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Human and Environmental Factors Shape Tree Species Assemblages in West African Tropical Forests

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Abstract

> Human activities exert a pronounced influence on forest ecosystems, impacting both biodiversity and function across multiple scales. Despite this, the consequences of low-intensity human activities on tropical forest ecosystems are

difficult to assess and, therefore, remain poorly explored. Here, the influence of human activities and other site-specific variables on forest tree assemblages in central-west Africa was investigated. By dividing forest tree species into edible (from the perspective of humans) and inedible species, we aimed to assess the differential impacts of human resource use on different species; in particular, the greatest impact of human activity was expected to be seen on edible tree species. Tree data from 66 plots across Nigeria and Cameroon collected between 2002 and 2019 and Generalized Dissimilarity Models (GDMs) were used to assess pairwise beta-diversity between plots, accounting for candidate factors including proximity to human presence, elevation, and stem density. The analysis revealed that human activity significantly affects beta-diversity within the Nigeria-Cameroon forest region. The key variables that shape total beta-diversity included geographical distance between plots, plot elevation, stem density, proximity to human presence, and forest species composition. The forest species composition (monodominant or mixed forest) appeared to influence dissimilarity in beta-diversity, specifically for edible tree species. This pattern was not observed for inedible species, likely linked to the cultural practices in the region. While stem density contributed to the edible species models, elevation was more relevant for inedible species. These findings underscore the critical role of human influence in shaping tree species assemblages in African tropical forests and stress the necessity for further research in this area.

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1. Introduction

Forest biodiversity and the functions it provides are rapidly changing at local, regional, and global scales due to large-scale habitat loss and modification from anthropogenic activities (McMichael et al., 2017a; Bush et al., 2015; Piperno et al., 2015; Clement et al., 2015; Helmus et al., 2014; Steadman, 1993; Stahl, 2015; Jarzyna and Jetz, 2018). In the tropics, anthropogenic activities such as selective harvesting, illegal logging, clear-cutting for agricultural purposes, foraging of fruit/seed for food, and conservation all modify the species composition and distribution of species within forests (Benchimol and Peres, 2013; Asuk et al., 2022; Elo et al., 2018). However, the impact of anthropogenic activities can vary depending on the type (like the use of species for food, timber, medicine, alongside other uses), intensity, and duration of the activity, and the type of species affected (Asuk et al., 2023; Adeyemi, 2016; Adnan et al., 2015; Aigbe and Omokhua, 2015; Jimoh et al., 2012). For example, forests subjected to clear-cutting prior to the attainment of a “protected” or “reserve” status might be at an early stage of succession and dominated by fast-growing pioneers compared to forests which were left to their natural growth (Aigbe and Omokhua, 2015). Also, since forest-dependent human communities have a history of migrating from place to place, their practice of deliberately planting preferred tree species can lead to widespread changes in the species composition of forests (McMichael et al., 2017a; Adnan et al., 2015; Aigbe and Omokhua, 2015; Jimoh et al., 2012).

Studies of the effects of anthropogenic activities on forest biodiversity have focused primarily on the high-intensity impacts, such as deforestation, fragmentation, and degradation (Swenson et al., 2011; Gallardo-Cruz et al., 2009;

Alahuhta et al., 2017; Donoso et al., 2017; García-Navas et al., 2020). Growing evidence suggests that low-intensity human activities such as foraging for food, selective species conservation, dispersal of seeds of desirable species (e.g., species with fruits eaten by humans), and enrichment planting may modify forest ecosystems more than previously thought, and thus potentially affect ecological and macroecological patterns (McMichael et al., 2017a; Piperno et al., 2015; Singh et al., 2022; Chaturvedi et al., 2017; Asuk et al., 2023). For example, the modern floristic composition and structure of some areas of natural forests in Amazonia have been linked to past low-intensity human activities (e.g., plant cultivation, seed dispersal and propagation, and incidental domestication) (Levis et al., 2017). However, the general effects of low-intensity anthropogenic impacts on spatial ecological patterns in tropical forests are poorly understood (Jarzyna and Jetz, 2018; Anderson et al., 2011), likely due to the difficulty in measuring impacts (McMichael et al., 2017a; Stahl, 2015; Piperno et al., 2015; Asuk et al., 2023). Given that remote sensing of forests easily detects coarse structural changes (e.g., deforestation, logging) much more than subtle floristic changes induced by management, without extensive ground surveys, it is likely that the extent of human impact on forest communities will be underestimated.

One way to assess the impact of low-intensity drivers on tropical forest composition is by measuring the effects of human activities such as foraging, preferential planting, and deliberate conservation on the spatial beta-diversity of the forest (Singh et al., 2022; Biswas and Mallik, 2011; Bush et al., 2015; Roberts et al., 2021; Asuk et al., 2023). Spatial beta-diversity, defined as the dissimilarity in species composition between two or more communities separated in space (Pound et al., 2019; Anderson et al., 2011), has been successfully used to analyse differences in tree species composition in forests, as well as the drivers of change (Condit et al., 2002). While there have been numerous ecological studies on the beta-diversity of forest tree species, these have mostly focused on identifying high-intensity drivers of change in beta-diversity at global scales, as well as mainly being focused on temperate forests, with less work focused solely on tropical forests (Jarzyna and Jetz, 2016; Herault et al., 2010; Barnagaud et al., 2017; Aspin et al., 2018; Waddell et al., 2020; Fu et al., 2019; Swenson et al., 2011; Devictor et al., 2010; Biswas and Mallik, 2011; García-Navas et al., 2020; Lueder et al., 2022; Biswas and Mallik, 2010; Zambrano et al., 2020).

African forests are biodiversity hotspots with numerous endemic species (Myers et al., 2000; Agaldo et al., 2016; Oates et al., 2004; Seifert et al., 2022). They play a vital role in climate regulation by absorbing atmospheric carbon dioxide, thus mitigating climate change effects (Núñez et al., 2022; Oyewole et al., 2019; Artaxo et al., 2022). In a study conducted by Hubau et al. (2020) until 2015, intact Afrotropical forests have maintained a consistent carbon sink in live aboveground biomass, averaging about 0.66 tonnes of carbon per hectare per year. These forests have also indicated a more resilient and stable carbon sink in contrast to the Amazonian forests over the same period (Hubau et al., 2020). Furthermore, African forests contribute to water cycle regulation, soil conservation, agriculture support during crop failure, and ecological balance (Raj et al., 2022; Meinhold and Darr, 2022). Understanding the processes that have shaped the forests in Africa is essential for developing effective conservation and management strategies. Yet, these forests remain largely understudied, particularly in terms of spatial composition patterns.

