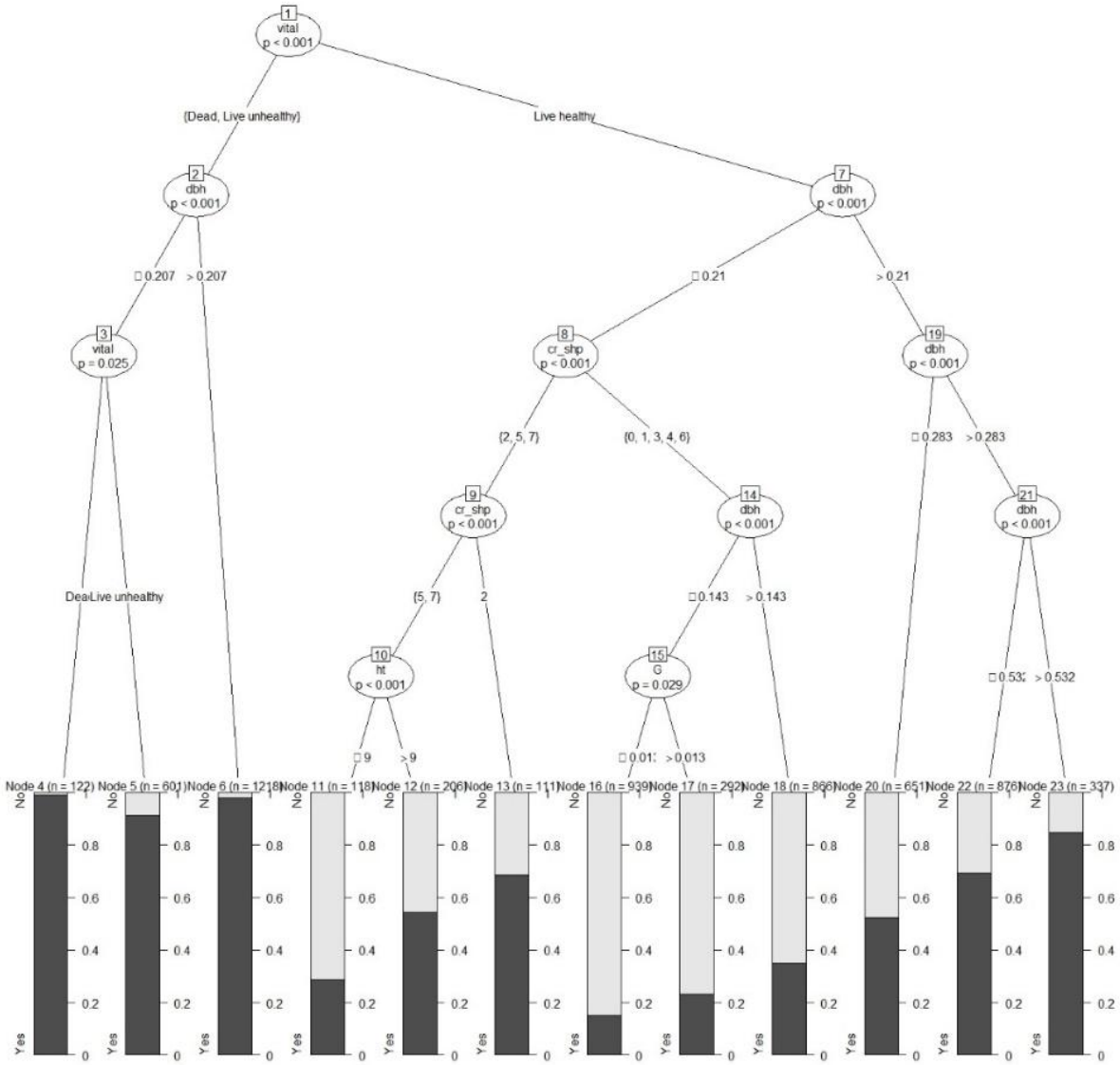


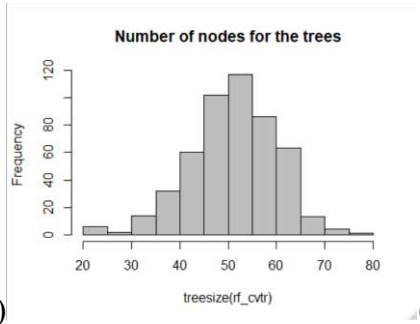
Figure 8: Probability of presence of tree microhabitats based on the tree characteristics, the grey scale bars represent probability of presence and absence of tree microhabitat (dark grey colour for presence light grey for absence)

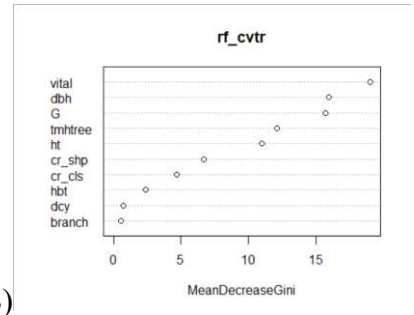
Tree characteristics related to presence/absence of tree cavity

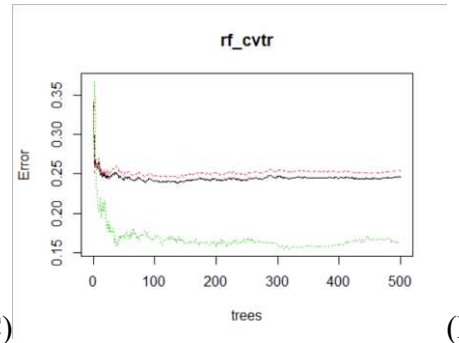
The proportion of trees with cavity was 8.7% and absence was 91.3%. Model predicted cavity presence with 76.1% Accuracy (p = 1; ci_l = 0.7514, ci_u = 0.7704). The Mcnemar's p value was <2e-16, sensitivity 87.6%, specificity 75.0%, and detection rate 7.5%. The importance value of tested variables showed vitality of tree, dbh of trees, basal area of trees, presence of

any microhabitat, height of trees, crown shape, crown class, habitat, decay stage, branchiness were important for cavity occurrences on trees (Figure 9B). The ROC curve showed that approximately 86% of the data lies under the curve which validates the model (Figure 9D). The hierarchical decision tree had 24.8% precision due to very low true presence value. The recall score was 87.6% indicating that the model was able to detect the presence correctly. Precision gain was estimated to be 70 % and Recall gain was 98.6 %. The F1 gain was 84.3 % showing that the model was efficient to predict the cavity presence in the dataset.

