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Human and environmental factors shape tree species assemblages in West African tropical forests.

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HUMAN AND ENVIRONMENTAL FACTORS SHAPE TREE SPECIES ASSEMBLAGES IN WEST AFRICAN TROPICAL FORESTS

Drivers of tree diversity in West Africa

ABSTRACT

Aim
This study investigated how human activities and local environmental variables shape tree assemblages (species composition in a defined location), comparing their effects on edible and inedible tree species. Three hypotheses were tested: (1) Environmental filtering impacts spatial beta-diversity more than dispersal limitation, (2) human activities significantly influence regional tree beta-diversity, and (3) predictors of beta-diversity differ between edible and inedible species.

Location
Tropical forest in Nigeria and Cameroon in West and Central Africa.

Methods
Tree data were collected between 2002 and 2019 from sixty-six forest plots. Species were categorised as edible and inedible by humans using interviews and online databases. Pairwise beta-diversity (partitioned into total beta-diversity and turnover) between plots was analysed using Generalised Dissimilarity Models (GDMs) with geographical distance, plot-specific variables (forest composition, climate, elevation, stem density, human influence indicators), and human influence indicators (distance to closest human presence (DCHP), and nearest anthropogenic edges (DNAE)) as predictors.

Results
The dataset included 236 edible species (11,097 stems) and 472 inedible species (17,202 stems), with high species turnover (>90%) dominating beta-diversity patterns. Due to local plot-level factors, environmental filtering (deviance explained for all species: 37.4%, edible: 18.9%, and inedible: 31.4%) exerted greater influence on species assemblages than geographical distance alone. Beta-diversity drivers differed between edible and inedible species: elevation strongly influenced turnover in inedible species, whereas forest composition significantly shaped the assemblage of edible species, reflecting patterns of human-mediated species selection and species dominance. Human presence impacted the overall beta-diversity of inedible species but only influenced the turnover component of edible species.

Main Conclusions
Tree assemblages in the Nigeria-Cameroon forest region were primarily structured by local environmental conditions and human activities rather than by dispersal limitation. Effective conservation should incorporate sustainable human activities and traditional ecological knowledge, with further research needed to explore the long-term anthropogenic impacts on these forests.

Keywords: West Africa, beta-diversity, species turnover, human presence, tree species assemblages, tropical forest, generalised dissimilarity models (GDMs), environmental gradients, elevational variability, forest composition

1. INTRODUCTION

Forest biodiversity and forest function are rapidly changing at local, regional, and global scales, due to large-scale habitat loss and modification from anthropogenic activities (Bush et al., 2015; Clement et al., 2015; Helmus et al., 2014; Jarzyna & Jetz, 2018; C. H. McMichael et al., 2017; Piperno et al., 2015; Stahl, 2015; Steadman, 1993). Anthropogenic activities such as selective harvesting, illegal logging, clear-cutting for agricultural purposes, foraging of fruit/seed for food, planting and conservation all modify the composition and distribution of species in tropical forests (Asuk et al., 2022; Benchimol & Peres, 2013; Elo et al., 2018). The form and magnitude of these impacts can vary depending on forest utilisation (e.g., for food, timber, medicine), intensity of use, duration of human activity, and the type of species being utilised (Adeyemi, 2016; Adnan et al., 2015; Aigbe & Omokhua, 2015; Asuk et al., 2023; Jimoh et al., 2012). Investigations into the effects of anthropogenic activities on forest biodiversity have focused primarily on high-intensity human activities, such as logging, farming, infrastructure development and other activities that result in deforestation, fragmentation, and forest degradation (Alahuhta et al., 2017; Donoso et al., 2017; Gallardo-Cruz et al., 2009; García-Navas et al., 2020; Swenson et al., 2011). However, growing evidence suggests that low-intensity human activities such as foraging for food, selective species conservation, dispersal of seeds of desirable species (e.g., with human-edible fruits) and enrichment planting may modify forest ecosystems more than previously thought, and thus potentially affect ecological and macroecological patterns (Asuk et al., 2023; Chaturvedi et al., 2017; Levis et al., 2017; C. H. McMichael et al., 2017; Piperno et al., 2015; Singh et al., 2022).

Low intensity human activities can intentionally or unintentionally have long-lasting effects on the forest (C. N. H. McMichael, 2021). These ecological legacies, from human activities, might vary depending on the species and the intensities of their utilisation (enrichment or depletion) and ultimately induce post-disturbance succession affecting the trajectory of ecosystem processes over time (Asuk et al., 2023; C. N. H. McMichael, 2021). Historical low-intensity activities, such as deliberate planting and conservation of preferred tree species and selective logging, leave ecological

legacies which have been linked to the modern floristic composition and structure of some areas of natural forests in Amazonia (Bousfield et al., 2023; Levis et al., 2017; C. N. H. McMichael, 2021). African forests harbour biodiversity hotspots with numerous endemic species (Agaldo et al., 2016; Myers et al., 2000; Oates et al., 2004; Seifert et al., 2022) and regulate the global climate by absorbing atmospheric carbon dioxide, thus mitigating climate change effects (Artaxo et al., 2022; Hubau et al., 2020; Núñez et al., 2022; Oyewole et al., 2019). In addition, African forests contribute to water cycle regulation, soil conservation, agricultural support during crop failure, and ecological balance (Meinhold & Darr, 2022; Raj et al., 2022). Evidence from long-term studies revealed that African forest species are more resilient to the impacts of El Niño-related droughts (Bennett et al., 2021, 2023; Choury et al., 2022; Sullivan et al., 2020) and have a more stable carbon sink than Amazonian forests (Hubau et al., 2020). Although climate impacts forest ecosystems differently, these findings suggested that spatial and temporal changes in the composition of Afrotropical forests could be due to factors other than climate. Understanding the processes which 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 plant composition patterns, and the effects of low-intensity human impacts on such patterns.

