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Impact of human foraging on tree diversity, composition, and abundance in a tropical rainforest

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Abstract

Tropical forest tree communities are structured by a range of large-scale drivers including elevation, certain high-impact anthropogenic activities (e.g., deforestation), and fires. However, low-impact human activities such as foraging may also be subtly but notably altering the composition of tropical forest tree communities. The study assessed the (i) differences in species diversity, patterns of relative abundance, and pairwise beta diversity between trees with edible and inedible fruits and seeds along an elevation gradient, and (ii) impact of human foraging on the forest tree communities in Oban Division of Cross River National Park, Nigeria. Fifteen permanent 40 by 40 m plots were established along an elevational gradient (120–460 m above mean sea level). All trees of 0.1 m diameter at breast height (dbh) and above were measured, identified, and, with the aid of structured questionnaires, classified into those with edible and inedible fruits/seeds. A total of 35 edible species with density of 128 stems/hectare and basal area of 11.99 m^2/hectare, and 109 inedible species with density of 364 stems/hectare and basal area of 22.42 m^2/hectare were sampled. However, the evenness of edible and inedible species was similar at pooled and plot levels. For inedible species, there was a positive relationship between pairwise beta diversity and elevation, and this was driven mainly by turnover. In contrast, edible species exhibited a non-significant trend between elevation and beta diversity. Thus, the study showed that human foraging of edible fruits may have subtly influenced patterns of species diversity and community structure in this tropical forest.

KEYWORDS
Africa, beta diversity, edible trees, evenness, human foraging, inedible trees, species abundance distribution, tropical rainforest

1 | INTRODUCTION

Anthropogenic activities leading to large-scale habitat loss are known to have substantially impacted forest biodiversity (Bush et al., 2015; Clement et al., 2015; Helmus et al., 2014; Levis et al., 2017; Piperno et al., 2015; Stahl, 2015; Steadman, 1993). However, there is growing evidence that less intense, more subtle human impacts may also affect ecological communities, and in turn alter what we consider to be "natural" ecological and biogeographical patterns (Chaturvedi et al., 2017; Levis et al., 2017; Piperno et al., 2015; Singh et al., 2022).

For example, the modern floristic composition and structure of some natural forests, like the Amazonian forest, have been linked to past human activities in the forest (Levis et al., 2017). These activities, such as cultivation, seed dispersal and propagation, in situ tending of useful resources, and hunting of large mammals that aid in seed dispersal have the capacity to both extend and reduce the abundance and distribution of tree species (Levis et al., 2017; Socolar et al., 2016). However, in contrast to the coarse-scale effects of forest loss and degradation (Alahuhta et al., 2017; Donoso et al., 2017; Gallardo-Cruz et al., 2009; García-Navas et al., 2020; Swenson et al., 2011), smaller scale impacts of anthropogenic activities on ecological patterns in tropical forests are left largely understudied, likely due to the difficulties in measuring and quantifying them. Thus, we still lack a comprehensive understanding of the magnitude and dynamics of impacts from low-intensity anthropogenic activity on natural forest ecosystems (Levis et al., 2017; Piperno et al., 2015; Stahl, 2015).

One widespread example of low-intensity activities is the utilization of forests for food by forest-dependent human communities, which in some cases has been found to leave lasting impacts on forest ecology and dynamics (Bush et al., 2015; Socolar et al., 2016; Steadman, 1993). The most important plant parts found to be utilized for food by human communities in tropical countries are underground storage organs, fruits and leaves (Welcome & Van Wyk, 2020). Friant et al.'s (2019) examination of dietary differences and associated changes in agriculture-forest frontiers of Cross River State, Nigeria, revealed that in addition to human hunting of wild animals, the forest also acts as a source of nuts, seeds, and vegetables. These plant foods are thought to comprise a significant component of the daily diets of forest-dependent human communities. Although food-producing tree species have been largely identified and documented in many tropical forest regions, very little is known about the effect of varying degrees of human foraging on their abundance, and distribution in space. The continuous influence of humans on the forest, and at varying intensities, could, in principle, lead to a change in the forest community that might be reflected in contrasting distribution and abundance patterns between different species (Verberk, 2012). Although it is expected that a typical tropical forest ecosystem will comprise a few species with high abundance and many species with low abundance (ter Steege et al., 2013), human activities can alter the species richness of, and the distribution of abundance between, tree species either through preferential planting or conservation of beneficial trees, or through intentionally or inadvertently influencing the propagule pool (McGill et al., 2007; Socolar et al., 2016). Thus, it is important to understand how less overtly destructive anthropogenic activities, such as foraging, can over time influence the species composition, and ultimately function, of the forest.

The hypothesis that harvesting tree-based food products affects community composition and relative abundance can be evaluated through a focus on two commonly studied biogeographical patterns: beta diversity and the species abundance distribution (SAD). Beta diversity is the dissimilarity in species composition between two or more communities (Anderson et al., 2011; Pound et al., 2019), and has been used as an effective indicator for assessing the impact of anthropogenic activities on the composition of species in terrestrial and aquatic ecosystems (Da Silva et al., 2018; Dantas de Miranda et al., 2019; Elo et al., 2018; Gradstein et al., 2007; Kessler et al., 2009). Changes in beta diversity along elevational gradients have been a particular area of research interest in ecology (García-Navas et al., 2020; Guerin et al., 2013; Nascimbene & Spitale, 2017; Socolar et al., 2016; Yu et al., 2017). Elevation has also been used as a proxy for temperature to assess relationships with plant community diversity (Gallardo-Cruz et al., 2009; Nascimbene & Spitale, 2017; Swenson et al., 2011; Xu et al., 2017) and functional traits of plant species (Yu et al., 2017).

The SAD characterizes the abundance of all species found within a defined community (Matthews & Whittaker, 2015; McGill et al., 2007). It is an important ecological and biogeographical concept because it provides insight on the structure, function, and other less visible aspects of ecological communities (Matthews et al., 2014; Verberk, 2012). Two primary types of empirical SAD shape are commonly observed in nature: logseries (with a dominance of very rare species) and lognormal (dominance of species with intermediate abundance) type shapes. Empirical SADs have been used to study the responses of ecological communities to anthropogenic disturbances such as land-use change and pollution, by evaluating how the form of the SAD changes in response to disturbance (Matthews et al., 2014; Matthews & Whittaker, 2015).