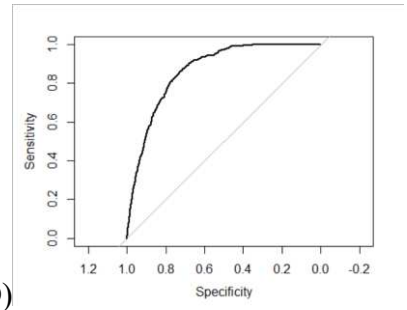
The decision tree showed vitality of trees was the most important factor and mother node to group the hosts placing all the unhealthy in one group and healthy and dead in another (Figure 10). The next node was dbh, trees in small diameter class (lesser than 0.274 m had probability of hosting cavity, if it hosted other microhabitats. Unhealthy trees in larger diameter classes (>0.274 m) were likely to have cavity only in presence of other microhabitats. Among the healthy and dead trees, trees with large basal area (>0.594 sq m per ha) had moderate probability to host cavity irrespective of presence or absence of other microhabitats. Healthy and dead trees in evergreen habitat with basal area up to 0.594 sq m per ha had high probability of hosting cavities. However, further the height of trees and its crown class made it more potential as cavity host. In deciduous habitat trees with basal area up to 0.594 sq m per ha had probability of hosting cavities if other microhabitats were present.

(A) 

(B) 

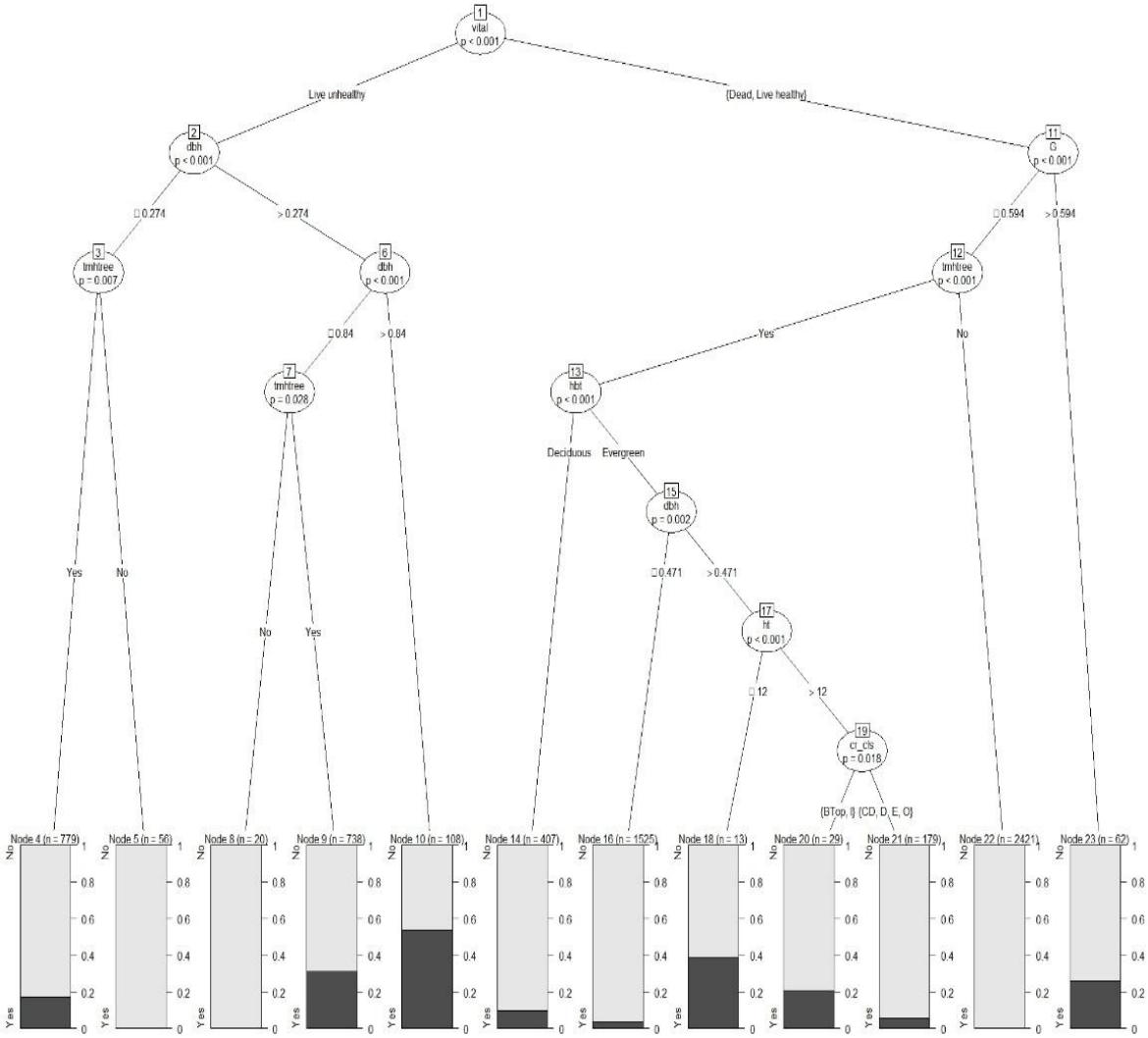


(C)