Large-scale trends of deliberate planting and conservation of preferred tree species have been reported in the Amazonia Forest (Levis et al., 2017). The selective logging of certain species while other species are preserved in these forests can also result in a spatial and temporal change in the species composition due to the turnover of species within the forest over time (Bousfield et al., 2023). A study on the “human experience of nature” in Africa revealed that forests respond differently to the intensity of usage to which they are exposed (Cazalis et al., 2023). A localised study in Oban Forest, a tropical African rainforest located in Nigeria, assessed the impact of low-intensity anthropogenic activities on tree species diversity by comparing patterns in tree species that were foraged for food and those that were not (Asuk et al., 2023). The results of the study suggested that beta-diversity trends, as well as patterns of relative species abundance, varied according to the use of the tree species (i.e., those utilized for food by humans and those not used for food by humans). This finding pointed to a potentially pervasive impact of low-intensity human foraging practices on tropical forest composition. For example, humans may disperse the seeds of edible species across the landscape and conserve those trees by not cutting them for timber due to the fruits/seeds they produce being highly valued as food sources. Similarly, with regard to timber harvest, while certain species of trees are cut down, some tree species with food value have been reported to remain in the forest estate or within old, abandoned farm estates (Ellis et al., 2021; Jansen et al., 2020; Asuk et al., 2023; Levis et al., 2017). However, whether such effects are prevalent across tropical ecosystems in West Africa at larger scales is unknown. A better understanding of the magnitude and dynamics of impacts from low-intensity anthropogenic activities on beta-diversity at a regional scale or how these activities interact with other drivers is essential to accurately predict the future impacts of humans on tree community composition and dynamics (McMichael et al., 2017b; Piperno et al., 2015; Stahl, 2015; Wayman et al., 2021). Due to the rugged topography and remote nature of some West African forests, the intensity of impact from human activities on the ecosystem could reasonably vary depending on the accessibility of these forests to people (Asuk et al., 2023). This variability has been observed locally (Asuk et al., 2023), but it is unclear if the same will be seen at a regional scale. This study seeks to address this research gap for the Nigeria-Cameroon region, which has a continuous forest area with varied human access and elevational variability. In addition, the studied ecosystem is threatened and poorly studied, yet it is one of the most culturally and biologically diverse forest regions in all of tropical Africa (Fotang et al., 2021a, 2021b).

In this study, a beta-diversity framework was used to evaluate the impact of low-intensity anthropogenic activities on the composition of tree assemblages in tropical West Africa at regional scales. Using a regional dataset of West African tropical forests, containing presence/absence information of tree species categorized into edible (produce seeds and fruits eaten by humans) and inedible (not eaten by humans) species, patterns of spatial beta-diversity alongside predicted drivers were calculated and analysed to answer the following question: is there an influence of human presence on the spatial beta-diversity of forest trees at a regional scale, and does this influence differ between those species used for food and those which are not? Based on previous work (Asuk et al., 2023) at local spatial scales, it was hypothesised that the impacts of humans on the distribution and composition of tree species observed at a local scale should clearly emerge at the larger regional scale.

2. Materials and Methods

2.1. Plot and species composition data

The study was carried out using tree data from long-term plots established in the tropical forests of Nigeria and Cameroon, bordering countries located in the West and West-Central regions of Africa, respectively (Figure 3.1). The forests of both countries are contiguous via their common borders (Nigerian National Park Service, 2019; Enuoh and Ogogo, 2018). The species composition data used for the study comprised single census tree-by-tree samples collected between 2002 and 2019 from five plots established in Nigeria (Asuk et al., 2022, 2023) and 61 plots established in Nigeria and Cameroon, accessed from the ForestPlots.net database (Lopez-Gonzalez et al., 2009; ForestPlots.net et al., 2021). The selected plots in Cameroon all measured 100m x 100m except for one plot that measured 40m x 100m (see Appendix S1, Table S1). The plots in Nigeria were smaller than those in Cameroon, measuring 40m x 120m (see Appendix S1, Table S1).

The plots were grouped into four spatial clusters based on their spatial proximity (Fig. 1). The associated plot metadata also included information on elevation, average plot slope, longitude, and latitude, stand density, forest status, and forest composition. Elevation was recorded as the elevation of plots in metres above mean sea level during field inventories. The average slope of the plots was measured at a 20m distance, and the slope was scaled into intervals: flat (0 – 2 degrees), almost flat (2 to 5 degrees), slightly sloping (5 to 10 degrees), moderately sloping (10 to 20 degrees), and steep (greater than 20 degrees). Geographical data consisted of information on longitude and latitude in metres (UTM) at the centre of the plot collected during forest inventories (used to measure geographical distance between plots). Stand density, which refers to the number of living individual tree stems per unit area, was generated by counting the total number of stems in each plot. To produce forest composition data, the composition of each plot was classified as either mixed forest, monodominant, or savanna following ForestPlots.net (see Appendix S1, Tables S2 and S3). Forest status data contained information about the status of the forest within the plots in relation to past or present anthropogenic disturbance as described by ForestPlots.net, including old-growth, secondary forest, logged, burned, and other mixed classifications (Lopez-Gonzalez et al., 2011).