The impact of low-intensity drivers on tropical forest composition can be assessed indirectly through the analysis of spatial beta-diversity, defined as the dissimilarity in species composition between two or more communities separated in space (Anderson et al., 2011; Asuk et al., 2023; Biswas & Mallik, 2011; Bush et al., 2015; Pound et al., 2019; Roberts et al., 2021; Singh et al., 2022). This is because the patchiness of human activities such as foraging, preferential planting and deliberate conservation within the forest leaves imprints on spatial patterns of species composition.

Spatial beta-diversity has been successfully used to analyse differences in tree species composition within and between forests (Condit et al., 2002), as well as to identify key drivers of spatial dissimilarity in the community composition of forest plots in Oban Forest in Nigeria (Asuk et al., 2023). Regarding the latter study, the impact of low-intensity anthropogenic activities on tree species

diversity was assessed by comparing different ecological patterns in tree species that were foraged for food by humans and those that were not (Asuk et al., 2023). It was found that spatial beta-diversity patterns and patterns of relative species abundance varied according to the use of the tree species by humans (i.e., those utilised for food and those not utilised for food). In particular, species used for their fruits, nuts and seeds (edible) showed no trends in spatial beta-diversity, while inedible species showed marked differences in species composition across space due to turnover across an elevational gradient (Asuk et al., 2023). This highlighted 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 or seeds that they produce being highly valued as food sources, thus reducing spatial beta-diversity. Similarly, with timber harvest, certain species of trees are cut down, but some tree species with food value remain in the forest estate or within old, abandoned farm estates (Asuk et al., 2023; Ellis et al., 2021; Jansen et al., 2020; Levis et al., 2017). However, the pervasiveness of these effects across tropical ecosystems in West Africa at larger scales is largely unknown.

While there have been numerous ecological studies on the spatial beta-diversity of forest tree species, these have mostly focused on identifying high-intensity drivers of dissimilarity at global scales, as well as mainly being focused on temperate forests, with less work focused solely on tropical forests (Aspin et al., 2018; Barnagaud et al., 2017; Biswas & Mallik, 2010, 2011; Devictor et al., 2010; Fu et al., 2019; García-Navas et al., 2020; Herault et al., 2010; Jarzyna & Jetz, 2016; Lueder et al., 2022; Swenson et al., 2011; Waddell et al., 2020; Zambrano et al., 2020). In addition, due to the rugged topography and remote nature of some West African forests, the intensity of impact from human activities on the ecosystem may vary depending on the accessibility of these forests to people (Asuk et al., 2023). As such, whether similar patterns to those observed by Asuk et al. (2023) in Oban Forest, Nigeria, hold at larger, regional and international scales remains unclear.

Here, we use plot data from eight National Parks and Forest Reserves across Nigeria and Cameroon, which have continuous forests with varied human access and elevational variability and include some

of the most diverse forests on the continent, to test the effect of low-intensity human impacts on spatial beta-diversity at a regional scale. We focus on the Nigeria-Cameroon region, a system that is threatened and poorly researched, yet remains one of the most culturally and biologically diverse forest regions in tropical Africa (Fotang, Bröring, Roos, Enoguanbhor, Abwe, et al., 2021; Fotang, Bröring, Roos, Enoguanbhor, Dutton, et al., 2021). The forests where our plots were established have been exposed to varied intensities of human activities, ranging from farming, logging, fire, and gathering non-timber forest products before they were made National Parks and Reserves (Choury et al., 2022; Funoh, 2014; Owono, 2001; Rainforest Foundation UK, 2016). Despite the creation of National Parks, these forests still face immense pressure from the inhabitants of hundreds of villages that rely on the forest for their livelihoods, thus impacting the forest in different ways.

The pressure on forest resources for human livelihoods, in combination with other variables such as forest composition, climate variables, elevation and other plot-level variables, contributes to the process of environmental filtering, and thus the signal of such pressure is potentially visible in spatial patterns of tree species assemblage composition (Adnan et al., 2015; Asuk et al., 2023; Malizia et al., 2020; Verrico et al., 2020; Yano et al., 2021). In addition, variation in species composition across space is influenced by dispersal limitation (Mokany et al., 2022) imposed by geographical distance and barriers between plots, including water bodies, forest fragmentation by major roads, and the presence of human settlements (Abiem et al., 2022; He et al., 2020; Wayman et al., 2021; Yang et al., 2015; Zahawi et al., 2021). To explore dissimilarity in species composition between forest plots in the Nigeria-Cameroon region, a beta-diversity framework was used to evaluate the impact of low-intensity anthropogenic activities, climatic variables (temperature and precipitation) and other plot-based variables on the composition of tree assemblages in tropical West Africa. Across all plots in our regional dataset, tree species were categorised into edible (produce seeds and fruits eaten by humans) and inedible (not eaten by humans) species. Spatial beta-diversity was then calculated for the different species groups, with the drivers of beta-diversity identified using generalised dissimilarity modelling. These analyses were used to test the following hypotheses: (1) environmental

filtering due to plot-level predictors (forest composition, climate, human influence, elevation and stem density) has a higher impact on tree species assemblages in the region than dispersal limitation, (2) human influence (measured as the distance to the closest human presence (DCHP) and the distance to the nearest anthropogenic edge (DNAE)) significantly impacts the spatial beta-diversity of forest trees at a regional scale, and (3) the predictors of spatial beta diversity will differ between edible and inedible species.