(D)

Figure 9: Variables identified to be important for increasing the probability of presence of tree cavities: (A) number of nodes in the trees generated from model; (B) plot showing Mean Decrease Gini of variables; (C) error plot; (D) AOC for the final model (area under the curve = 0.8638)



572 Figure 10: Probability of presence of tree cavities based on the tree characteristics, the grey
573 scale bars represent probability of presence and absence of tree cavities (dark grey colour for
574 presence light grey for absence)

575

576 **Discussion**

577 **Habitat characteristics important for diversity and abundance of tree microhabitats**

578 There was a significant difference in the stand structure of evergreen and deciduous habitats,
579 which may explain the observed variation in the diversity and abundance of microhabitats.
580 Using non-parametric ordination analysis, the role of specific stand attributes in influencing
581 tree microhabitat abundance within each habitat type was identified.

582 In evergreen habitats, microhabitat abundance correlated strongly with diversity indices
583 Shannon Index, Simpson Index, Fisher's alpha, and evenness. These indices incorporate both
584 species richness and the abundance of dominant species, highlighting the importance of not
585 just the number of species but also the presence of numerous individuals of dominant tree
586 species. In contrast, in deciduous habitats, the Berger-Parker index showed a high correlation
587 with microhabitat abundance. Despite lower species richness, the presence of a large number
588 of individuals from a few dominant species contributed substantially to microhabitat hosting
589 capacity. The strong correlation between microhabitat abundance and evenness in these habitats
590 suggests that dominant species play a crucial role in supporting microhabitats in deciduous
591 forests. These key habitat attributes have also been shown to influence tree microhabitat
592 diversity and abundance in other forest types. The findings of this study align with previous
593 research by Winter and Möller (2008), Michel and Winter (2009), Vuidot et al. (2011), Larrieu
594 and Cabanettes (2012), Regnery et al. (2013), Larrieu et al. (2014), Kozak et al. (2018), Asbeck
595 et al. (2019), and Paillet et al. (2019). In particular, observations from deciduous stands are

596 consistent with the results of Asbeck et al. (2019) and Courbaud et al. (2022), who
597 demonstrated that even trees in lower diameter classes can serve as important hosts, especially
598 in stands where they are abundant. Microhabitat diversity was also highly correlated with
599 microhabitat abundance, suggesting that existing microhabitats may facilitate the formation or
600 establishment of additional microhabitats through ecological interactions and structural
601 changes.

602 In present study, stand characteristics were limited to tree species-related attributes; geographic
603 variables such as altitude, slope, and forest age were not included due to the restricted number
604 of sampling sites. Furthermore, to avoid bias from anthropogenic influences, the study was
605 conducted exclusively in protected forests. Therefore, conclusions regarding the effects of
606 forest management practices could not be drawn.

607 **Tree characteristics important for diversity and abundance of tree microhabitats**

608 The vital stage of the trees was the most important characteristic followed by the dbh of trees
609 hosting microhabitats. This is in contrast to the observations from temperate regions, where
610 diameter of the trees was most important factor followed by the vitality (Paillet et al. 2019).
611 The unhealthy and dead trees of any dbh class had high potential for hosting tree microhabitats
612 (Figure S2D). This was applicable to forests in temperate regions (Vuidot et al. 2011; Paillet et
613 al. 2019), Mediterranean (Winter et al. 2015; Larrieu et al. 2018; Marziliano et al. 2021), boreal
614 (Martin et al. 2021a; Kõrkjas et al. 2023) and similarly in tropical regions based on the present
615 study. However, live unhealthy trees host more diversity of microhabitats compared to the dead
616 individuals in both tropical evergreen and deciduous habitats (Figure S2E). The proportion of
617 individuals hosting microhabitats was high in the deciduous (71.5 %) compared to the
618 evergreen (57.2 %). In addition to cavities, snags hosted four other microhabitats in deciduous
619 habitat and six other tree microhabitats in evergreen (excluding crown deadwood). The

620 proportion of growth forms was highest in the healthy individuals compared to other
621 microhabitats in both habitats.

622 Growth forms also form cavities and make healthy trees high-potential hosts for tree cavities.
623 However, features related to these structures are specific to tree species such as *Cullinea*
624 *exarillata*, *Drypetes venusta* in evergreen and *Xylia xylocarpa* in deciduous habitat. For
625 example, spruce has been observed to have high richness of microhabitats favouring the
626 abundance of dead branches, rot holes and fungal fruiting bodies (Kõrkjas et al. 2021). Other
627 deciduous tree species reported to host cavities in the tropical forests are *Tectona grandis*,
628 *Dalbergia latifolia*, *Garuga pinnata* (Mukardamwala et al., 2025). *Terminalia* sp. which was
629 observed to host cavities in the deciduous forests southern Western Ghats were not observed
630 with cavities in the Dangs area. This emphasises the importance of tree species as a
631 characteristic of host tree as well as influence of site factor on wood and presence of other
632 microhabitats such as specificity of tree species and rot fungi. Malvaceae, Combretaceae,
633 Olecaceae, Myristicaceae, Euphorbiaceae, Elaeocarpaceae were the dominant microhabitat
634 host tree families in the studied tropical area. The dominant cavity host tree families were
635 Myristicaceae, Malvaveae, Lauraceae, Elaeocarpaceae, Fabaceae, Combretaceae,
636 Dilleniaceae, Combretaceae. The tree families Fabaceae, Anacardiaceae, Moraceae and
637 Meliaceae are observed to host more cavities compared to others in human-dominated
638 landscapes (Koli et al., 2025). Individuals of these families are prone to rot by white and brown
639 fungi, which make them suitable cavity hosts (Suryanarayanan et al., 2011). Therefore,
640 unhealthy and dead individuals and species of these families are potential habitat resources in
641 resource-deficient landscapes such as urban parks, community lands, and residential areas.