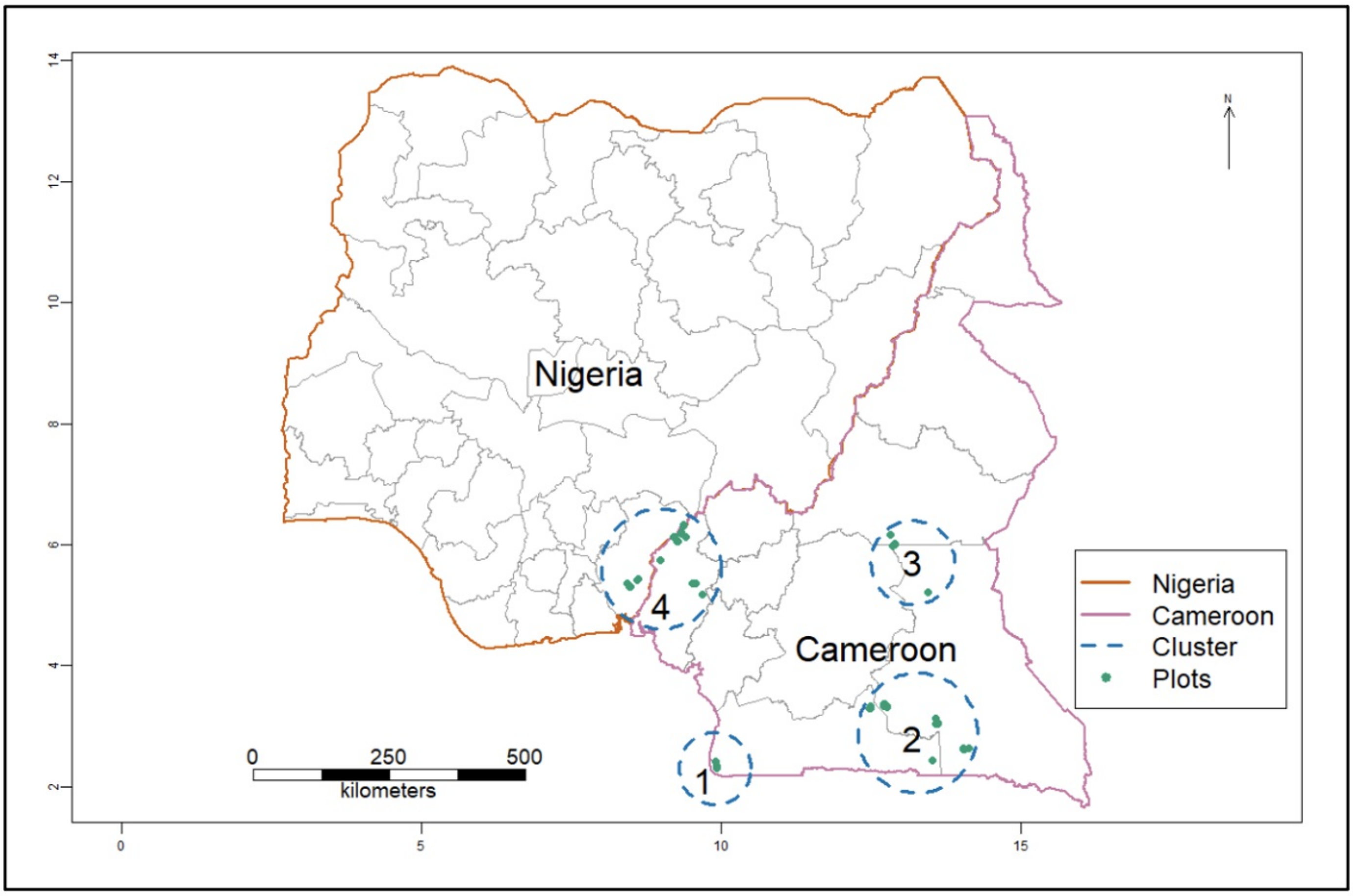

Figure 1. *Map of Nigeria and Cameroon showing the location of the 66 plots used for the study. The plots were grouped into four spatial clusters (blue broken lined circles), numbered 1 to 4.*

2.1.1. Plot selection criteria

To reduce any area effect on tree composition and thus ensure a justifiable pairwise comparison of the plot data, differences in plot dimension/area (i.e., plots that were much larger/smaller compared to other plots) were reduced. Data from the last tree censuses collected between 2002 and 2019 were filtered from the multiple census tree data for the study. Only plots that fell within the size range of 40 by 100 m and 100 by 100 m, with mixed and monodominant species composition in old-growth and secondary forest ecotones, were selected for the study. Specifically, for the Nigerian plots, five groups of three adjacent plots that were below 100 m by 100 m in size were merged into plots of size 40 m by 120 m. GPS coordinates for the centre plot amongst the three adjacent plots were used as the centre point for the new plot. Filtering and joining the plots resulted in a dataset consisting of 66 plots across the study region (i.e., Cameroon and Nigeria), with an average size of 94.6 m (std. 17.4 m) by 101.5 m (std 5.3 m) and containing a total of 28,299 individual trees. All other plots that did not meet the above criteria were discarded, leaving a total of 66 plots.

As outlined above, due to the geographic distances between plots, the 66 plots were further grouped into four clusters based on the geographical proximity of the plots. Cluster one had three plots, cluster two had 25 plots, cluster three had seven plots, and cluster four had 31 plots.

2.2. Species categorization

Tree species were categorized into those with fruits, nuts, and seeds that are edible and those that are inedible for human consumption. The categorization was based on a combination of structured questionnaires (see Appendix S2) administered to four forest-dependent/support zone communities within Oban Forest in Nigeria (Asuk et al., 2023), and secondary data on the utilization of tree species collected from online databases between December 2021 and February 2022. These online databases included the Useful Tropical Plants database (https://tropical.theferns.info/), the PlantUse database (https://uses.plantnet-project.org/en/), the Royal Botanic Gardens Kew/Plants of the World Online database (https://powo.science.kew.org/), PlantZAfrica (http://pza.sanbi.org/), World Agroforestry (https://apps.worldagroforestry.org/usefultrees/), and ebooks and journal publications. Only species identified to produce fruits, nuts, and seeds consumed by humans were classified as edible. All other species were classified as inedible.

2.3. Human influence/presence

Two variables were used as proxies to assess the impact of humans on the tree species composition in the region (see Appendix 3):

1. Distance to the nearest anthropogenic edge (DNAE), calculated as the straight-line distance from the plot centre to the nearest anthropogenic edge of the forest at the time of the census. Information on the nearest anthropogenic edge was available for the plots in the Oban Division dataset, but few other plots in the forestplots.net dataset. For plots without this information, OpenStreetMap and Google Earth were used to measure a straight-line distance from the GPS location of the centre of each plot to the nearest sign of anthropogenic edge (e.g., farm, settlement, construction but excluding footpaths). DNAE was used as an indicator to measure the possible presence of relatively high-impact human activity in the region.
2. Distance to the closest human presence (DCHP) – calculated as the straight-line distance from the GPS centre point of the plot to the closest identified footpaths, often used to forage for food and hunting; thus, it was used as an indicator for relatively low-impact human activities. Human presence measurement was generated from OpenStreetMap and validated on Google Earth. Because of a combination of data from censuses carried out in different years, Google Timelines on Google Earth were used to select an available aerial image closest to the years the census measurements were taken (see Fig. S1 and S2 in Appendix S3). DCHP generally had shorter distances than DNAE and is arguably a more accurate measure of low-impact human presence in the forest region.

2.4. Data analysis

Data analysis involved three main steps: the generation of a tree species presence-absence matrix for each plot, calculation of Sørensen’s pairwise beta-diversity between plots (partitioned into nestedness and turnover components), and the use of Generalized Dissimilarity Models (GDMs) to identify variables that drive spatial beta-diversity. The data were analysed using R (R Core Team, 2022).

2.4.1. Presence-absence matrix and beta-diversity calculation

For each plot, a presence-absence matrix was constructed separately for all species (a combination of edible and inedible species), edible species, and inedible species. Then the pairwise dissimilarity (beta-diversity; Sørensen index) was computed between each plot and every other plot within the dataset for each presence-absence matrix. The pairwise dissimilarity was partitioned into the turnover (which is independent of richness differences) and nestedness components (Baselga, 2012). All beta-diversity components were calculated using the “betapart” package in R (Baselga et al., 2018; R Core Team, 2022).

2.4.2. Generalized Dissimilarity Models (GDM)

GDMs and variance partitioning are valuable tools for disentangling what proportion of the variation in dissimilarity between communities is due purely to the effect of distance between the communities, what proportion is explained uniquely by environmental (including anthropogenic) gradients, and what proportion of variance is shared between the two (Buzatti et al., 2019; Guerin et al., 2013; He et al., 2020; Wayman et al., 2021).