2. METHODS

2.1. Plot location and human population demographics

The plots used for the study were spread across eight National Parks and Forest Reserves in Nigeria and Cameroon (see Appendix S1, Table S1). For all reserves, there are villages in proximity to the forest that rely on the forest for their livelihoods, with farming as one of the main occupations. Oban Division of Cross River National Park, located in Nigeria, has a lowland rainforest ecosystem with thirty-nine villages and an estimated human population of 40,000 (Asuk et al., 2023; UNESCO World Heritage Centre, 2020). Takamanda National Park has thirty-two support zone communities with a total of 28,000 inhabitants and, according to the Wildlife Conservation Society (WCS), 12,000 of these directly affect the Park (Ndobe & Mantzel, 2014). The Campo Ma'an Reserve has a moist equatorial forest located in the centre of the forest belt that extends from Cross River (Nigeria), Mayombe Region (Congo and Gabon) and covers a part of South-west Equatorial Guinea with an estimated population of about 300,000 people (Owono, 2001). Deng Deng National Park has about sixteen villages with an estimated population of 1,300 inhabitants in proximity to the forest (Diangha, 2015). Dja Faunal Reserve has about thirty-seven villages with 3000 people living in the reserve and surrounding the reserve along boundary roads, an additional population of about 22,500 people (1.5 people per square kilometre) directly impacting the forest (International Union for Conservation of Nature, 2017; Nguiffo, 2001). Mbam Djerem National Park has about seventy-four forest-dependent villages with an estimated population of 30,000 people who rely on the forest resources for their livelihood (Wildlife Conservation Society, 2021). Ngoyla has about 13,000 inhabitants (Funoh,

2014). Nguti forest has an estimated population of 20,060 people in about fifty-four villages (Rainforest Foundation UK, 2016).

2.2. Plot and species composition data

The study was carried out using tree data (min 10 cm DBH) from long-term plots established in the tropical forests of Nigeria and Cameroon, bordering countries in West and West-Central Africa, respectively (Figure 1). The forests of both countries are contiguous via their common borders (Enuoh & Ogogo, 2018; Nigerian National Park Service, 2019). 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 by the lead author (Asuk et al., 2022, 2023) and a further 61 plots established in Nigeria and Cameroon by colleagues, accessed via the ForestPlots.net database (ForestPlots.net et al., 2021; Lopez-Gonzalez et al., 2009). The selected plots in Cameroon all measured 100 x 100m except for one that measured 40 x 100m (see Appendix S1, Table S2). The plots in Nigeria were smaller than those in Cameroon, measuring 40m x 120m (see Appendix S1, Table S2).

The associated plot metadata included information on elevation, average plot slope, longitude, latitude, stem density, forest status and composition. Elevation above mean sea level was recorded during field inventories. The average slope of plots was measured at 20 m distance and scaled into five 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) slope. Geographical data consisted of information on longitude and latitude in metres (UTM) at the centre of the plots, collected during forest inventories (used to measure geographical distance between plots). Stem density (the number of living individual tree stems per hectare) was generated by counting the number of stems in each plot with a minimum DBH of 10 cm. The forest composition in each plot was classified as either mixed (44 plots) or monodominant (12 plots) following ForestPlots.net protocols for vegetation and compositional data (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).

2.2.1. 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 by selecting plots that were more similar in size. Data from the last three censuses collected between 2002 and 2019 were filtered from the multiple census tree data for the study. Only plots that fell between 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 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 sixty-six 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.

2.3. Species categorisation

Tree species were categorised into those with fruits, nuts and seeds that are edible to humans, and all other species were classified as inedible. The categorisation 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 utilisation of tree species collected from online databases between December 2021 and February 2022. These online databases included Useful Tropical Plants database (https://tropical.theferns.info/), the PlantUse database (https://uses.plantnet-project.org/en/), the Royal Botanical 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.

2.4. 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 (e.g., farm, settlement, construction, but excluding footpaths) at the time of the census. Information on the nearest anthropogenic edge was available for the plots in the Oban Division dataset, but for only a few other plots in the forestplots.net dataset. For plots without this information, OpenStreetMap and Google Earth were used to approximate a straight-line distance from the GPS location of the centre of each plot to the nearest sign of anthropogenic edge, and to assess historical maps. OpenStreetMap is a community map with contributions from areas where data are missing in other online maps and has been used frequently in science and research (Grinberger et al., 2022; Sehra et al., 2013; Zhou et al., 2022). 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. The 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 measurement was taken (see Figures 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.

2.5. Precipitation and Temperature Data Collection

The study utilised 5 km resolution Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) daily precipitation data (version 2.0; Funk et al., 2015) to generate mean yearly

precipitation data for each plot. CHIRPS is considered a reliable source for studying precipitation trends in tropical Africa (Didi Sacré Regis et al., 2020; Dinku et al., 2018; Paredes-Trejo et al., 2020). Maximum surface temperature data were generated from TerraClimate monthly temperature data with a 4 km resolution (Abatzoglou et al., 2018). Maximum temperature was used because of the known resilience of Afrotropical forests to recent temperature increases (Doughty et al., 2023; Hubau et al., 2020). These monthly data were aggregated into yearly means for the study.

2.6. Data analysis

Data analysis involved three main steps: the generation of a tree species presence-absence matrix for each plot, the calculation of Sørensen's pairwise beta-diversity between plots, and the use of Generalised Dissimilarity Models (GDMs) to identify variables that drive spatial beta-diversity. Overall beta-diversity (i.e., Sørensen's dissimilarity) was partitioned into turnover, to assess compositional shifts due to species replacement between plots, and nestedness-resultant dissimilarity (herein 'nestedness') to assess if species-poor plots are nested subsets of species-rich plots (Ferrier et al., 2007). Predictor variable distribution plots, Spearman's correlation between predictor variables, and Mantel correlations between other predictor variables and geographic distance were computed (see Figures S3 to S5 in Appendix S3). All analyses were completed using R (R Core Team, 2022).