Human foraging in tropical forest could affect the beta diversity and SAD patterns of tree communities in various ways. For example, during food (seeds and fruits) gathering, forest-dependent communities cover a wider area of the forest as well as higher elevational gradients and in the process, promote the dispersal of edible species (Levis et al., 2017), which may result in increasing their relative abundance and distribution, shifting the SAD from more uneven shapes (which are common in tropical tree communities; ter Steege et al., 2013) to more even shapes, and lowering the spatial beta diversity of edible species.

While low-intensity food collection should theoretically leave an imprint on beta diversity and the SAD (Adeyemi, 2016; Socolar et al., 2016; Verberk, 2012), higher-intensity activities, such as harvest of trees for timber, would also be expected to leave an imprint on stem diameter and density distributions of the forest (Adeyemi, 2016). However, high-intensity activities should affect species independently of their foraging value to humans, whereas low-intensity foraging should specifically alter the patterns of edible species. Analysis of forest structure can thus provide complementary insights to help narrow the range of possible causes behind changes in beta diversity or SADs.

The present study analyzes a tropical forest elevational gradient and utilizes tree diameter distribution, stem density, beta diversity patterns, and SADs to assess how the utilization of tree species by humans for food influences the community composition and structure of food producing (herein "edible") and non-food producing (herein "inedible") tree species in Oban Forest of Cross River

State, Nigeria. In turn, this enabled us to assess how low-intensity anthropogenic activities have influenced the ecological dynamics of the forest along an elevational gradient. We tested the following hypotheses:

1. Human movement of propagules along the elevational gradient will lead to more even distribution of abundance of edible species compared to inedible species.
2. Edible and inedible species will exhibit different turnover patterns along the elevational gradient in the forest.
3. Tree species utilization along elevational gradient will have different effects on tree stem density and diameter class distributions of edible and inedible trees.

2 | MATERIALS AND METHODS

2.1 | Study location

The study was carried out in an area of tropical rainforest located in Oban Division of Cross River National Park (CRNP), Nigeria (Figure 1b). The forest is situated between longitude 8°10′ and 8°55′ East and latitude 5°00′ and 5°50′ North and covers an estimated area of ~251,345 ha (Adeyemi, 2016; Jimoh et al., 2012; Olajide et al., 2008). In the North, South, and West, the forest is bounded by a number of forest-dependent and small-holder agricultural communities, and it is continuous with the Korup National Park and Ejagham Forest Reserve of Cameroon in the East (Adeyemi, 2016; Agaldo et al., 2016; Jimoh et al., 2012; Oluwatosin & Jimoh, 2016).

The forest vegetation is lowland and submontane moist tropical rainforest with mean annual precipitation ranging between 3000 and 3500 mm, mean monthly temperature range of 23–37°C, rugged terrain and elevation ranging from ~100 m to over 1000 m above mean sea level (Agaldo et al., 2016; Aigbe & Omokhua, 2015; Jimoh et al., 2012). The forest is the last stronghold of pristine tropical forest in Nigeria (Agaldo et al., 2016). The Oban forest is also part of the "Gulf of Guinea biodiversity hotspots of conservation concerns" in West Africa (Agaldo et al., 2016). It is known to house a large number of endemic flora and fauna species (Oates et al., 2004), including most of the 935 tree species identified in Nigeria (Lock & Keay, 1991), other herbaceous plant species, and a rich diversity of butterflies, birds, reptiles, amphibians, and a wide range of mammal species including ungulates, cats, buffalo, elephants, and primates, including the world's rarest lowland gorillas and others plant and animal species (Asuk et al., 2018).

2.2 | Plot establishment

To assess the impact of elevation on species diversity and the impact of humans along these elevational gradients, plots were established along an elevational gradient rising from about 100 to 500 m above sea level (Agaldo et al., 2016; Aigbe & Omokhua, 2015; Jimoh

et al., 2012). Plot location was also consistent with some additional considerations (see Section S1.1 in Appendix S1) from ForestPlots. net (Phillips et al., 2018).

Between August 23, 2019, and September 9, 2019, along an elevational band of between 100 and 500 m above sea level, five plot clusters were established in three areas of the forest for the study (see Appendix S1, Table S1): one cluster in Erukut, and two clusters in Aking and Osomba each (Figure 1a,c,d,e). Three 40 by 40 m plots with varying elevation were established in each of the clusters, making a total of 15 sample plots (Figure 1c–e) with a total area of 2.4 hectares. Due to the steep topography of Aking and Osomba locations, plots were established at closer horizontal intervals based on elevational differences of about 20 m.

2.3 | Data collection

All trees with a minimum of 10 cm dbh in all 15 plots were measured and tagged with a unique number. The collected data included plot information (plot number and GPS coordinate of the four corners of plots using Garmin eTrex 10 Outdoor Handheld GPS Unit), tree dbh (diameter of a tree at 1.30 m from the base) using a diameter tape and LaserAce 1000 rangefinder for points of measurement too high for a diameter tape, species name, assigned tag number, and species group (edible and inedible species). Measurement of buttress trees, folk trees, leaning trees, or trees on a slope was completed using the African Tropical Rainforest Observation Network (AfriTRON) protocol (Phillips et al., 2018). Trees were identified to species level by a field taxonomist and in cases where there was uncertainty in the identification of species, tree locations were noted, and specimens collected and stored in herbarium presses for further taxonomic work.