The “gdm” R package (Ferrier et al., 2007; Mokany et al., 2022) was used to fit the GDMs, which involved modelling a measure of compositional difference between sites (here, the total pairwise beta-diversity and separately the turnover and nestedness components) against the selected environmental variables and geographic distance to assess which predictor variables drive spatial taxonomic dissimilarity between plots. GDMs utilize the pairwise dissimilarities from beta-diversity matrices as the response variable and transform this dissimilarity to allow for meaningful comparison with combinations of predictor variables on different scales in the form of site pairwise distances (Mokany et al., 2022). A linear combination of I-spline basis functions fit using non-negative least squares regression was used to transform each predictor variable in the GDM (Mokany et al., 2022). The spline function of each predictor variable is relatively flexible in shape. However, because GDMs assume that dissimilarity can only increase between two sites that become more different in their predictor variables, I-splines are constrained to increase monotonically (Mokany et al., 2022).

Separate GDM models were fitted for total beta-diversity, turnover, and nestedness calculated from each of the three presence-absence matrices (all species, edible species only, and inedible species only) (Mokany et al., 2022). These models included all the environmental variables (elevation, average plot slope), plot-level variables (stand density, forest status, and forest composition), and a measure of distance between each plot. The direct impact of each variable along the dissimilarity gradient was assessed by applying a permutation and backwards selection approach, allowing the calculation of variable significance and variable importance (applied using the function ‘gdm.varImp’ within the ‘gdm’ package (Mokany et al., 2022; Ferrier et al., 2007)). This approach fits a model using all the unpermuted predictor variables. The rows containing the variables are then permuted 100 times between the plots (columns), and a separate GDM is fitted to each. Deviance between the unpermuted and permuted models is then calculated. The process is then repeated for each individual predictor, whilst holding the others constant, to calculate importance scores and significance for each one. The least significant predictor is then dropped, and the permutation is repeated with the remaining predictors until a model is found where all those remaining are significant ($p < 0.05$; model 1). The predictor importance for each variable was calculated from the percent change in deviance explained between the unpermuted and permuted models for that variable (Mokany et al., 2022; Ferrier et al., 2007).

Geographical distance (the Euclidean distance between sites based on the x and y coordinates) was included as a predictor to account for the direct or indirect likelihood of distance-induced dissimilarity between site pairs through dispersal limitations (Mokany et al., 2022). However, the dissimilarity driven by environmental gradients could be suppressed or wrapped up in the dissimilarity from the distance between sites, leading to the variance explained by each to be shared. Therefore, two more models were fitted for each response: one containing only geographical distance (model 2) and one with only environmental predictors that were significant in the model selection process (model 3). The shared variance between the environmental predictors and geographical distance was generated using the formula (Ray-Mukherjee et al., 2014) below.

$$V_s = V_{full} - (V_{full} - V_g) - (V_{full} - V_e) \qquad \text{Equation (1)}$$

where V_s is the shared variance explained between the environmental and geographical variables, V_{full} is the total variance explained by the model (model 1), V_g is the variance explained by the model containing only geographical variables (model 2), and V_e is the variance explained by the environmental model only (model 3).

The distinct cluster groups were coded from 1 to 4 (Fig. 1) and included cluster identity as a variable in the Generalized Dissimilarity Models (GDMs) to check the effect of cross-cluster variation. Then the GDMs were also run with data from each of the four cluster groups individually to compare within-cluster variation and drivers. In addition to this, the model was also run with and without cluster as a variable.

3. Results

3.1. Regional, Taxonomic Beta-Diversity, Turnover, and Nestedness

Among the 66 plots, there were a total of 28,299 individually sampled trees with a gamma diversity of 708 species within 316 genera. From a perspective of human consumption, 236 species were classified as edible, and 472 species were classified as inedible, with 11,097 and 17,202 stems, respectively (Table S4 in Appendix S4). The mean total pairwise beta-diversity between sites was similar (Figure 2) for all species (0.74 ± 0.13), edible species (0.73 ± 0.14), and inedible species (0.75 ± 0.13). The turnover component of beta-diversity was the main determinant of the overall beta-diversity, while nestedness contributed a very small proportion in the region and in the clusters. For all species, turnover (0.67 ± 0.15) accounted for 90.5% of total beta-diversity, while nestedness resultant dissimilarity (0.07 ± 0.08) was responsible for 9.5%. For inedible species, turnover (0.67 ± 0.16) was responsible for 90.1% of total beta-diversity, while nestedness (0.07 ± 0.09) described 9.9% of total beta-diversity. Similarly, 89% of total beta-diversity for edible species was due to turnover (0.65 ± 0.17), and 11% was due to nestedness resultant dissimilarity (0.08 ± 0.08). However, for the nestedness GDMs, no explanatory variables explained any variation and, therefore, they are excluded from further discussion.