642 Epiphytes may also show host preference leading to high richness of microhabitats on specific
643 species (Vuidot et al. 2011; Regnery et al. 2013), and more abundance in large diameter classes
644 (Vuidot et al. 2011). The importance of specific tree species due to wood characteristic has

been also highlighted in the temperate broadleaved forests (Regnery et al. 2013). Based on these characteristic features trees can be grouped into functional groups which host specific microhabitats (Asbeck et al. 2020). For example, species with growth forms structures like buttress and flutes which host mostly natural cavities and rot by fungal decay host excavated cavities. However, in present study some of the species were observed to host most of the microhabitats such as cavities as well as epiphytes. Therefore, further study involving clustering of microhabitats at stand level and species level for fungi and epiphytes may be required at multiple scales (Kõrkjas et al. 2023) for identification of functional groups in tropical regions.

In both habitats, the richness and occurrences of some of the microhabitats (such as injuries and epiphytes) was higher in the unhealthy and dead trees compared to the healthy trees. Across the habitats there was significant increase in the microhabitat occurrences with increase in the diameter of trees (F = 2.0952, p = 0.063). Therefore, the abundance of potential dead and unhealthy host trees with large basal area will be an important factor for increasing the abundance of tree microhabitats in any habitat (Martin et al. 2021; Großmann 2021; Santopuoli et al. 2022).

Pairwise comparison of trees in the six dbh-range shows that the occurrences of microhabitats in the higher diameter classes from 0.91-1.10 m and > 1.11 m was not significant (t = 0.9579, p = 0.3382). But it was observed that there was increase the proportion of some of the microhabitats with diameter of trees such as injuries and epiphytes, cavities and growth forms in the healthy trees in deciduous habitat similar to the observations from temperate regions (Paillet et al. 2019). In evergreen habitat, the increase in the proportions of the microhabitats remained nearly similar across all the diameter classes. Among snags, in both the habitats there was increase in the proportions of fungal fruiting bodies and cavities with increase of diameter

669 of host trees. Snags add microhabitats in the habitat irrespective of the size of tree in tropical
670 forests (Figure 8 and 10), and in medium to very large tress trees in temperate forests (Paillet
671 et al., 2017).

672 The difference in the diversity and abundance of microhabitats was highly significant with the
673 increase in diameter of trees in different vitality classes similar to the observations of Martin
674 et al. (2021). The difference was significant only in the occurrences of microhabitats between
675 the live unhealthy trees and snags. But among the diameter classes 0.51-0.70 m, 0.71-0.90 m,
676 0.91-1.10 m and >1.11 m the microhabitat occurrences had no significant difference based on
677 the health status of the host trees. Large trees, regardless of their health condition, have a high
678 potential to host microhabitats. This may explain why trees with a diameter greater than 0.274
679 m are more likely to fall into larger diameter classes that have a higher probability of hosting
680 microhabitats and cavities. Our observations align with findings from temperate regions
681 (Paillet et al. 2019; Marziliano et al. 2021), where tree size was the most important predictor
682 of microhabitat richness and abundance. In contrast, in the tropics, tree health was found to be
683 a significant factor only for specific structures, such as cavities and epiphytes.

684 Some studies suggest that plot-level information on tree characteristics—such as bark features,
685 phyllotaxis, developmental stage of tree species, compartmentalization (e.g., forking), and
686 physiological state at the individual tree level—and their comparisons across multiple scales
687 may serve as better predictors of tree microhabitats (Larrieu et al. 2022; Kõrkjas et al. 2023).
688 These parameters require micro-scale observations and were not included in the present study.

689 Factors such as the decay class of dead trees, the availability of crown deadwood, and the
690 presence of rot agents have been identified as important for the occurrence of cavities, whether
691 naturally formed or excavated (DeGraaf and Shigo 1985; Sedgwick and Knopf 1986; Schepps
692 et al. 1999; Remm and Lõhmus 2011; Zahner et al. 2012). Even in live trees, a low proportion

693 of live branches in the canopy is preferred by excavators (Ross et al. 1997). In the present
694 study, crown class and crown shape were also observed to increase the probability of cavity
695 occurrence, often correlating with the presence of other microhabitats such as crown deadwood
696 and fungal fruiting bodies. While woodpeckers are known to prefer large, old trees (Rudolph
697 and Conner 1991), cavities created by primary excavators and those formed naturally were also
698 observed in medium-sized trees, which were frequently used by secondary cavity users (Patel
699 et al. 2022, 2023).

700 Tree species characteristics, such as the presence of latex and resins, may influence tree
701 selection for cavity excavation; however, this may also depend on the abundance of preferred
702 species (Ross et al. 1997). The observation that large *Mesua ferrea* trees host rot-induced holes
703 but lack excavated cavities suggests that intrinsic wood characteristics, specifically the
704 presence of resins, may act as a biological deterrent to excavating fauna despite the availability
705 of softened wood.

706 Probably because of the association between the tree species and types of microhabitats it hosts
707 host more microhabitats such as oak and beech in French forests (Vuidot et al., 2011). Modified
708 habitats such as urban landscapes usually have fewer species and small size, which reduce the
709 diversity and abundance of microhabitats (Gallego et al., 2025). While managed landscapes are
710 poor in microhabitats, in natural forests, by virtue of the 'habitat heterogeneity hypothesis'
711 (Simpson 1949; MacArthur and Wilson 1967; Müller et al. 2018), the higher number of tree
712 species adds to the habitat resources and niche for many plants and animals (Bazzaz 1975;
713 Taboada et al. 2010; Jung et al. 2012).