Information on tree species producing edible fruits, nuts, and seeds for humans was collected from four out of 39 forest dependent/support zone communities within the Oban Division of Cross River National Park (Enuoh & Ogogo, 2018; Ewah, 2013) using structured questionnaires (see Appendix S2). Two of the villages, Nsan and Aking, were selected based on proximity to the plot while Obutong, and Mkpot were selected to ensure a spread around the National Park. Mixed method interviews (Friant et al., 2019) comprising of group interviews with the council of chiefs, farming/gathering household heads, and individual interviews. The respondents were restricted to those above 25 years of age who had lived in the area long enough to provide information on forest tree species use. The information generated from the interviews was compiled into a comprehensive list and used to categorize tree species into those producing edible products and those which only produce inedible ones (see Appendix S1 for further details). The study was reviewed and approved by the Humanities and Social Sciences Ethical Review Committee of the University of Birmingham. Consent letters on the collection, use and storage of data by research team, were read to all participants. Only respondent who consented voluntarily participated in the study.
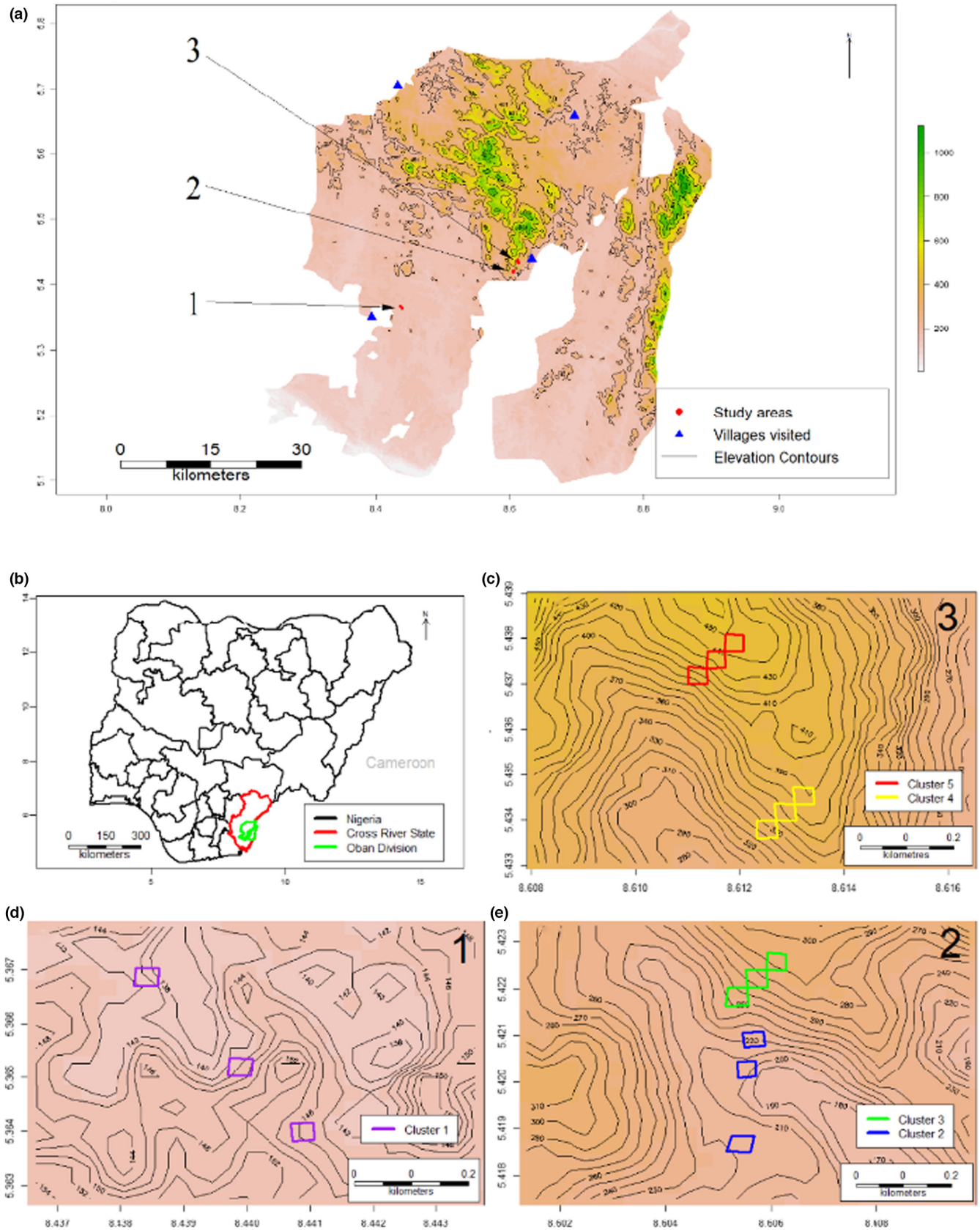
FIGURE 1 Topographic map of Oban Division showing the three areas selected for location of permanent sample plots and forest-dependent communities used for the study (a). Map of Nigeria showing the location of Oban Division of Cross River National Park (b). Clusters of plot clusters along elevational band withing the three study areas (c–e).

2.4 | Data processing and analysis

R (version 4.0.3) was used for all analyses (RStudio Team, 2021).

2.4.1 | Comparing species abundance distributions (SADs) and the evenness of edible and inedible tree species along the elevational gradient

Species abundance distributions were calculated for the different species groups at the community level (i.e., all plots combined) using the "sads" and "gambin" R packages (Matthews et al., 2020; Prado et al., 2018). The histogram form of SAD plotting was used (Connolly & Dornelas, 2011; Matthews & Whittaker, 2014). As an additional SAD test, the gamma-binomial (gambin) model was fitted to the SAD data on a histogram of log-transformed octaves (Matthews & Whittaker, 2014). To create the abundance octaves, $\log_2$ transformation was used to double the abundance class of previous octave (Matthews et al., 2014). Thus, beginning from 0, each octave had an interval that was twice the preceding one (octave 0 = "1 individual", 1 = "2–3", 2 = "4–7", 3 = "8–15", 4 = "16–31", and 5 = "32–63"; Matthews et al., 2014; Prado et al., 2018; Verberk, 2012). The gambin model is a flexible SAD model with one free parameter (alpha) that provides a metric of SAD shape (Matthews et al., 2014), allowing us to compare the shape of edible and inedible species SADs. 95% confidence intervals around the alpha values were calculated using bootstrapping. As SAD form is known to be affected by sample size, we also calculated standardized alpha by subsampling all samples down to the smallest number of individuals in a plot (Matthews et al., 2014). The number of individuals in the smallest group was randomly sampled from the groups with larger sample size, alpha value calculated and then this process repeated 999 times to generate the mean alpha values and standard deviations (Matthews et al., 2014).

Pielou's evenness index was used for comparing the evenness between edible and inedible species at the plot level and at the combined (pooled) plot level (Pielou, 1966). Pielou's evenness index (Equation 1) was computed using the vegan package in R (Oksanen et al., 2022), and plot level evenness for edible and inedible species were compared using a t-test from the "car" package in R (Fox et al., 2022).

$$J = \frac{H}{\log(S)} \tag{1}$$

where J = Pielou's evenness index, H = Shannon's diversity index, S = species richness.

2.4.2 | Beta diversity and spatial species turnover along the elevational gradient

Pairwise beta diversity between all plots along the gradient was calculated using Sorensen's dissimilarity index (β_{sor}). We also analyzed the turnover component of β_{sor}, Simpson's dissimilarity index (β_{sim}), which measures the replacement of species between pairs of plots independently of richness differences (Aspin et al., 2018; Baselga, 2010; Jarzyna & Jetz, 2018). The formulas (Equations 2 and 3) for the computed indices are shown below (Baselga, 2010, 2012).

$$\beta_{sor} = \frac{b + c}{2a + b + c} \tag{2}$$

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)} \tag{3}$$

where a = number of species common to both locations, b = number of species present in the first location but absent in the second location and c = number of species present in the second site but absent in the first location.