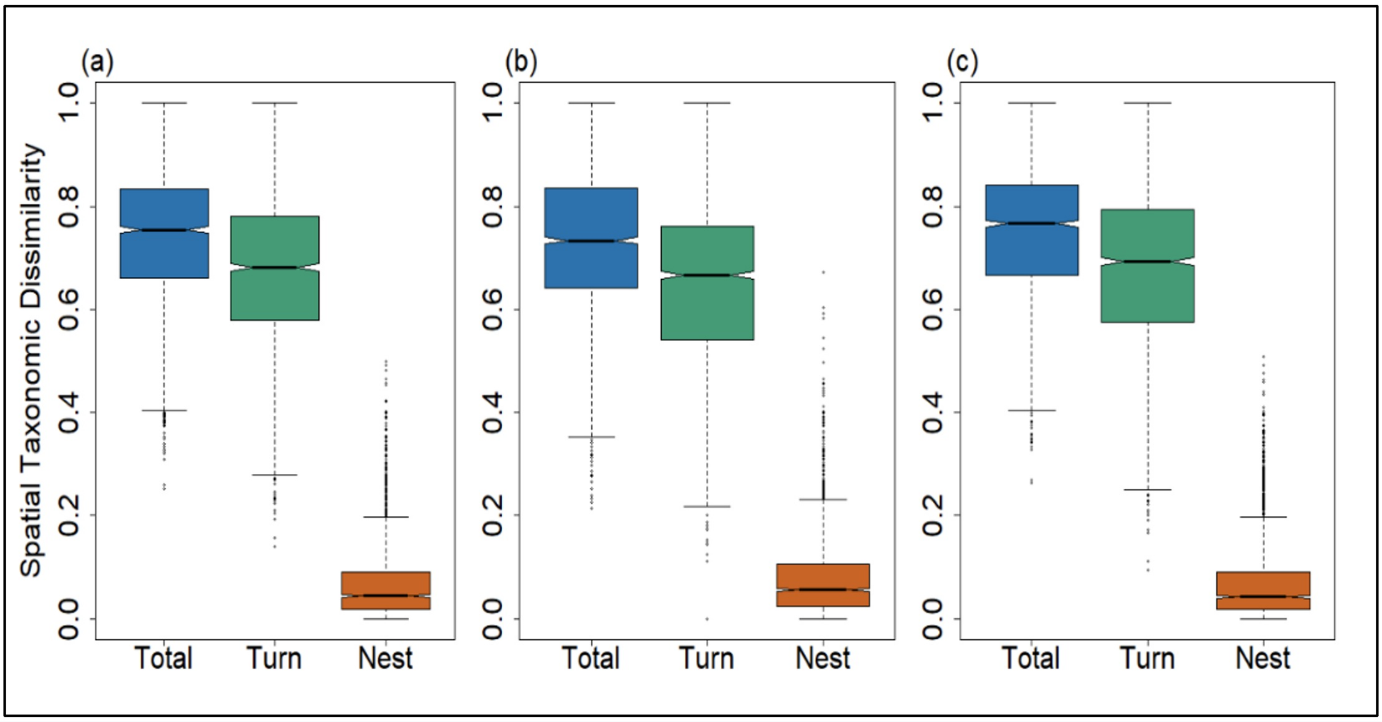

Figure 2. *Boxplots of pairwise spatial dissimilarity of all (a), edible (b), and inedible (c) tree species found in the region. Plots display total beta-diversity (Total) as well as the turnover (Turn) and nestedness (Nest) components.*

3.2. GDM Results

As expected, Model 1 (a combination of geographical distance and environmental variables) had the highest variance explained, with 40.9%, 36.8%, and 31.8% explained for total beta-diversity, for the models containing all, inedible only, and edible only species groups, respectively. Similarly, Model 1 also recorded the highest percentage of variance explained in turnover (species replacement) for the inedible, all, and edible species groups, with 43.5%, 41.6%, and 27.7%, respectively (Table 1). Model 3 (models run with environmental variables only) recorded the second highest variance explained for total beta-diversity, with 30.9%, 23.1%, and 24.8% (all, edible, inedible species groups, respectively), while Model 2 had the least variance explained in total beta-diversity, between 18.3%, 13.2%, and 17.4% for all, edible, and inedible species groups, respectively (see Table 1). A low shared explained variance between geographical distance and environmental predictors was observed, with percentages ranging from 8.3%, 5.4%, and 4.6% for dissimilarity due to total beta-diversity and 5.9%, 4.2%, and 5.8% in dissimilarity due to turnover in all, edible, and inedible species groups, respectively (see Table 1).

Table 1. *Results from the generalized dissimilarity models analysing the spatial dissimilarity between forest plots. "Total" refers to total Sørensen's beta-diversity while "Turn" refers to the Simpson's turnover partition of beta-diversity. NA values indicate where variables were non-significant within models. Shared variance (%) was calculated from the variance explained by the full model, the geographical distance only model, and the environment only model. Model 1 (all significant predictor variables), Model 2 (only geographical distance), and Model 3 (only significant environmental predictors from model 1) rows show the percentage deviance explained for the models. Variable importance is percent change in deviance explained between the unpermuted and permuted models for that variable. DNAE is the ground distance of plots to nearest anthropogenic edge. DCHP is the ground distance to closest human presence to each plot. "m" is ground distance measured in metres.*

Groups	**All**		**Edible**		**Inedible**	
	Total	**Turn**	**Total**	**Turn**	**Total**	**Turn**
GDM Deviance	104.19	127.37	157.09	208.10	120.16	142.20
Null Deviance	176.20	218.03	230.25	287.99	190.19	251.47
Intercept	0.66	0.50	0.66	0.42	0.71	0.48
Model 1	40.87	41.58	31.77	27.74	36.82	43.45
Model 2	18.26	17.30	13.22	13.19	17.38	15.54
Model 3	30.89	30.13	23.12	18.75	24.83	33.70
Shared Variance (%)	*8.28*	*5.85*	*4.57*	*4.20*	*5.39*	*5.79*
Variable importance						
Geographical distance (m)	24.38	27.51	27.18	32.36	32.54	22.42
Elevation	19.83	25.23	NA	NA	19.99	26.98
Stem density (stems/ha)	NA	NA	19.31	15.04	NA	NA
DNAE (m)	NA	NA	NA	15.24	NA	NA
DCHP (m)	18.35	24.34	14.07	24.01	21.54	26.65
Forest composition	18.25	NA	26.86	NA	NA	NA

3.2.1. Drivers of spatial taxonomic beta-diversity across all, edible, and inedible species

A total of six variables (geographical distance, elevation, stem density, DNAE, DCHP, forest composition) out of the eight variables imputed in model 1 significantly affected beta-diversity at varying levels of importance across all groups (all, edible, and inedible) (Table 1).

All species models

In the all-species model (all; Table 1), geographical distance, elevation, DCHP, and forest composition were significant predictors of total beta-diversity. Geographical distance, the variable with the highest importance in most models (except in the model for turnover of inedible species), showed a rising trend up to 200-300 km before levelling off (Figure 3a). Elevation, the second most important, increased gently up to 500-700 m, then sharply increased after that point (Figure 3a). DCHP, the third key predictor, had a slight initial rise followed by a steady increase (Figure 3a). Forest composition had a minor yet significant linear relationship with beta-diversity (Figure 3a). The turnover model identified geographical distance, elevation, and DCHP as significant, with trends similar to those in the total beta-diversity model (see Figure 4a, Tables 1 and S5 in Appendix S5), but interpretations should be made with caution as the data spread shown on the x-axis was skewed, with only a few forest plots having high values of DCHP or DNAE (see x-axis in Fig. 3).