714 The present study explores the relationship between forest stand features and the presence of
715 microhabitats in evergreen and deciduous forests. Irrespective of forest type and number of
716 trees, the presence of unhealthy trees, species richness and diversity, and the number of trees

717 with tree microhabitats or cavities were key factors for ensuring the availability of
718 microhabitats. Dead and unhealthy trees, though fewer in number, were found to serve as key
719 hosts for tree microhabitats. A greater tendency to host tree microhabitats was observed in dead
720 trees compared to unhealthy live ones. Healthy trees in the smallest size category, taller
721 individuals with reduced canopy cover, were more likely to host tree microhabitats. As the size
722 of healthy trees increased, likelihood of tree hosting more microhabitats increased. Unhealthy
723 trees with a dbh more than 0.34 meters are more likely to host cavities. This pattern suggests
724 that factors such as fungal decay and physical damage may play a role in cavity development,
725 particularly in smaller unhealthy trees. Cavity formation was found to be influenced by more
726 factors than other tree microhabitats. Availability of suitable trees and substrates is important
727 factor in bomartinth managed and unmanaged habitats (Maya-Elizarrarás et al., 2025). The live
728 and dead trees more than 0.59 meters dbh hosted cavities hosted natural cavities and
729 dendrothelms which serve as essential nesting structures for various organisms. Conservation
730 strategies should prioritize the retention of key host species like *Cullenia exarillata* and
731 establish specific diameter targets for 'unhealthy' trees, recognizing them as essential
732 biodiversity hotspots rather than mere forest hazards.

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Supplement A

NMDS was performed using the metaMDS function in the vegan package, treating stand characteristics as sites and tree microhabitat types and subtypes as species. this function accommodates raw data and dissimilarity matrices, so no further transformation was applied. the stressplot function was used to visualize tree microhabitat abundances in two-dimensional space. The stressplot draws a Shepard Plot with Observed Dissimilarities in X axis and Ordination Distance in Y axis. The correlation is calculated based on stress using the formula:

$R^2 = 1\text{-}S^2$

where, Stress (S) = $\sqrt{\frac{\sum_{i \neq j}[\theta(d_{ij}) - \tilde{d}_{ij}]}{\sum_{i \neq j} \tilde{d}_{ij}^2}}$

The 'fit based R^2' is the correlation between the fitted values and ordination distances. The null model of linear fit assumes that all ordination distances are equal and fit is flat horizontal line. The NMDS was performed with random seed set at 50, distance method selected as '*bray*', iterations set to 99 and auto-transformation set as FALSE.

Bray distance is calculated by the formula: $d_{jk} = \frac{A + B - 2J}{A + B}$

The properties of the distance matrix are:

for A = B $d_{AB} = 0$ if the sites are identical, distance is zero

for $A \neq B$ $d_{AB} > 0$ if sites are different, their distance is larger than zero

$d_{AB} = d_{BA}$ distances are symmetric

$d_{AB} \leq d_{Ax} + d_{xB}$ the shortest distance between two sites is a line, and it cannot be improved by going through other sites

995 Table S1: Families of host tree species of tree microhabitats (number of individuals ≥10)

Evergreen				Deciduous	
Family	**Number of individuals**	**Family**	**Number of individuals**	**Family**	**Number of individuals**
Achariaceae	17	Myristicaceae	330	Apocynaceae	69
Anacardiaceae	146	Myrtaceae	80	Bignoniaceae	16
Annonaceae	33	Oleaceae	63	Combretaceae	173
Burseraceae	13	Phyllanthaceae	125	Dilleniaceae	83
Calophyllaceae	148	Polygalaceae	73	Euphorbiaceae	79
Clusiaceae	114	Putranjivaceae	191	Fabaceae	338
Dipterocarpaceae	49	Rosaceae	13	Lamiaceae	64
Eabaceae	34	Salicaceae	28	Lythraceae	50
Elaeocarpaceae	148	Sapindaceae	296	Malvaceae	108
Euphorbiaceae	103	Sapotaceae	373	Phyllanthaceae	24
Icacinaceae	22	Stemonuraceae	14	Rubiaceae	23
Lauraceae	410	Symplocaceae	18		
Malvaceae	339	UN_62	24		
Meliaceae	156	Urticaceae	18		
Moraceae	40				

996

997 Table S2: Host tree species of tree microhabitats (number of individuals ≥10)

Evergreen				Deciduous	
Species	**Number of individuals**	**Species**	**Number of individuals**	**Species**	**Number of individuals**
Actinodaphne sp.	43	*Glochidion* sp.	23	*Bauhinia malabarica*	10
Aglaia perviridis	10	*Heritiera papilio*	25	*Bombax ceiba*	10
Aglaia sp.	10	*Holigarna beddomei*	10	*Bombax insigne*	31
Agrostistachys borneensis	62	*Holigarna* sp.	56	*Cassia fistula*	11
Antidesma sp.	54	*Hopea parviflora*	46	*Catunaregam spinose*	10
Apodytes dimidiate	22	*Hydnocarpus* sp.	13	*Cleistanthus collinus*	27
Artocarpus heterophyllus	29	*Ligustrum robustum subsp. perrottetii*	52	*Dillenia pentagyna*	82
Bischofia javanica	27	*Litsea* sp.	52	*Grewia tiliifolia*	49
Calophyllum sp.	12	*Macaranga peltata*	20	*Lagerstroemia microcarpa*	36
Canarium strictum	13	*Mesua ferrea*	118	*Macaranga peltata*	56
Cinnamomum sp.	36	*Myristica malabarica Lam.*	257	*Radermachera xylocarpa*	13
Cryptocarya sp.	10			*Tabernaemotana alternifolia*	10
Cryptocarya wightiana	150	Unknown1	63	*Tectona grandis*	61
Cullenia exarillata	311	*Neolitsea scrobiculata*	26	*Terminalia bellerica*	13
Dimocarpus longan	292	*Olea dioica*	11	*Terminalia paniculata*	150
Diospyros sp.	32	*Oreocnide integrifolia*	18	*Wrightia tinctoria*	48
Drypetes sp.	17	*Palaquium ellipticum*	367	*Xylia xylocarpa*	282
Drypetes venusta	174	*Persea macrantha*	56		
Dysoxylum malabaricum	55	*Poeciloneuron indicum*	30		
Dysoxylum sp.	54	*Polyalthia coffeoides*	13		