The "betapart" R package was used to calculate the dissimilarity indices using a vector of species incidence (Baselga et al., 2018). The incidence-based pairwise dissimilarities were regressed against elevation using a linear regression model to determine any general trend. Due to the non-independence of the data, Mantel correlation tests were undertaken relating the dissimilarity matrices to a matrix of elevational differences between plots to generate the correlation coefficient (and its significance) and respective confidence intervals, using the "ecodist" package in R (Goslee & Urban, 2017). In addition, to remove any possibility of spatial autocorrelation, a partial Mantel test (Legendre et al., 2015) was conducted using the species dissimilarity metrices, plot elevational matrix and plot distance matrix. This was done using the "vegan" R package (Oksanen et al., 2022). These analyses were undertaken for edible and inedible species separately.

Two null models were run to confirm that the trends in tree beta diversity and turnover with elevation observed in the edible and inedible species category were not due to chance (see details in Appendix S3). In addition, two sensitivity tests were conducted to check the effect of the ground distance between plots in Erukut and those in Aking and Osomba on the βsor and βsim trends observed in the edible and inedible species categories (see details in Appendix S3).

2.4.3 | Stand density, basal area, and diameter size distribution

The dbh of all trees in the study area were transformed using natural logarithms and visualized on a relative density plot using the ggplot2 package in R (RStudio Team, 2021; Wickham, 2016). Stand density per plot was also computed for each species category. The basal area (BA) and total BA of each measured tree were calculated from their diameter at breast height (Aigbe & Omokhua, 2015; Ojating, 2008).

Linear regression analysis was used to compare the effect of the elevational gradient, and the edible-inedible species category, on tree density (tree per ha) and total basal area (m^2 per ha). Moran's I test (Moran, 1950) was used to check for spatial autocorrelation in the linear regression residuals. This was done with the "DHARMa" R package (Hartig, 2017). To determine whether the slopes and intercepts of the

linear regression lines differed between the species categories, for each dependent variable, ANCOVA was used. The ANCOVA models were developed using the "aov" function and type III sums of squares, using the "car" package (Fox et al., 2022) in R (see details in Appendix S4).

3 | RESULTS

3.1 | Summary of site information

We sampled 492 tree stems per hectare, with total basal area density of 34.41 m^2 per hectare across the 15 plots (Table 1; Asuk et al., 2022). The sampled individuals were distributed among 144 species in 105 genera and 49 families. Species identified as edible from group interviews with local villagers are shown in the Appendix S5 and Table S5. The total richness in this study was divided into 35 edible species that provided food in the form of fruits and seeds for rural communities and 109 inedible species. Among the edible and inedible categories, 67.35% of families, 75.24% of the genera, 75.69% of the total species richness, and 65.15% of the total basal area belonged to the inedible species. The mean BA was higher in edible species (0.09 (SD: 0.37)) due to the presence of larger stems among the edible species category compared to inedible species. The 15 most abundant species had a total density of 10 stems per hectare, while the total stem density across all plots was 213 stem/ha. The 15 most abundant species represented 43.29% of the total tree stand, and 23.37% of the total basal area.

These prevalent species included five edible species making up 26.76% (57 stem/ha) of the stem density and 10 inedible species making up 73.24% (156 stem/ha) stems density.

3.2 | SADs and evenness of edible and inedible species

3.2.1 | All plots combined

The SAD of all species combined (Figure 2b) showed there were few highly abundant species and a higher proportion of rarer species,

with the modal octave containing 2–3 individuals representing the peak of the distribution. The alpha parameter of the gambin model was 3.1 (confidence interval of 2.4–4.4). The alpha parameter of the gambin model was slightly lower for inedible (α = 3.1 and confidence interval of 2.2–4.4) compared to edible (4.0 and confidence interval of 2.1–7.1) species. However, the confidence intervals of the two alpha values overlapped. A lower alpha was recorded for inedible category of 1.83 (SD = 0.30 and 95% CI of 1.37–2.41) after standardizing the population of both categories. At this scale, the pooled (all plots combined) evenness index of the edible category was not different from the inedible.

3.2.2 | Individual plots

At the scale of individual plots, Pielou's evenness index (Figure 2a) showed that the edible species had similar (p value < .348) evenness at the plot level compared to the inedible category. For edible species, evenness ranged from 0.840 to 0.988 while for inedible species it ranged from 0.790 to 0.964.

3.3 | Beta diversity and the turnover of edible and inedible species along the elevation gradient

3.3.1 | Relationship between beta diversity and elevation in edible and inedible tree species

Pairwise dissimilarity plots (Figure 3a,d) showed that elevation had a strong positive effect on the differences in composition between plots in the study area when all species were considered together. There was a significant (p = .001) Mantel correlation value of 0.43 between both total beta diversity (a) and turnover (b) and elevation, indicating that both pairwise total beta diversity and turnover increased with increasing difference in elevation between plots.

Both the pairwise total beta diversity and replacement component for edible species (Figure 3b,e) remained constant as the difference in elevation between plots increased. In contrast, inedible

Variable	Edible	Inedible	Total
Families	16 (32.65%)	33 (67.35%)	49
Genera	26 (24.76%)	79 (75.24%)	105
Total species richness	35 (24.31%)	109 (75.69%)	144
Total stem density (stem/ha)	128 (26.02%)	364 (73.98%)	492
Total Basal Area (m^2/ha)	11.99 (34.85%)	22.42 (65.15%)	34.41
Mean Basal Area (m^2/ha)	0.59 (SD: 0.42)	0.39 (SD: 0.12)	
Prevalent species count	5 (33.33%)	10 (66.67%)	15
Prevalent species stem density (stem/ha)	57 (26.76%)	156 (73.24%)	213
Prevalent species basal area (m^2/ha)	2.23 (27.74%)	5.81 (72.26%)	8.04