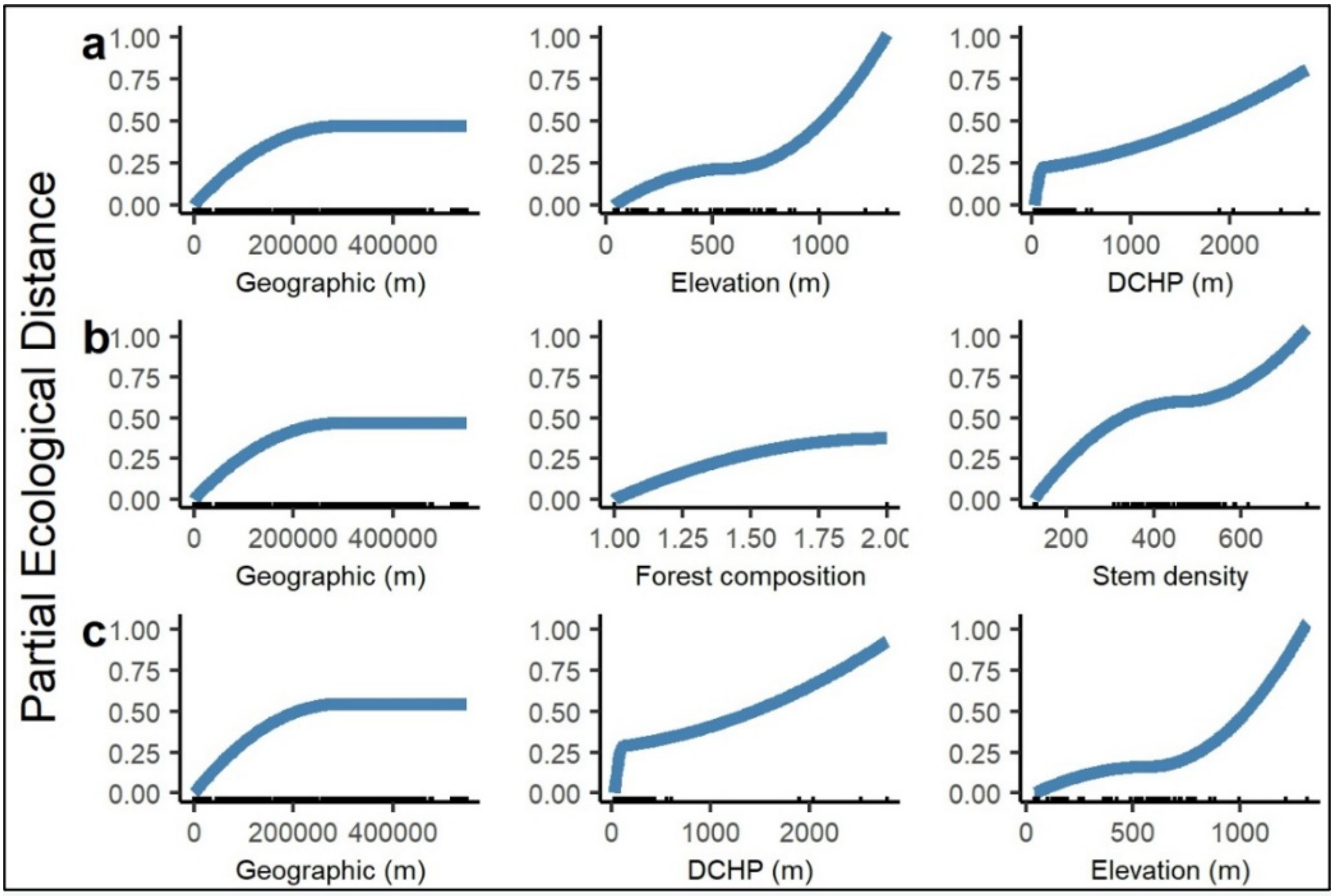

Figure 3. *Plotted I-splines of the three variables with the highest importance scores from the GDMs analysing the spatial relationship between geographical gradients, environmental variables, and tree species composition. Plots are the Total Sørensen's beta-diversity for the entire region (a), for the edible species category (b), and for the inedible species (c). Plots are organized from left to right in order of decreasing importance.*

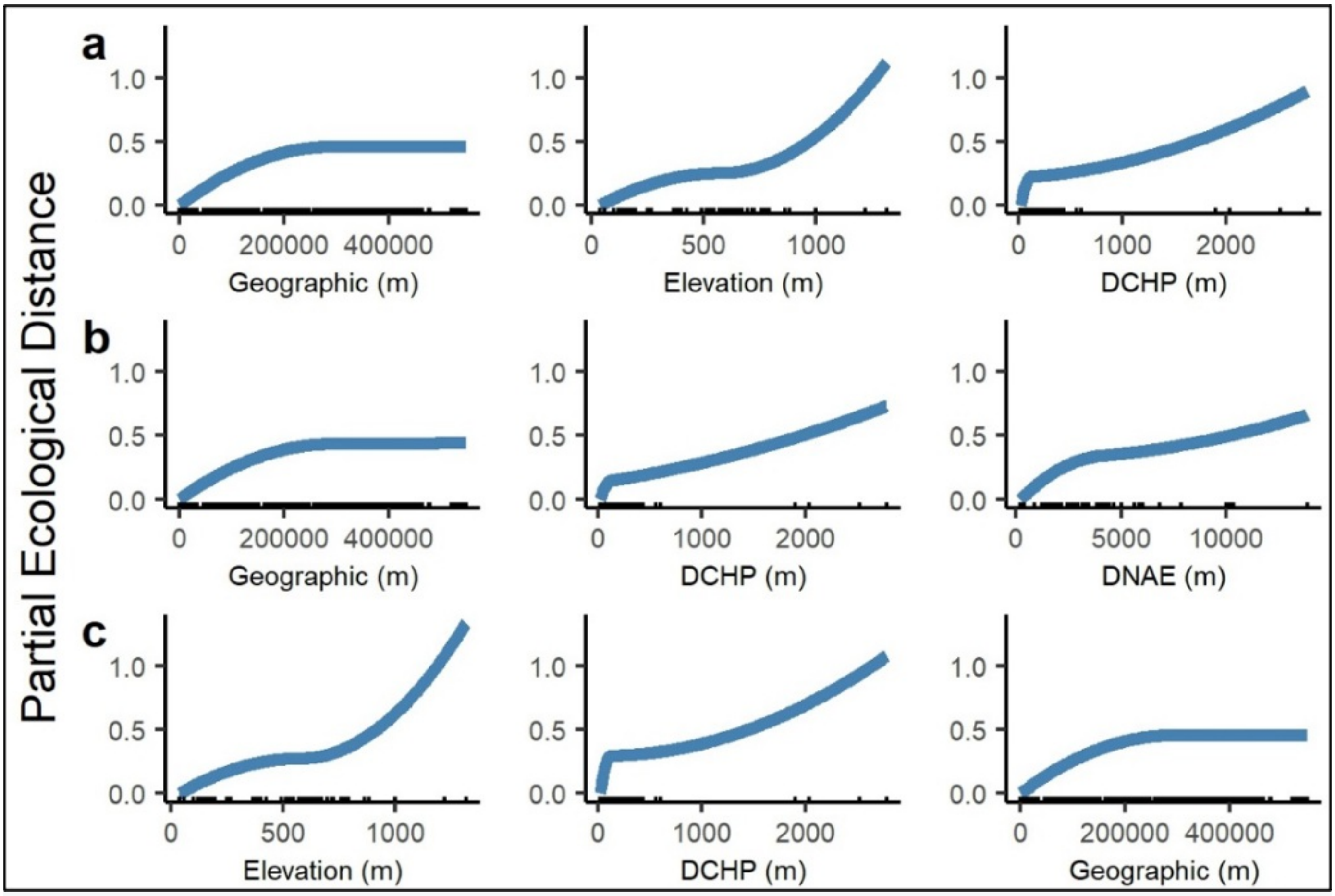

Figure 4. *Plotted I-splines of the three variables with the highest importance scores from the GDM analysing the spatial relationship between the turnover component of Sørensen's beta-diversity and geographical gradients, environmental variables, and tree species composition. Plots on row (a) are for all species, (b) are for the edible species category, and (c) for the inedible species. Plots are organized from left to right in order of increasing importance.*