Evergreen				Deciduous	
Species	**Number of individuals**	**Species**	**Number of individuals**	**Species**	**Number of individuals**
Elaeocarpus munroii	18	*Polyalthia fragrans*	13		
Elaeocarpus tuberculatus	112	*Prunus ceylanica*	12		
Elaeocarpus variabilis	11	*Symplocos sp.*	18		
Flacourtia montana	17	*Syzygium cumini*	21		
Garcinia morella	27	*Syzygium gardeneri*	25		
Garcinia pushpangadaniana	23	*Syzygium* sp.	31		
Garcinia sp.	43	Unknown2	24		
Glochidion ellipticum	11	*Xanthophyllum arnottianum*	73		

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1000 Table S3: Families of host tree species of tree cavities (number of individuals ≥10)

Evergreen				Deciduous	
Family	**Number of individuals**	**Family**	**Number of individuals**	**Family**	**Number of individuals**
Annonaceae	14	Myrtaceae	19	Apocynaceae	19
Calophyllaceae	87	Oleaceae	18	Bignoniaceae	12
Clusiaceae	14	Phyllanthaceae	30	Combretaceae	80
Dipterocarpaceae	31	Polygalaceae	48	Dilleniaceae	59
Elaeocarpaceae	70	Putranjivaceae	93	Euphorbiaceae	48
Euphorbiaceae	27	Sapindaceae	62	Fabaceae	181
Lauraceae	102	Sapotaceae	50	Lamiaceae	23
Malvaceae	113			Lythraceae	22
Meliaceae	31			Malvaceae	39
Moraceae	16			Phyllanthaceae	20
Myristicaceae	158			Rubiaceae	17

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1003 Table S4: Host tree species of tree cavities (number of individuals ≥10)

Evergreen				Deciduous	
Species	**Number of individuals**	**Species**	**Number of individuals**	**Species**	**Number of individuals**
Actinodaphne sp.	14	*Ligustrum perrottetii*	16	*Cleistanthus collinus*	38
Agrostistachys borneensis	17	*Litsea sp.*	29	*Dillenia pentagyna*	59
Antidesma sp.	18	*Mesua ferrea*	77	*Grewia tiliifolia*	23
Artocarpus heterophyllus	12	*Myristica dactyloides*	40	*Lagerstroemia microcarpa*	13
Cryptocarya wightiana	29	*Myristica fatua*	103	*Macaranga peltata*	20
Cullenia exarillata	109	*Myristica sp.*	13	*Radermachera xylocarpa*	10
Dimocarpus longan	60	*Palaquium ellipticum*	50	*Tectona grandis*	15

Evergreen				Deciduous	
Species	Number of individuals	Species	Number of individuals	Species	Number of individuals
Drypetes venusta	91	*Poeciloneuron indicum*	10	*Terminalia paniculata*	74
Dysoxylum malabaricum	20	*Syzygium sp.*	11	*Wrightia tinctoria*	10
Elaeocarpus tuberculatus	57	*Xanthophyllum arnottianum*	48	*Xylia xylocarpa*	155
Hopea parviflora	29			*Cleistanthus collinus*	38

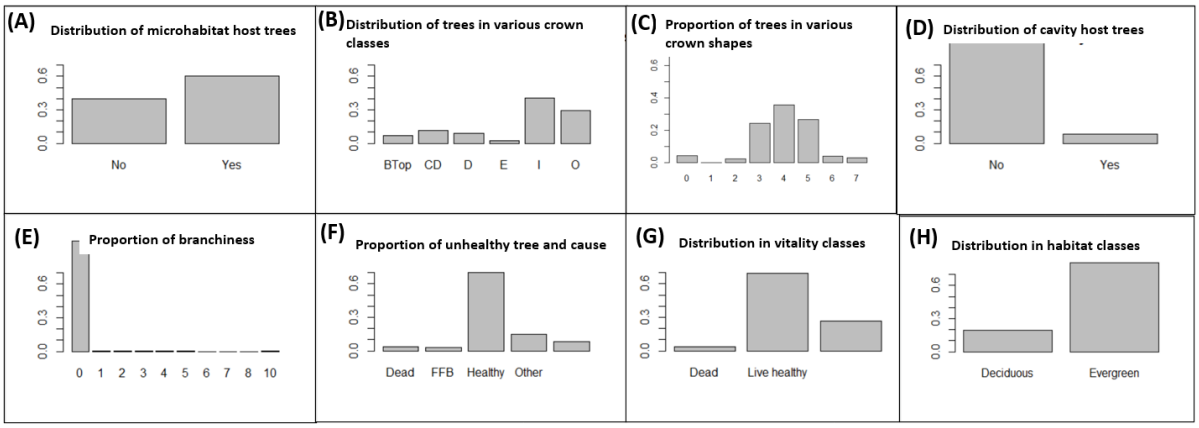


Figure S1: Proportion of trees and their characteristics observed and analysed for the presence and abundance of tree microhabitats