TABLE 1 Summary of total species, tree density per hectare, and total basal area in the forest
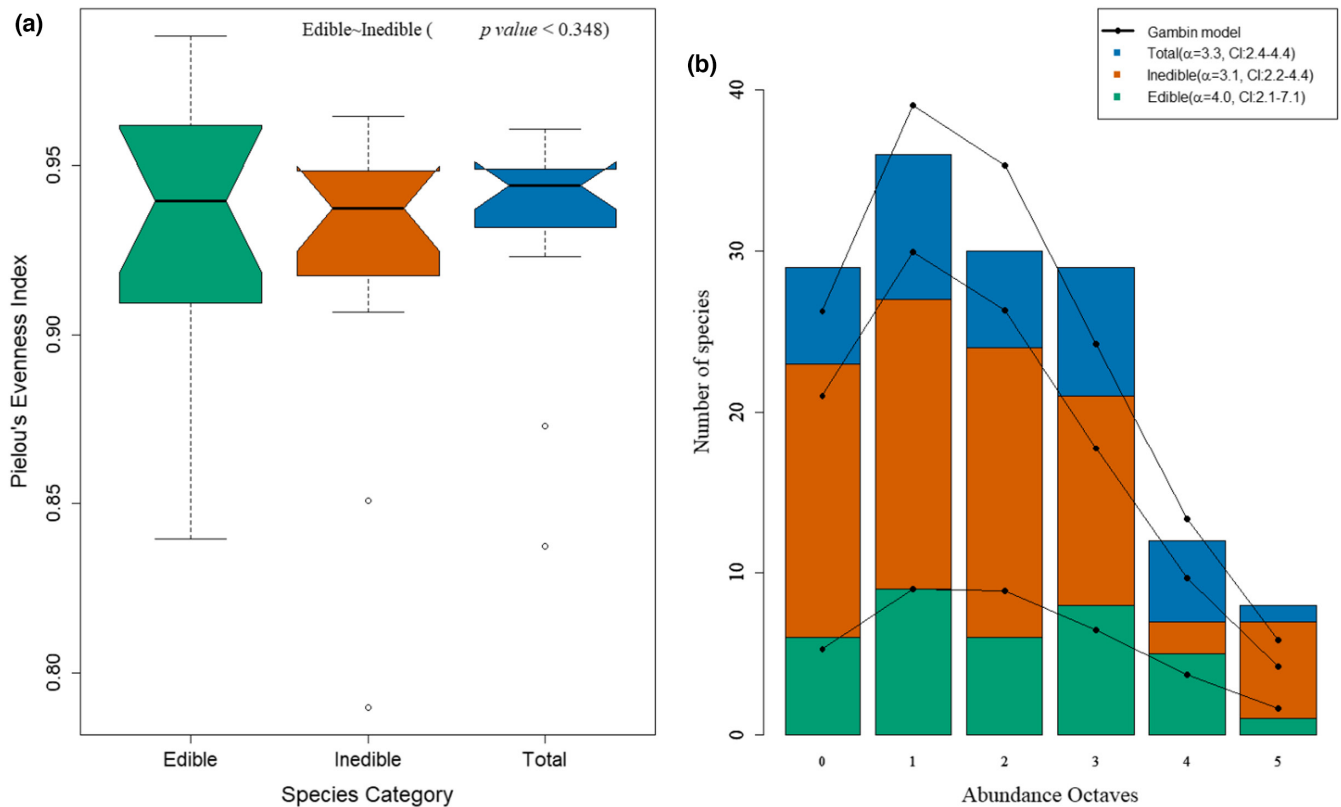
Abbreviation: SD, standard deviation.

FIGURE 2 (a) Boxplot of plot level Pielou's evenness index for edible, inedible and total species categories (pooled evenness total = 0.887, edible = 0.871 and inedible = 0.869) and (b) a species abundance distribution octave plot with the fit of the gambin model for edible, inedible, and all tree species in the forest. (octaves: 0 = "1 individual", 1 = "2–3", 2 = "4–7", 3 = "8–15", 4 = "16–31", and 5 = "32–63"). The brown bars are overlayed on the blue bars while the green bars are overlayed on the brown bars to preserve origin at zero.

species exhibited a significant positive correlation between total beta diversity and the replacement component, and elevation (Figure 3c,f). For both the total beta diversity and turnover plots, the Mantel correlation coefficients for edible and inedible species did not overlap, indicating significant differences in the patterns between the two subsets.

3.3.2 | Sensitivity test and null model analyses

The sensitivity test to check the effect of the ground distance between plots on the β_{sor} and β_{sim} trends observed (see Appendix S6, Figures S1 and S2) yielded similar trends for both species categories, suggesting that the distance between plots in Erukut from those in Aking and Osomba were not driving the observed patterns. The p values from the partial Mantel's test which accounted for spatial autocorrelation in the data yielded similar results as the Mantels test (see Appendix S6, Table S6). The fixed-fixed null model analysis (see Appendix S6, Table S7) revealed that the Mantel correlations for edible species were not significantly different from observed, but the observed correlations (both β_{sor} and β_{sim}) for the inedible species were significantly higher than expected. The interspecies randomized null model (see Appendix S6, Table S6) provided slightly contrasting

results. The correlations for the edible species, for both β_{sor} and β_{sim}, were found to be significantly lower than expected, given the null model. Again, the observed correlations for inedible species were higher than expected, although they were non-significant.

3.4 | Effect of tree species utilization on diameter size distribution, tree stem density, and BA along the gradient