Edible species models

For the edible species model, total dissimilarity in the community assemblage was significantly influenced by geographical distance, forest composition, stem density, and DCHP, in order of decreasing variable importance (Table 1). The I-splines indicated that the relationship between geographical distance and total beta-diversity had an initial steep linear trend that then plateaued. Forest composition exhibited a slight linear trend, while stem density had a steeper linear trend (Figure 3b). DCHP exhibited a very steep initial increase, followed by a continuous linear increase (Figure 4b). The turnover resultant beta-diversity of edible species was driven by four significant variables: geographical distance (most important variable), DCHP, DNAE, and stem density (least important variable) (Table 1), although DNAE and stem density had similar importance scores. The I-splines indicated that the relationship between geographical distance and total beta-diversity had an initial steep linear trend that then remained constant at the peak, just as seen in total beta-diversity. Both DCHP and DNAE exhibited positive roughly linear relations with beta-diversity. However, caution should be taken when interpreting this relationship as most of the trend in DCHP was driven by four points with higher values while other plots were skewed (Figure 4b).

Inedible species models

The models for total and turnover resultant beta-diversity using the inedible species data produced the same three significant predictors of dissimilarity but with varied importance values (Table 1). Significant predictors with the highest variable importance for the total beta-diversity of inedible species were geographical distance, DCHP, and elevation, in order of decreasing importance. The geographical distance increased (based on the I-splines) with a steep linear trend and then remained constant at its peak. DCHP exhibited a very steep initial increase followed by a continuous linear increase, while elevation showed a gentle trend that levelled off at about 600m followed by a sharp continuous increase (Figure 3c). Inedible turnover resultant beta-diversity models showed that elevation had the highest variable importance, followed by DCHP and geographical distance. However, the variable importance values for DCHP (26.65) and elevation (26.98) were similar.

The total beta-diversity models for edible and inedible species had two common variables that were significant (geographical distance and DCHP). While there were differences in the variable importance hierarchy, the maximum I-spline values for these variables were higher when using the inedible species data than when using the edible data.

3.2.2. Effects of spatial clusters on the model outcome

When the plot clusters (Table S6 to S7 and Figure S3 to S4 in Appendix S5) were included as predictors in the models, there was an increase in the overall GDM deviance and a slight decrease in the variance explained for total beta-diversity in each model group (all, edible, and inedible species). When attempting to run the GDMs for individual clusters, the models for clusters one, two, and three did not run due to too few data points. In cluster four, there was an increase in the variable importance of human influence variables (DCHP and DNAE) as predictors of the total beta-diversity of inedible species, while they were less important for edible species (Figure S5 to S6 in Appendix S5).

4. Discussion

4.1. Drivers of West African tropical forest tree beta-diversity

The dissimilarity in tree species composition observed in the Nigeria-Cameroon regional forest was mainly driven by the replacement of species across space, which could be due to dispersal limitation, competition, and environmental filtering along environmental gradients (Jiang et al., 2021; Verrico et al., 2020; He et al., 2020). Environmental filtering in the tree species community composition of the region was reflected in higher values for variance explained in the models with environmental variables alone compared to that explained by geographical distance. In addition, the finding that distance had the largest variable importance score, combined with the low shared variance explained between models with geographical distance alone and environmental variables alone, further supported that dispersal limitation may play a key role in the spatial beta-diversity patterns observed. A similar study in the Cuitzeo basin, Mexico, revealed that environmental heterogeneity has a greater impact on beta-diversity due to niche-based processes than geographical distance (Vega et al., 2020). Another study conducted in Hainan, China, demonstrated that environmental variables, including temperature, precipitation, and evapotranspiration, had far more significant effects on tree species compositional dissimilarity than geographical distance, again highlighting the importance of niche-based processes rather than dispersal limitation (He et al., 2020). Although the current study did not account for climate variables like He et al. (2020), the difference in regional species composition can be driven by spatial changes in climate variables between plots.

The region has seen a shift from sustainable, small-scale agricultural and logging practices to large-scale industrial farming and extensive commercial logging, which has profoundly impacted forest ecosystems (Fongnzossie et al., 2020; FAO, 1999). The shift from nomadic life to settled living near forests, driven by urbanization and technology (Asuk et al., 2023; Adnan et al., 2015), has changed forest resource use. The indigenous human communities have maintained their medicinal, land management, and conservation customs tied to cultural and spiritual forest connections (FAO, 1999; Falconer, 1993). Sustainable foraging and wildcrafting, embedded in cultural heritage, continue in the Nigeria-Cameroon forest region, and these practices could have a different impact on the tree species assemblage.

4.2. The impact of human influence on regional beta-diversity

The combination and intensity of variables driving species composition in edible and inedible species groups in the regional forest differed. This might result from the history and frequency of forest disturbance, successional processes, varying distances of plots from high-intensity and low-intensity human activities, differences in topography, climate, and soil conditions (Williams et al., 2020; Fotang et al., 2021c; Yuan et al., 2022; Asuk et al., 2023). Low-intensity human influence (DCHP - distance to closest human presence) was one of the leading predictors of dissimilarity in tree species composition across all species types in the regional forest. While low-intensity human influence (DCHP) had a higher impact on inedible species than edible species, high-intensity human activities (DNAE - distance to nearest anthropogenic edge), such as logging, agricultural expansion, and other large-scale disturbance, drove the turnover of only edible species. This was different from the finding in a previous local study within one of the locations in the same region, which suggested that high-impact human activities could increase the turnover of all species while low-impact activities reduced the turnover of edible species (Asuk et al., 2023). Studies suggest that human activities, including logging, agricultural expansion, and harvesting for livelihood, significantly alter habitats and species composition in African tropical forests (Auliz-Ortiz et al., 2024; Assede et al., 2023; Hussein, 2023; Asuk et al., 2023).

In addition to DNAE, beta-diversity of edible species was driven by the composition of the forest (either mixed forest or monodominant), and in combination with stem density, it was a predictor of turnover. These variables, however, were not observed to be significant in inedible species. The forests studied included both mixed forest and monodominant forest. Monodominant forests are characterized by one single species making up more than 60% of the tree canopy, resulting from coppicing (sprout or regrowth formed at the tree base or root) and edaphic factors (ter Steege et al., 2019). Edible species have cultural and agroforestry values beneficial to different communities in the Nigeria-Cameroon region (Falconer, 1993; Fongnzossie et al., 2020); thus, the predominance of a single species belonging to the edible or inedible category in one location could contribute to the beta diversity observed (Shiembo et al., 1996; FAO, 1999; Hundera, 2007; Klein et al., 2003). Some of the species managed and used by local communities include African Walnut (*Coula edulis*), Bush Mango (*Irvingia spp.*), Kola Nut (*Cola spp.*), Baobab (*Adansonia digitata*), African Bush Mango (Irvingia gabonensis), Safou (*Dacryodes edulis*), African Breadfruit (*Treculia africana*), Bitter Kola (*Garcinia kola*), African Star Apple (*Chrysophyllum albidum*), and Monkey Kola (*Cola lepidota* and *Cola pachycarpa*) (Shiembo et al., 1996; FAO, 1999; Hundera, 2007; Klein et al., 2003; Fongnzossie et al., 2020).