2.6.1 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).

2.6.2 Generalised Dissimilarity Models (GDM)

GDMs and deviance partitioning are valuable tools for disentangling what proportion of variation in dissimilarity between communities is due purely to the effect of distance between the communities, what proportion is explained uniquely by environmental gradients (plot-level variables including climatic and anthropogenic variables), and what proportion of deviance is shared between the two (Buzatti et al., 2019; He et al., 2020; Guerin et al., 2021; Ferrier et al., 2007). The "gdm" R package (Ferrier et al., 2007; Mokany et al., 2022) was used to fit the GDMs by modelling a measure of the compositional difference between plots (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. The environmental (climatic, anthropogenic, and ecological) variables included elevation (masl), stem density (stems/hectare), nearest anthropogenic edge (m), human presence (m), forest composition, total precipitation (mm/year), and maximum temperature (°C). Geographic distance (m) was also included as a predictor. GDMs utilise the pairwise dissimilarity 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 plot 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 plots 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, precipitation, and temperature), plot-level variables (stem density 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 (randomly shuffling the values of each predictor variable across the 66 plots) and a backwards selection approach, allowing the calculation of variable significance and variable importance (applied using the function 'gdm.varImp' within the 'gdm' package (Ferrier et al., 2007; Mokany et al., 2022)). This approach first fits a model using all the unpermuted predictor variables. The row containing a given predictor variable is 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 predictor in turn, whilst holding the others constant, to calculate importance scores and significance for each one. The least significant predictor is then dropped, and the permutation procedure is repeated with the remaining predictors until a model is found where all those remaining are significant ($p < 0.05$). The predictor importance for each variable was calculated from the percent change in deviance explained between the unpermuted and permuted models for that variable (Ferrier et al., 2007; Mokany et al., 2022). The variable (predictor) importance measures the influence of a variable in explaining changes in the response variable. The variable importance was then used to compute the absolute importance, which is a percentage-based measure of how much each predictor variable contributes to the total variation in beta-diversity explained by the model.

Geographical distance (the Euclidean distance between plots based on the x and y coordinates) was included as a predictor to account for the likelihood of effects of distance on plot-pairwise dissimilarity due to dispersal limitation (Mokany et al., 2022). However, the dissimilarity driven by environmental gradients could be suppressed or wrapped up in the dissimilarity from the distance between plots, leading to the deviance explained by each to be shared. Therefore, four models were fitted for each response: Model 1 (full model containing all significant predictor variables), Model 2 (containing only geographical distance), Model 3 (only environmental and human predictors that were significant from Model 1), and Model 4 (only significant human predictors from Model 1; see Table 2). Models 2–4 were used to calculate the shared amount of deviance explained between the geographical distance and the environmental predictors. Because Models 2 and 3 were made up of

significant predictors from Model 1, they were not used to compute variable importance. The shared deviance between the environmental predictors and geographical distance was generated using the formula (Ray-Mukherjee et al., 2014):

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

where V_s is the shared deviance explained between the environmental and geographical variables, V_{full} is the total deviance explained by the model (model 1), V_g is the deviance explained by the model containing only geographical variables (model 2), and V_e is the deviance explained by the environmental model only (either model 3 or model 4).

3. RESULTS

3.1. Regional taxonomic beta-diversity, turnover and nestedness

Among the 66 plots, a total of 28,299 individual trees were sampled with total (gamma) diversity of 708 species (including 157 morphospecies) from 316 genera. 236 of these species were classified as edible to humans, and 472 species as inedible, with 11,097 and 17,202 stems respectively (Table S4 in Appendix S4). The mean total pairwise beta-diversity between plots 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. 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) accounted for 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 (0.08 ± 0.08). In addition to nestedness representing a low proportion of overall dissimilarity (Figure 2), no explanatory variables significantly explained variation in the GDMs with nestedness as a response, and, therefore, the metric and associated models were excluded from further discussion.

3.2. GDM results

As expected, Model 1 (a combination of geographical distance, environmental variables, and human variables) had the highest deviance explained, with 46.7%, 41.0% and 25.9% 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 deviance explained in turnover (species replacement) for the inedible, all and edible species groups with 47.9%, 43.5% and 27.7% (Table 1). Model 3 (models run with environmental and human predictors only) recorded the second highest deviance explained for total beta-diversity with 37.4%, 31.4%, and 18.9% (all, edible, inedible species groups, respectively), while the deviance explained in total beta-diversity for Model 2 (models run with only geographical distance as predictor) was 18.3%, 17.4%, and 13.2% for all, inedible and edible species groups respectively (see Table 1). Finally, the deviance explained for total beta-diversity recorded in Model 4 (only human variables) was 18.0%, 13.4%, and 7.24% in all, inedible and edible species. However, Model 4 had a higher deviance explained for turnover in inedible species than Model 2. In some cases, half of the deviance explained by environmental variables alone (Model 3) is tied up with distance (Model 2), with percentages of shared deviance ranging from 9.0%, 7.8%, and 6.2% for dissimilarity due to total beta-diversity to 9.5%, 5.8%, and 4.2% for dissimilarity due to turnover in all, inedible, and edible species groups, respectively (see Table 1).