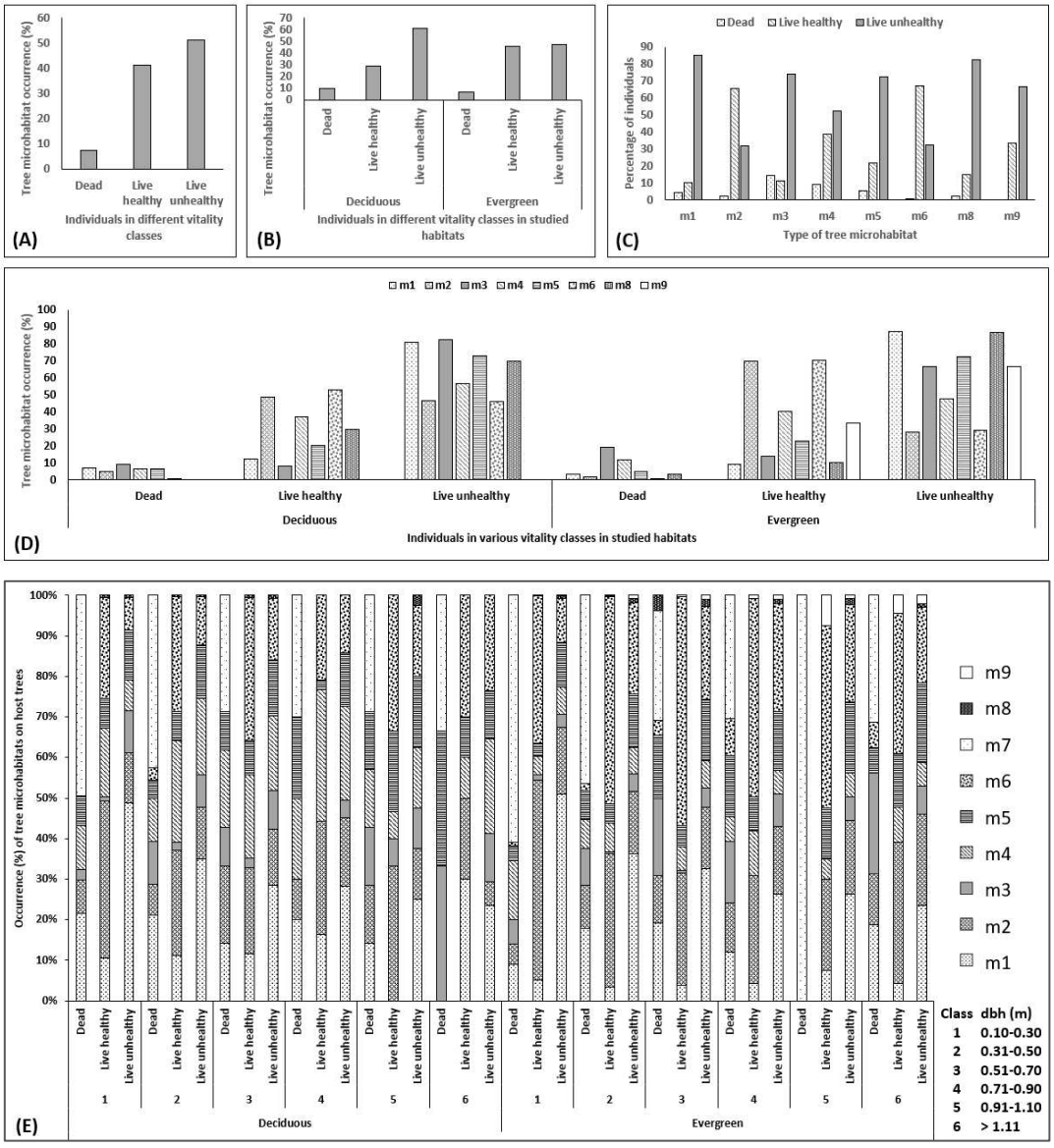


Figure S2: Percentage occurrences of various tree microhabitats in trees in different vitality classes in the studied habitats. The tree microhabitat category deadwood (m7) was not included as dead trees (snags) in figures A to D as one of the vitality classes itself shows the proportions for this category.

Hazard or habitat: injured and unhealthy trees host most of the microhabitats in tropical forests

Supplement A

NMDS was performed using the metaMDS function in the vegan package, treating stand characteristics as sites and tree microhabitat types and subtypes as species. this function accommodates raw data and dissimilarity matrices, so no further transformation was applied. the stressplot function was used to visualize tree microhabitat abundances in two-dimensional space. The stressplot draws a Shepard Plot with Observed Dissimilarities in X axis and Ordination Distance in Y axis. The correlation is calculated based on stress using the formula:

$R^2 = 1\text{-}S^2$

where, Stress (S) $= \sqrt{\frac{\sum_{i \neq j}[\theta(d_{ij}) - \tilde{d}_{ij}]}{\sum_{i \neq j} \tilde{d}_{ij}^2}}$

The 'fit based R^2' is the correlation between the fitted values and ordination distances. The null model of linear fit assumes that all ordination distances are equal and fit is flat horizontal line. The NMDS was performed with random seed set at 50, distance method selected as '*bray*', iterations set to 99 and auto-transformation set as FALSE.