High stem density in tropical forests can create complex and heterogeneous microhabitats that support different tree species with unique environmental requirements. The effect of stem density on total beta diversity and turnover of edible species might translate to high migration of the species in space, either naturally through propagation or through the management and cultivation influence of humans. Alpha diversity is positively correlated with stand structural heterogeneity (either tree DBH inequality, height inequality, or stand density) (Abbasi et al., 2023; Godlee et al., 2021; Yano et al., 2021). However, the dynamics differed as stand density was not a predictor of beta-diversity in inedible species with higher alpha diversity than edible species. This might be due to the influence of other ecological factors such as greater adaptability to survive in smaller, isolated habitats or possibly other species uses such as medicine, gum, and others (Bailey et al., 2010; Fahrig, 2003; de Lima Filho et al., 2021). Comparing results of this study with those of Asuk et al. (2023) indicates that these processes are apparent for inedible species at both local and regional scales in West African tropical forests but differ for edible species. More broadly, findings from other studies, for example, those undertaken in the Amazon, have suggested that the selection and stewardship of desired tree species by indigenous populations over time could leave strong imprints on patterns of forest composition (Roberts et al., 2021; Levis et al., 2017; Scerri et al., 2022).

4.3. Effects of spatial distance and elevation on the beta-diversity of tree species in the region

Although the combined effect of environmental variables (see model 3 in Table 1) was greater than the geographical distance (see model 2 in Table 1), in the overall model (model 1), the geographical distance between sites had a stronger individual effect on the pairwise dissimilarity between plots than any other single environmental variable (except for the turnover of inedible species, where elevation had the strongest effect). This suggested that a large geographical distance between plots, in addition to water bodies, could act as a biogeographical barrier, inducing some level of dispersal limitation in species, driving turnover (Abiem et al., 2022; He et al., 2020; Wayman et al., 2021; Yang et al., 2015; Zahawi et al., 2021). Thus, human impact on the forest could vary based on the distance covered – shorter for intense activities like timber harvesting, and wider for foraging (Asuk et al., 2023; Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022).

Elevation plays a crucial role in the composition and spatial distribution of tree species in forest ecosystems (Asuk et al., 2023; Malizia et al., 2020; Yano et al., 2021). Elevation exerts varying niche-based effects on species due to changes in climate, soil, the identity of seed dispersers, and the activities of humans along the elevational gradient, which could result in strong environmental filtering and the replacement of species along the gradient (Adnan et al., 2015; Asuk et al., 2023; Verrico et al., 2020). Elevation was a significant variable in all species and inedible species models, which was expected given that the study area is generally characterized as having rough terrain with strong elevational gradients. However, elevation was not a significant predictor of total beta-diversity and turnover of edible species. This could also be linked to the level of access to the forest, type of activities, and biome type that drive changes in tree species community (Fotang et al., 2021c; Yuan et al., 2022; Williams et al., 2020). This implied that human impact varies with elevation, more intense at lower levels and decreasing with altitude (Yano et al., 2021; Malizia et al., 2020), influencing beta-diversity patterns in edible and inedible species differently across elevations (Asuk et al., 2023).

The interaction between elevation and human activities (Asuk et al., 2023; Yano et al., 2021; Malizia et al., 2020) could result in an uneven distribution of activities along elevational gradients, which could potentially affect the pairwise turnover between plots (Asuk et al., 2023; Verrico et al., 2020; Adnan et al., 2015; Aigbe and Omokhua, 2015). However, low-intensity activities (e.g., foraging for food) may occur across the elevational gradient, leading to more similar species composition across the gradient (due to humans spreading the seeds of edible species; Jansen et al., 2020; Williams et al., 2020; Guo et al., 2022; Scerri et al., 2022; Asuk et al., 2023) and explains why elevation was not a significant predictor in the edible species models. Although these forests were intact at the time of the census, any past timber harvesting would likely have been restricted to lower elevations (Adnan et al., 2015; Asuk et al., 2023; Socolar et al., 2016; Verrico et al., 2020), which will have increased the effect of elevation on dissimilarity (Asuk et al., 2023; Ellis et al., 2010). Landscape transformation could drive species turnover, where some species decline or disappear, unable to adapt, and others better suited to these changes thrive. Additionally, selective pressure due to species preferences could reduce populations of certain species, causing a marked turnover in species composition.

4.4. Limitations associated with the study

Understanding the impact of human influence on tree species dissimilarity in the Nigeria-Cameroon forest region using this dataset presents significant challenges, primarily due to the lack of historical data. The study was limited to the data available and plots that fit the selection criteria. This limitation hindered a comprehensive assessment of past human impacts on the forest, an essential factor in understanding the current state of these ecosystems. Against this backdrop, the evolution of human interaction with forests over the years is particularly noteworthy (Vellend et al., 2017; Edwards et al., 2019; Ulian et al., 2020).

5. Conclusion

This study evaluated the drivers of beta-diversity in tree species, while emphasizing the impact of human activities in the Nigeria-Cameroon forest region. The primary driver of tree species dissimilarity was found to be turnover. Key factors driving beta-diversity included geographical distance, plot elevation, stem density, human proximity, and forest species composition, with environmental variables playing a more substantial role than geographical distance, although the latter was the most important individual variable in most models.

The variables observed to predict beta-diversity differed between edible and inedible tree species. While forest composition (mixed or monodominant forest) significantly influenced beta-diversity in edible species, this pattern was not observed in inedible species. Geographical distance was a more dominant factor in plot dissimilarity than any single environmental factor, and elevation was particularly influential in the diversity of inedible species, suggesting the importance of niche-filtering and human activities along elevational gradients (Asuk et al., 2023).

Despite these limitations and based on what is currently possible with the available data, our findings suggest that human influence is an important driver of beta-diversity in the Nigeria-Cameroon forest region. As discussed, the type, intensity, and duration of different human activities can exert a different response on the beta-diversity of different species. The study highlights the role of environmental filtering, spatial factors, and human influence in shaping tree species diversity in this region. However, further research is necessary to understand the links between species dissimilarities and tree traits, and the effects of various disturbances. This could involve a combination of socio-economic and ecological data to develop sustainable conservation and management strategies, particularly focusing on sustainable resource use to support forest-dependent communities. This research is vital for guiding conservation efforts in Afrotropical forests, considering the significant impact of human activities on tree species assemblages.

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