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 included (including temperature and precipitation) 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 2), geographical distance (with an absolute importance of 24.73%), elevation (21.58%), DCHP (20.15%), forest composition (18.42%), and stem density (15.11%) were significant predictors of total beta-diversity. Geographical distance, the variable with

the highest importance in three of the six models (total beta-diversity for all and inedible species and turnover in edible species), showed a rising trend up to 200-300 km before levelling off (Figure 3a,f,h). The I-spline for elevation, the second most important variable, increased gently up to 500-700 m, then sharply increased after that point (Figure 3b,g,j). The I-spline for DCHP, the third key predictor, had a slight initial rise followed by a steady increase (Figure 3c). Forest composition had a minor yet significant linear relationship with beta-diversity (Figure 3d,k), while stem density within plots had the lowest variable importance values (Table 2, Figure S6 in Appendix S5). The turnover model identified DCHP (30.49%), elevation (28.59%), geographical distance (22.65%), stem density (10.74%) and DNAE (7.53%) as significant predictors, with trends similar to those in the total beta-diversity model (Figure 4a, Tables 1 and Figure S7 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 rug plot on the x-axis in Figure 3a, Figure 4a,h and Figure S4).

Table 1. Results from the GDMs analysing the dissimilarity in species composition between forest plots and the deviance explained (DE) by each model in percentages. "Total" refers to total Sørensen's beta-diversity while "Turn" refers to the Simpson's turnover partition of beta-diversity. Shared deviance (%) was calculated from the deviance explained by the full model, the geographical distance only model, and the environment only model. Model 1 (all significant predictor variables; see Table 2) was partitioned into Model 2 (only geographical distance), Model 3 (only significant environmental and human predictors from Model 1), and Model 4 (only significant human predictors from Model 1; see Table 2). Models 2 and 3 were only used to calculate the shared amount of deviance explained. Rows in bold show the percentage deviance explained for the models.

Groups	**All**		**Edible**		**Inedible**	
	Total	**Turn**	**Total**	**Turn**	**Total**	**Turn**
Model 1 (*DE* %)	**46.73**	**47.91**	**25.89**	**27.74**	**41.01**	**43.45**
GDM Deviance	93.86	113.58	170.63	208.1	112.2	142.2
Null/Predicted Deviance	176.20	218.03	230.25	287.99	190.19	251.47
Intercept	0.62	0.41	0.74	0.42	0.66	0.48
Model 2 (*DE* %)	**18.26**	**17.3**	**13.22**	**13.19**	**17.38**	**15.54**
Model 3 (*DE* %)	**37.43**	**40.09**	**18.88**	**18.75**	**31.43**	**33.70**
Shared Deviance (Model 3 and 2 in %)	*8.96*	*9.48*	*6.21*	*4.20*	*7.80*	*5.79*
Model 4 (*DE* %)	**17.95**	**14.88**	**7.24**	**13.22**	**13.36**	**17.55**
Shared Deviance (Model 4 and 2 in %)	*4.11*	*1.28*	2.55	*3.18*	*1.49*	*1.48*
GDM Deviance	144.56	185.59	189.01	221.1	164.78	207.33
Intercept	1.02	0.93	0.77	0.46	1.18	0.91

Table 2. Results from the GDMs showing variable importance from Model 1 (all significant predictor variables) and Model 4 (only human predictors from Model 1). Variable importance is the percentage change in deviance explained between the unpermuted and permuted models for that variable, while absolute importance is the percentage of the explained deviance that each variable contributed to the GDM model. "Total" refers to total Sørensen's beta-diversity while "Turn" refers to the Simpson's turnover partition of beta-diversity. DNAE is the ground distance of plots to the nearest anthropogenic edge. DCHP is the ground distance to the closest human presence to each plot. "m" is the ground distance measured in metres. Values within brackets are the absolute importance of each variable in relation to other variables. Dashed lines indicate where variables were non-significant within models.

Groups	**All**		**Edible**		**Inedible**	
	Total	**Turn**	**Total**	**Turn**	**Total**	**Turn**
Variable importance (*Absolute importance*) – Model 1						
Geographical distance (m)	19.89 *(24.73)*	16.31 *(22.65)*	27.05 *(32.82)*	32.39 *(37.20)*	23.31 *(30.26)*	22.42 *(29.58)*
Elevation (masl)	17.36 *(21.58)*	20.58 *(28.59)*	18.51 *(22.46)*	-	21.39 *(27.78)*	27.04 *(35.67)*
Stem density (stems/ha)	12.16 *(15.11)*	7.73 *(10.74)*	-	15.47 *(17.77)*	-	-
DNAE (m)	-	5.42 *(7.53)*	-	15.08 *(17.33)*	-	-
DCHP (m)	16.21 *(20.15)*	21.95 *(30.49)*	-	24.12 *(27.70)*	22.11 *(28.71)*	26.35 *(34.76)*
Forest composition	14.82 *(18.42)*	-	36.86 *(44.72)*	-	10.20 *(13.25)*	-
Temperature	-	-	-	-	-	-
Precipitation	-	-	-	-	-	-
Variable importance (*Absolute importance*) – Model 4						
Geographical distance (m)	40.02 *(50.82)*	51.804 *(54.52)*	59.56 *(70.74)*	43.00 *(50.63)*	54.29 *(57.67)*	44.44 *(47.08)*
DNAE (m)	15.62 *(18.04)*	-	24.64 *(29.26)*	15.33 *(18.05)*	-	-
DCHP (m)	26.99 *(31.15)*	43.21 *(45.48)*	-	26.59 *(31.31)*	39.85 *(42.33)*	49.96 *(52.92)*

Edible species models

For the edible species model (Figures 4e,f,g), total beta-diversity was significantly influenced by forest composition (44.72%), geographical distance (32.82%), and elevation (22.46%), in order of decreasing variable importance (Table 2 and Figure 3). The I-splines indicated that the relationship between forest composition and total beta-diversity exhibited a slight linear trend (Figure 3d), geographical distance had an initial steep linear trend that then plateaued, while stem density had a steeper linear trend (Figure 3e,f,g). The turnover resultant beta-diversity of edible species was driven by four significant variables: geographical distance (highest absolute variable importance score – 37.2%), DCHP (27.7%), stem density (17.8%), DNAE (lowest variable importance score – 17.3%)

(Table 2 and Figure 4e,f,g,h). The I-splines indicated that the relationship between geographical distance and turnover had an initial steep linear trend that then remained constant at the peak (Figure 4i), just as seen in turnover total beta-diversity. The turnover I-spline for DCHP exhibited a very steep initial increase, followed by a continuous linear increase (Figure 4f), while for stem density it increased gently then plateaued between 400 to 500 stems per hectare before increasing again (Figure 4g), and for DNAE it exhibited a positive roughly linear relationship (Figure 4h). 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 4f).