Bray distance is calculated by the formula: $d_{jk} = \frac{A + B - 2J}{A + B}$

The properties of the distance matrix are:

for A = B	$d_{AB} = 0$	if the sites are identical, distance is zero
for $A \neq B$	$d_{AB} > 0$	if sites are different, their distance is larger than zero
	$d_{AB} = d_{BA}$	distances are symmetric

1040	$d_{AB} \leq d_{Ax} + d_{xB}$	the shortest distance between two sites is a line, and it
1041		cannot be improved by going through other sites

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Supplement B

Script for Decision Tree

```
> rfdata = read.csv("D:/Ob4data.csv", header = T)
> str(rfdata)

> ### Summaries of categorical variables
> barplot(prop.table(table(rfdata$cavity)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Distribution of cavity host trees")
>
> barplot(prop.table(table(rfdata$hbt)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Habitat class distribution")
>
> barplot(prop.table(table(rfdata$vital)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Vitality class distribution")
>
> barplot(prop.table(table(rfdata$unh_cause)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Proportion of unhealthy trees with cause")
>
> barplot(prop.table(table(rfdata$branch)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Proportions of branchiness")
>
> barplot(prop.table(table(rfdata$cr_shp)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Proportions of trees in various crown shapes")
>
> barplot(prop.table(table(rfdata$cr_cls)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Distribution of trees in various crown class")
>
> barplot(prop.table(table(rfdata$tmhtree)),
+       col = "gray",
+       ylim = c(0, 0.7),
+       main = "Distribution of microhabitat host trees")

> ######## Random Forest for presence of Tree Microhabitats
> ###### Decision Tree #########
> library(FSelector)
> library(rpart)
> library(rpart.plot)
> library(dplyr)
> library(caret)
> library(xlsx)
> library(data.tree)
> library(caTools)
> library(Rfast)
> ## Random Forest libraries
> library(ROSE)
> library(randomForest)
> library(caret)
> library(e1071)
```

```
> library(AUC)
> #### Data Partition: partition the dataset into train dataset and test dataset based on set.seed
> set.seed(123)
> rfind <- sample(2, nrow(rfdata), replace = TRUE, prob = c(0.7, 0.3))
> rftrain <- rfdata[rfind==1,]
> rftest <- rfdata[rfind==2,]
> #### Predictive Model Data: Let create a model based on the training dataset and look at the classification in the training dataset
> rftmhset <- table(rftrain$tmhcounts)
> rftmhset
> # Discriminant analysis in R
> prop.table(table(rftrain$tmhtree))
> # Based on proportion table 70% in one class and 30 % in another class
> summary(rftrain)
> # Predictive Mode: The Random Forest model is using for prediction purposes
> trainmod1 <- randomForest(tmhcounts~hbt+dbh+ht+G+vital+dcy+cr_shp+cr_cls+branch, data = rftrain)
> # Cross-validation based on test data
> trainmod1cross <- confusionMatrix(predict(trainmod1, rftest), rftest$tmhcounts, positive = 'Yes')
> # Cross-validation based on test data
> trainmod1cross <- confusionMatrix(predict(trainmod1, rftest), rftest$tmhcounts)
> ### Random Forest Model
> rf_tmhtr <- randomForest(tmhcounts~hbt+dbh+ht+G+vital+dcy+cr_shp+cr_cls+branch, data = rfdata)
> rf_tmhtr_confusemat <- confusionMatrix(predict(rf_tmhtr, rfdata), rfdata$tmhtree)
> rf_tmhtr_confusemat
> ## Error rate of Random Forest
> plot(rf_tmhtr)
> ## Tune Random Forest Model
> t_tmhtr <- tuneRF(rftmhset[,-9], rftmhset[,9], stepFactor = 1, plot = TRUE, ntreeTry = 2000, trace = TRUE, improve = 0.05)
> t_tmhtr
> ## Number of nodes per tree
> hist(treesize(rf_tmhtr), main = "Number of nodes for the trees", col = "gray")
> ## Variable Importance
> varImpPlot(rf_tmhtr)
> varImpPlot(rf_tmhtr, sort = TRUE, n.var = 9, main = "Important variable for abundance of tree microhabitats")
> importance(rf_tmhtr)
> varUsed(rf_tmhtr)
> ## Partial Dependence Plot
> partialplot (rf_tmhtr, rftrain, G, "1", "3", "Yes")
> ## Extract single tree from the forest
> getTree(rf_tmhtr, 1, labelVar = TRUE)

> ########### Random Forest for Cavity presence/absence
> ######### Solving imbalance data issue with caret and pROC package
> ####in training set instruct to do sampling in stratified random way and in each iteration take equal number of samples from the two
classes of dependent variable
> ######## Random Forest for presence of Tree Microhabitats
> #### Data Partition: partition the dataset into train dataset and test dataset based on set.seed
> ### Split data into training and testing data
> set.seed(1234)
> ind <- sample(2, nrow(rfdata), replace = TRUE, prob = c(0.7, 0.3))
> rftrain <- rfdata[ind==1,]
> rftest <- rfdata[ind==2,]
> #### Predictive Model Data: Let create a model based on the training dataset and look at the classification in the training dataset
> rfcvset <- table(rftrain$cavity)
> rfcvset

> # Discriminant analysis in R
> prop.table(table(rftrain$cavity))
> # Based on proportion table 65% in one class and 34% in another class
> summary(rftrain)
> # Predictive Mode: The Random Forest model is using for prediction purposes
> rf_cvtr <- randomForest(cavity~hbt+dbh+ht+G+vital+dcy+cr_shp+cr_cls+branch+tmhtree,
                  data = rfdata, strata = rfdata$cavity, sampsize = c(100,100), positive = "Yes")
> ### Confusion Matrix and Statistics
> rf_cvtr_confusemat <- confusionMatrix(predict(rf_cvtr, rfdata), rfdata$cavity, positive  = "Yes")
> rf_cvtr_confusemat
> ## Error rate of Random Forest
```

```
> plot(rf_cvtr)
> ## Number of nodes per tree
> hist(treesize(rf_cvtr), main =
        "Number of nodes for the trees", col = "gray")
> ## Variable Importance
> varImpPlot(rf_cvtr)
> varImpPlot(rf_cvtr, sort = TRUE, n.var = 9,
    main = "Important variable for occurrence of tree cavities")
> importance(rf_cvtr)
> varUsed(rf_cvtr)


> ## Extract single tree from the forest
> getTree(rf_cvtr, 1, labelVar = TRUE)
```