3.4.1 | Diameter size distribution

The diameter distribution for all species together, and edible and inedible species separately, all show a reverse J-shaped or negative exponential function characteristic of a natural uneven-aged tropical forest stand (Daniel et al., 2015; Marín et al., 2005), with the number of trees stems decreasing as tree dbh increases (Figure 4). The nonlinear relationship between dbh and stem density shown on the curve further indicated that there was regeneration and upgrowth of stems along diameter classes in the forest stand (Daniel et al., 2015; Marín et al., 2005). For lots of the dimeter distribution curves within plots (Figure 4b), the edible category (red line) was above the inedible (blue line) around point 4.
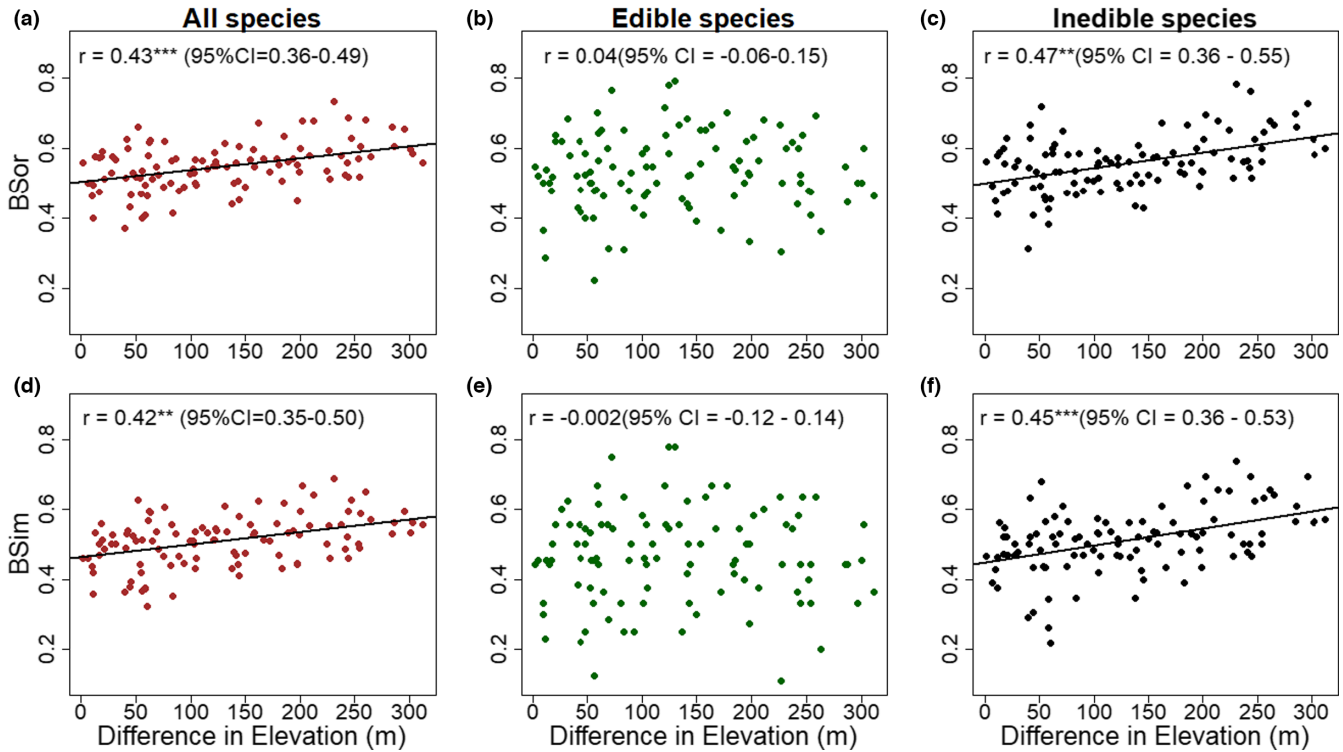
FIGURE 3 Pairwise dissimilarity trend showing the association between both total beta diversity, BSor (a–c) and turnover, BSim (d–f), and elevation (m) for edible and inedible species in Oban Forest. The *r* values and confidence intervals (CIs) were generated from mantel correlation tests. The solid lines show ordinary least squares regression fits, only for significant associations.
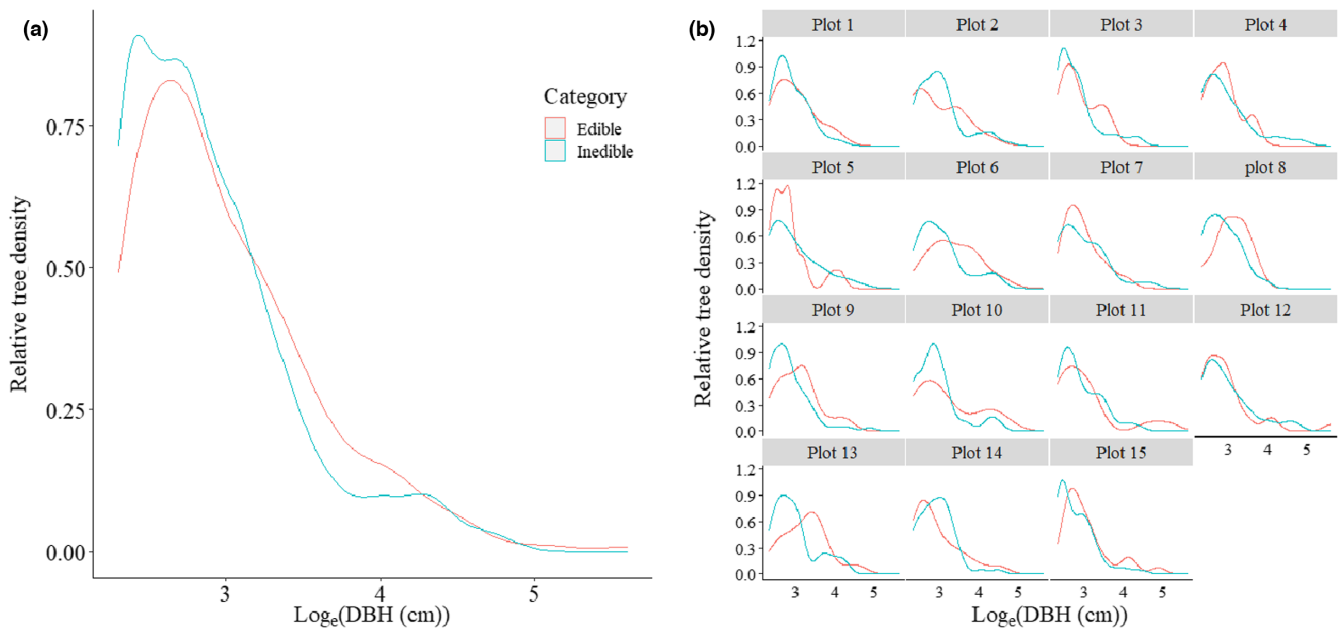

FIGURE 4 Tree diameter size distribution curve showing relative density of tree dbh in Oban Forest. (a) Tree diameter size distribution curve of all measured trees grouped into edible and inedible categories. (b) Tree diameter size distribution curve of trees measured in each plot categorized into edible and inedible.

3.4.2 | Tree stand and basal area densities along the elevational gradient

Linear regression models fitted to tree density (tree/hectare) against elevation (m) (Figure 5a) indicated a significant relationship

only for inedible species. The R^2 value (intercept = 141.25, slope = −0.05; *p* value = .65) for edible species was 0.02, while a significant (intercept = 283.50, slope = 0.29; *p* value = .02) positive association with elevation was observed for inedible species, with an R^2 value of 0.34. Results from the ANCOVA model (see

details in Appendix S4) with two covariates (species category and elevation) and with tree density as the dependent variable showed that the slopes of the regression lines differed between the edible-inedible categories (interaction term F value = 5.026; p value = .034). Results from the Moran's I test of spatial autocorrelation for edible and inedible species categories yielded p values that were greater than .05 in all cases, thus indicating that there was no spatial autocorrelation in the residuals (see details in Appendix S7, Table S8).