Inedible species models

The model for total beta-diversity using the inedible species data included four significant predictors: geographic distance, which had the highest variable importance value (contributing absolute importance of 30.26% to the total explained deviance in the GDM model.), DCHP (28.71%), elevation (27.78%) and forest composition (13.25%) (Table 1). The effects of geographical distance on total beta-diversity increased (based on the I-splines) with a steep linear trend and then remained constant at its peak (Figure 3h). The I-spline for DCHP exhibited a very steep initial increase followed by a continuous linear increase (Figure 3i), while for elevation it showed a gentle trend that levelled off at about 600m followed by a sharp continuous increase (Figure 3j), and for forest composition it had a minor yet significant linear relationship (Figure 3k). Inedible turnover resultant beta-diversity models showed that elevation had the highest variable importance value, contributing 35.67% to the model deviance, followed by DCHP (34.76%), and geographical distance (29.58%). The total beta-diversity models for edible and inedible species had three significant variables in common (geographical distance, elevation, and forest composition). While there were differences in the relative ranking of variables based on variable importance values, the maximum I-spline values for these variables were higher when using the inedible species data than when using the edible data.

4. DISCUSSION

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

The dissimilarity in tree species composition observed in the Nigeria-Cameroon forest region was primarily due to species replacement between plots, which was driven by geographical distance, elevation, human influence (relatively low and high intensity impacts), forest composition, and stem density. Geographic distance had the largest variable importance score for total beta-diversity in all and inedible species and turnover in edible species, and there was low shared explanatory power between distance and environment in the relevant model. This result indicates that dispersal limitation plays a strong role in driving the spatial beta-diversity patterns observed in the region. This dispersal limitation could be due to the possible impact of natural geographical barriers such as water bodies, or a result of fragmentation by large roads and human settlements, driving turnover in species composition (Abiem et al., 2022; He et al., 2020; Wayman et al., 2021; Yang et al., 2015; Zahawi et al., 2021).

Elevation, DCHP, and forest composition were also important variables explaining turnover in inedible and edible species. Elevation plays a crucial role in driving the composition of tree species assemblages, exerting varying niche-based effects on species due to changes in climate, wind, soil, the identity of seed dispersers, and the activities of humans along the elevational gradient, all of which could result in strong environmental filtering and the replacement of species (Adnan et al., 2015; Asuk et al., 2023; Malizia et al., 2020; Verrico et al., 2020; Yano et al., 2021).

The effects of plot-specific variables resulted in a large proportion of the model deviance being explained by environmental filtering, a finding that has also been reported in studies of a wetland nature reserve in China, a montane forest in North America, and a tropical island in South China (He et al., 2020; Jiang et al., 2021; Verrico et al., 2020). The impact of environmental filtering on the tree species community composition in the Nigeria-Cameroon region was further evidenced through higher explained deviance in the models with environmental variables alone (Model 3) compared to that explained by geographical distance solely (Model 2) or by only the human predictors (Model 4). A similar study in the Cuitzeo basin, Mexico, revealed that environmental heterogeneity has a greater

impact on spatial beta-diversity, due to niche-based processes, than geographical distance (Vega et al., 2020). Other work has shown that environmental heterogeneity can explain why turnover has greater effects on beta-diversity than nestedness (Ferenčík et al., 2024), as we observed here.

Climate variables (precipitation and max temperature) may theoretically also contribute to environmental filtering effects, despite not being significant individual predictors of beta-diversity in the Nigeria-Cameroon region. While He et al. (2020) reported that the difference in regional tree species composition can be driven by spatial variation in climate, Bennett et al (2023) showed that protected Afrotropical forests are less sensitive to fluctuations in climate variables compared to forests in the Amazon.

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

The indicators of human influence (DCHP and DNAE used in Model 4) were significant drivers of patterns of spatial beta-diversity in the region. The percentage of deviance in the GDMs explained by human influence (Model 4) was higher than geographic distance for the turnover models for both inedible and edible species. Collectively, human influence had higher variable importance values for the turnover models for all species (38%) and edible species (45%), while for inedible species, DCHP was the second most important variable in both the total beta-diversity (22%) and turnover (26%) models. In addition, the variable importance values observed for DCHP across the groups (All, Edible and Inedible) suggest possible modification of the forest due to the ecological legacies from humans that live in close proximity to the forest plots (Adnan et al., 2015; Asuk et al., 2023; Singh et al., 2022). Indigenous human communities, some of whom have historically transitioned from a nomadic lifestyle to stable settlements near or within forests (Asuk et al., 2023; Adnan et al., 2015), can transform the forest through forest resource utilisation, leaving footprints visible in the tree species assemblages (Jaeger et al., 2022; Lueder et al., 2022; Williams et al., 2020). There are about 250 forest-dependent villages that are culturally and spiritually connected to the Nigeria-Cameroon forest region studied here (Diangha, 2015; Funoh, 2014; Nguiffo, 2001; Owono, 2001; UNESCO World Heritage Centre, 2020; Wildlife Conservation Society, 2021), and the interaction of the villages'

inhabitants with the forest is linked to practices such as medicinal use, land management, food foraging, wildcrafting, and conservation traditions (Falconer, 1993; FAO, 1999). In addition, there has also been a historical shift in the region from sustainable, small-scale agricultural and logging practices to large-scale plantation farming (like cocoa plantations) and extensive commercial logging, which has likely impacted forest ecosystems to varying degrees (FAO, 1999; Fongnzossie et al., 2020). The different uses of forests and individual tree species can result in different impacts on tree species composition in different places, which explains why human influence is an important driver of spatial beta-diversity (Asuk et al., 2023; Ellis et al., 2021; C. N. H. McMichael, 2021; Piperno et al., 2015).

4.3. Predictors of the beta-diversity of edible and inedible species.

The identity and strength of effect of variables driving differences in species composition in the region differed between edible and inedible species. These observed differences could be attributed to the history and frequency of forest disturbance, successional processes, varying distances of plots from high-intensity and low-intensity human activities, and differences in topography, climate, and soil conditions (Williams et al., 2020; Fotang et al., 2021c; Yuan et al., 2022; Asuk et al., 2023). While low-intensity human influence (DCHP) had a higher impact on inedible species (34.8% and 28.7% absolute importance in turnover and total beta-diversity) than edible species (27.7% absolute importance), high-intensity human activities (DNAE - distance to nearest anthropogenic edge) such as logging, agricultural expansion and other large-scale disturbance was a more important driver of the turnover of edible species. However, no effect of human activities was observed on the total beta-diversity of edible species, and elevation was not a driver of the turnover of edible species.

A previous study in one of the areas in the region analysed here that used elevation as a proxy for the level of human impact (where local villages were located at low elevations) found a positive relationship between turnover and elevation for inedible species, which was not apparent for edible species (Asuk et al., 2023), the implication being that humans are spreading the seeds of the edible species along the elevational gradient, reducing turnover The non-significant influence of human

predictors on total beta-diversity, and elevation on the turnover of edible species compared to that of inedible species, observed in this study, partly align with these previous findings. (Asuk et al., 2023) More broadly, the results from the present study corroborate previous studies that showed that human activities, including logging, agricultural expansion, and harvesting for livelihoods (like firewood and other non-timber forest products), significantly alter species composition in African tropical forests (Assede et al., 2023; Asuk et al., 2023; Auliz-Ortiz et al., 2024; Hussein, 2023).

Forest composition (mixed or monodominant forest) was a significant predictor of the total beta-diversity of edible species, having the highest variable importance score for this model, but was a less important driver of the beta-diversity of inedible species. In addition, stem density was only a predictor of the turnover of edible species. Monodominant forests are characterised by one single species making up more than 60% of the tree canopy, and this condition could be due to coppicing (sprout or regrowth formed at the tree base or root), the presence of fast-growing species, or edaphic factors (ter Steege et al., 2019). *Gilbertiodendron dewevrei* (De Wild.) J.Léonard, a dominant inedible timber species in the Cameroon region (Heimpel et al., 2024), made up 68 to 87% of all trees in nine plots and 43 to 56% in three additional plots. More broadly, one (inedible) species dominated the plots in up to twelve locations (FAO, 1999; Hundera, 2007; Klein et al., 2003; Shiembo et al., 1996). Therefore, the differences in predictors of the beta-diversity of edible and inedible species could be attributed to higher stem density and dominance in inedible species, leading to high inter-specific competition for space and an increase in the dissimilarity observed in edible species. For example, a dominant inedible species like *Gilbertiodendron dewevrei* could reduce the number of edible species within the plot, causing greater spatial turnover.

Stem density being a non-significant predictor in the inedible species models may be due to the influence of other ecological and human factors influencing the community composition of inedible species, such as greater adaptability and ability to survive in smaller, isolated habitats, or possibly due to human uses that are not linked to being edible, e.g., for medicine and gum (Bailey et al., 2010; de Lima Filho et al., 2021; Fahrig, 2003).

Comparing the results of this study with those of Asuk et al. (2023) indicates that the factors driving the beta-diversity of inedible species are similar at both local and regional scales in West African tropical forests, while there are differences in regards to the beta-diversity of edible species. Findings from other studies in the Amazon, that have suggested that the selection and stewardship of desired tree species by indigenous human populations over time could leave strong imprints on patterns of forest composition, and that such impacts may vary across regions (Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022). Some of the primary species favoured by local communities for their food and trade value in the region include African Walnut (*Coula edulis* Baill), Bush Mango (*Irvingia spp.*), Kola Nut (*Cola spp.*), Baobab (*Adansonia digitata* L.), African Bush Mango (*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill), Safou (*Dacryodes edulis* (G. Don.) H. J. Lam), African Breadfruit (*Treculia africana* Decne. ex Trécul), Bitter Kola (*Garcinia kola* Heckel), African Star Apple (*Chrysophyllum albidum* G. Don), and Monkey Kola (*Cola lepidota* K. Schum. and *Cola pachycarpa* K. Schum.) (FAO, 1999; Fongnzossie et al., 2020; Hundera, 2007; Klein et al., 2003; Shiembo et al., 1996). However, the utilisation of these species can vary across the cultures in the region.

4.4. Study limitations

Understanding the impact of human influence on tree species dissimilarity in the Nigeria-Cameroon forest region using this dataset presents significant challenges. The lack of historical data on how long-term human impacts have shaped current forest structure and species composition limited the conclusions that could be drawn in terms of human impacts. In particular, the proxies for human activities from OpenStreetMap and Google Earth, combined with the lack of data on changes in human impacts through time, could result in an incomplete understanding of the historical drivers of spatial beta-diversity. The plot dataset lacked systematic sampling in space, particularly across key variables such as DCHP (Distance to Closest Human Population) and DNAE (Distance to Nearest Agricultural Expansion), making relatively small numbers of plots responsible for the strong gradients observed in the I-splines. This means that the attribution of a large role of DCHP must be

considered with some caution; however, it should be noted that even without these few data points above (Figures 3 and 4), the response shape was also positive across the narrower DCHP range.