No significant relationships were recorded between total BA and elevation (Figure 5b) for either category. ANCOVA with species category and elevation as covariates, and total basal area as the dependent variable (see Appendix S4), showed that the slopes of the regression lines for both categories were not significantly different from each other (interaction term F value = 1.421; p value = .244). Moran's I test yielded a non-significant p value, indicating that there was no spatial autocorrelation in the model's residuals (Appendix S7, Table S8).

4 | DISCUSSIONS

4.1 | Potential effect of human activities along the elevational gradient on SADs and species evenness

The SAD plots (Figure 2) for the total community indicate that the sampled area of the forest exhibited a log-left skewed lognormal distribution type SAD, a pattern commonly observed in tropical forests (Hubbell, 2001; Matthews & Whittaker, 2014). Pooled species richness was lower for edible species and higher for inedible species while the Pielou's evenness index was similar for both categories at

pooled and plot levels. However, at the plot level, edible tree species recorded the highest evenness while inedible species recorded the lowest.

Despite the difference in species richness and stand density between both categories, the high evenness in edible category at plot and pooled levels might be due to sample size effects (Mackey & Currie, 2001) or linked to historical impacts of human influence on the abundance of species along the elevational gradient (Wilsey & Potvin, 2000) through tree management, deliberate planting, and conservation for food production (see Section 4.3). Conservation efforts have concentrated on the present species richness of the forest but previous an assessment of species abundances shows how the forest species composition and abundance has modified over time (Ellis et al., 2010, 2021; Wilsey & Potvin, 2000). This is further evident in the beta diversity results whereby inedible species exhibited more turnover than edible species.

4.2 | Difference in beta diversity and turnover in edible and inedible species along the elevational gradient

Elevation is an important variable that affects the distribution of trees in tropical rainforests (Lan et al., 2011). The pairwise beta diversity trends observed here showed that there was a positive association between beta diversity and differences in elevation. The beta diversity and turnover trends of inedible species were similar to that for all species combined. In contrast, the beta diversity of edible species exhibited no trend with elevation (Figure 3).

In the absence of human influence, we may expect the constant turnover of species along the elevational gradient due to niche
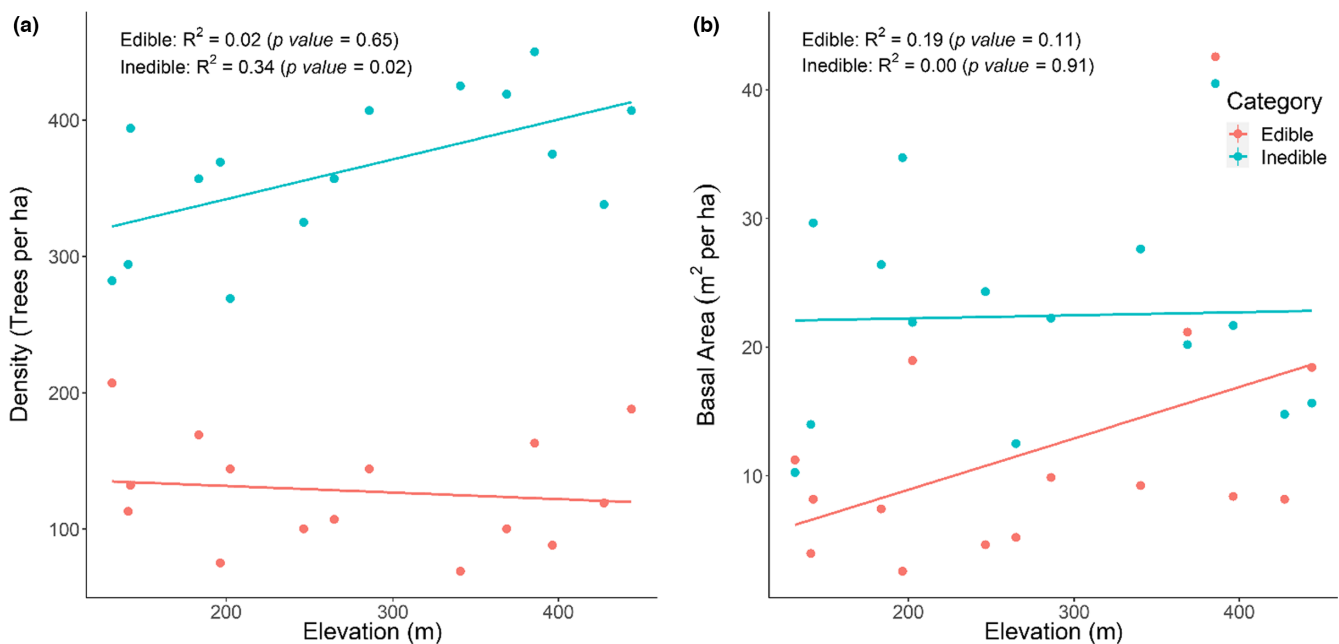

FIGURE 5 Trend in stem density (a) and total basal area per hectare (b) per plot with increasing elevation for edible and inedible species

filtering (i.e., the changing of abiotic conditions with increasing elevation) and/or dispersal limitation (Peters et al., 2019). This will result in increased pairwise spatial beta diversity between plots with increasing elevational distance, which is the pattern observed for inedible species. However, edible species did not exhibit a significant relationship between elevation and pairwise composition. This could be due to tree propagules being spread by humans along the gradient (both purposefully and indirectly), resulting in the spatial homogenization of community composition. However, for the spreading of seeds by humans to have this effect it must mean that (i) niche filtering is not a dominant assembly mechanism and instead dispersal limitation is driving tree distributions in this forest (Hubbell, 2001), (ii) human-aided dispersal is occurring at such a rate that mass effects (Shmida & Wilson, 1985) are overriding any niche filters, or (iii) a combination of the two. Further research is needed to fully explore these different possibilities.

4.3 | Trends in dbh distribution, tree species density, and BA along elevational gradient in the forest

The dbh, BA, and stem density distribution shown by certain species categories can indicate the type of human footprint in the forest (de Quesada & Kuuluvainen, 2020). Humans tend to favor propagation and conservation of certain tree species based on their utilization value. Thus, the dbh distribution of edible tree differed from that of inedible trees species (Marín et al., 2005). The interventions of humans include selective conservation, enrichment planting, and seed dispersal of desired species, while undesirable species may be harvested.

There was consistency of red line (edible) above blue line (inedible) around point 4 (Figure 4), which could be suggestive of a period of disturbance (mortality, gap in the forest that favor height growth or slowed diameter growth) in the inedible category not observed in the edible species category (Aigbe & Omokhua, 2015). However, the variability observed in individual plots of tree dbh also suggests that other variables maybe important. The diameter distribution of trees species can be affected by the mortality patterns in the forest (de Quesada & Kuuluvainen, 2020) or the distribution of species abundance. A study in an old growth forest in Costa Rica revealed that basal area and density of large trees is expected to increase with elevation (Muñoz Mazón et al., 2020). Even though inedible species had three times the species diversity, three times the stand density of edible species, they only had twice the total BA and a lower mean BA than edible species (see Table 1).

The level of impact that foraging by local communities has on forests is likely to be linked to accessibility in some way, although this is not necessarily a simple function of elevation given the activity is low intensity and does not require heavy machinery, and thus, foragers have the capacity to cover a wider spatial range and along varying elevational gradients (Jimoh et al., 2012). For example, the villagers interviewed stated that they often foraged in the higher elevations of

our gradient. However, there are additional human activities that may be more impactful at different parts of the elevation gradient, which may then influence species composition and distribution across the gradient (Socolar et al., 2016), although these should impact edible and inedible species equally. For instance, logging activities might be limited to more accessible areas at relatively low elevation.

Socolar et al. (2016) stated that human activities, taxa, and geographical location can determine the impact pattern on tree species composition and diversity. In a forest area, like the study location used here, with rough terrain, increasing elevational gradient, inaccessible roads, and reasonable distance away from human habitation, forest harvest for timber and/or farming at higher elevation might be difficult (Adeyemi, 2016; Aigbe & Omokhua, 2015; Jimoh et al., 2012; Olajide et al., 2008; Otu et al., 2012). Therefore, while some activities that occurred in the past may have been limited to the lower elevations or unevenly distributed along varying elevations, these activities such as harvesting of timber, farming, nomadic nature of some indigenous settlements, foraging, and others could have affected the distribution of tree stand density along the elevational gradient (Adnan et al., 2015; Aigbe & Omokhua, 2015; Asuk et al., 2021; Jimoh et al., 2012). In addition, conservation efforts by indigenous people would favor trees utilized for their seeds, fruits, and others more than those not used for food (Asuk et al., 2021). This would result in trees with food value having bigger girth with greater mean BA per hectare (see Table 1) and a more even distribution of stand density with elevation compared to species that may likely have been harvested prior to the creation of the National Park. Furthermore, as humans forage along the elevational gradient, they may be more likely to propagate seeds of desirable tree species at lower elevations in a bid to reduce their foraging distances. Although it is not possible to make a definitive attribution, the difference in BA and stand density trends observed in edible and inedible species for the study area (Figure 5) are therefore consistent with the expected impacts of human intervention.

However, it is worth highlighting that alternative explanations may also explain the observed patterns, or may be acting in tandem with the effects of human foraging (Adnan et al., 2015; Brockerhoff et al., 2017). First, edible and inedible species may have different trait values, especially if traits are linked with edibility (e.g., traits related to tissue density; Lueder et al., 2022; Waddell et al., 2020). If edibility-related traits also affect dispersal ability or the ability of species to cope with the abiotic environment (as in tissue density traits), then the edible-inedible comparison may not reflect the effect of humans but that of trait–environment interactions. Similarly, edible species might be functionally similar due to phylogenetic similarities, which are not accounted for in this study. Second, while we classified species as edible based on interviews with local villagers, we cannot discount the role of other animal taxa in dispersing the edible species (Teitelbaum & Mueller, 2019). As data on species traits and interaction networks in the study area are not available, we recommend conducting further study involving abiotic factors and functional traits to validate these findings (Lueder et al., 2022; Waddell et al., 2020).

4.4 | Implications and additional considerations

The disparity in the trends observed in edible and inedible species could be due to selective dispersal of propagule during foraging, deliberate conservation, and management of desired species by humans for food production. These low-impact activities are theorized to potentially modify the forest species composition overtime leaving observable footprints. Furthermore, large-scale disturbance of the forest due to timber harvesting, clear cutting for agriculture, or agroforestry practices are some other factors capable of modifying the forest. These human interactions, that potentially modified the forest prior to the creation of the National Park, might have left some footprints which are still visible in the dbh abundance-size distribution. Even though the forest is now protected, low-intensity activities of human may continue to modify the species composition and structure of the forest. This supports the findings of Aigbe and Omokhua (2015) who pointed out that the species composition of the Oban forest might be recovering from past disturbances from tree mortality which occurred prior to acquiring the National Park status. Notwithstanding the data indicating human impact, Adeyemi (2016) was of the opinion that the hilly terrain, poor road network, and large water bodies adjoining the forest may have assisted in reducing pressure on the forest from certain human activities such as logging, thus preserving the current species diversity of the forest. But as pointed out by Levis et al. (2017), some activities such as food gathering encourage forest-dependent communities to cover wider ranges thus promoting dispersal of edible species.

The results of this study, along with information of past disturbances that may have occurred in the forest (Adeyemi, 2016; Agaldo et al., 2016; Aigbe & Omokhua, 2015; Jimoh et al., 2012; Olajide et al., 2008; Otu et al., 2012), suggest that low-intensity human activities have influenced the forest species distribution and structure. Earlier research has shown that more than 50% of the global tropical broadleaf forest show evidence of similar low-intensity human impact (Ellis et al., 2010, 2021). Studies in the Amazon forests (Bush & Flenley, 2007; Clement et al., 2015; Piperno et al., 2015) also indicate that low-intensity human activity has modified the forest. Furthermore, studies have shown that indigenous human societies have historically modified the structure and composition of terrestrial biosphere dating back 12,000 years and 75% to 95% of these area might now be in seminatural states (Ellis et al., 2010, 2021; Helmus et al., 2014; Williams et al., 2020). Much focus has rather been placed on high-intensity activities such as logging, and it has been shown that many forests are not natural due to human farming, and nomadic settlements in the past. But our result show that even very low-intensity foraging, which is not visible from remote sensing and field inventories is also possibly changing forest dynamics, which throws into question whether any forest can be classified as "natural".

As a single case study, care is needed in extending these findings elsewhere and further work at a broader scale will be needed to assess whether these patterns and interpretations hold true more widely across the continent and indeed tropical forests as a whole. In our opinion, the results presented indicate a role of human foraging on the distribution and structure of edible tree species.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at 10.5061/dryad.kh189328z. More details have been provided in the supporting information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.