The available data from plots that fit the selection criteria were constrained in terms of the spatial and temporal scope, with single census data collected from a limited number of plots between 2002 and 2019. This limitation hindered the observation of long-term trends and changes in species composition and human influence, potentially not fully representing broader regional patterns.

While the study provides valuable insights, these limitations could impact the precision of inferences regarding past human impacts on tree species composition, as well as the spatial and temporal dynamics of tree species dissimilarity. Addressing these limitations in future research is essential for a more accurate and comprehensive understanding of human impacts on forest ecosystems.

5. CONCLUSION

Tree species dissimilarity in the Nigeria-Cameroon forest was primarily driven by the interplay between dispersal limitation, environmental filtering, and human influence. Environmental filtering due to plot-specific predictors had a greater impact on tree species assemblages than geographical distance, thus supporting the hypothesis that localised plot-specific conditions such as elevation, stem density, forest composition and, to some extent, climate exert a stronger influence on species turnover (with higher explanatory power) than geographical distance alone (Asuk et al., 2023; He et al., 2020). However, climate variables (temperature and precipitation) did not have an independent effect on tree species assemblage composition in the region.

Human influence significantly impacted tree species assemblage composition in the study area, with distinct impacts on edible and inedible species. While both low- and high-impact human activities shaped the regional turnover of edible species, only low-intensity use contributed to the total beta-diversity and turnover of edible species. This supported the notion that human proximity to forests alters species assemblages, potentially through foraging, seed dispersal, and selective harvesting. Elevation, by contrast, was the most important variable responsible for the turnover of inedible species and did not impact the turnover of edible species, likely due to the restriction of high-impact

activities like logging to lower elevations, while low-impact activities such as food gathering for seeds and fruits occurring across a wider elevational gradient (Asuk et al., 2023; Levis et al., 2017). Additionally, forest composition (mixed or monodominant forest) significantly influenced beta-diversity in edible species only, possibly due to the monodominance of inedible species such as *Gilbertiodendron dewevrei* in several plots.

Despite the aforementioned study limitation, our findings suggest that humans are not just agents of deforestation but also active participants in shaping forest diversity in the Nigeria-Cameroon forest region. Their varied use of tree species for food, materials, and other livelihoods can differentially influence species turnover, particularly in edible species, and interact with environmental filtering and geographic constraints to shape patterns of beta-diversity across the landscape. Conservation strategies should evolve from simplistic preservationist models to integrated strategies like community-managed food forests that use traditional knowledge, recognise the ecological impacts of seemingly low-impact human activities, and support sustainable land use for lasting forest resilience. Further research is needed to fully understand the long-term effects of anthropogenic disturbance on forest composition in Afrotropical ecosystems, and tropical forests more widely.

REFERENCES

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data*, *5*. https://doi.org/10.1038/sdata.2017.191

Abiem, I., Dickie, I., Kenfack, D., & Chapman, H. M. (2023). Factors limiting plant recruitment in a tropical Afromontane Forest. *Biotropica*, *55*(1), 221–231. https://doi.org/10.1111/btp.13179

Adeyemi, A. A. (2016). Site quality assessment and allometric models for tree species in the Oban Forest, Nigeria. *Journal of Sustainable Forestry*, *35*(4), 280–298. https://doi.org/10.1080/10549811.2016.1168306

Adnan, M., Tariq, A., & Shinwari, Z. K. (2015). Effects of human proximity and nomadic grazing on the diversity of medicinal plants in temperate hindukush. *Pakistan Journal of Botany*, *47*(1), 149–157.

Agaldo, J. A., Gwom, T. G., & Apeverga, P. T. (2016). An assessment of present threats and associated conservation implication to the Oban division Forest Cross river national park; Nigeria's biodiversity hotspot. *Ethiopian Journal of Environmental Studies and Management*, *9*(2), 938–950. https://doi.org/10.4314/ejesm.v9i2.1S

Aigbe, H. I., & Omokhua, G. E. (2015). Tree Species Composition and Diversity in Oban Forest Reserve, Nigeria. *Journal of Agricultural Studies*, *3*(1), 10. https://doi.org/10.5296/jas.v3i1.6461

Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M. M., Bolpagni, R., Bove, C. P., Chambers, P. A., Chappuis, E., Clayton, J., de Winton, M., Ecke, F., Gacia, E., Gecheva, G., Grillas, P., Hauxwell, J., Hellsten, S., Hjort, J., Hoyer, M. V., … Heino, J. (2017). Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *Journal of Biogeography*, *44*(8), 1758–1769. https://doi.org/10.1111/jbi.12978

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Artaxo, P., Christen Hansson, H., Augusto MachadoID, L. T., & RizzoID, L. V. (2022). Tropical forests are crucial in regulating the climate on Earth. *PLOS Climate*, *1*(8), e0000054. https://doi.org/10.1371/JOURNAL.PCLM.0000054

Aspin, T. W. H., Matthews, T. J., Khamis, K., Milner, A. M., Wang, Z., O'Callaghan, M. J., & Ledger, M. E. (2018). Drought intensification drives turnover of structure and function in stream invertebrate communities. *Ecography*, *41*(12), 1992–2004. https://doi.org/10.1111/ecog.03711

Assede, E. S. P., Orou, H., Samadori, ·, Biaou, S. H., Coert, ·, Geldenhuys, J., Fiacre, ·, Ahononga, C., Paxie, ·, & Chirwa, W. (2023). Understanding Drivers of Land Use and Land Cover Change in Africa: A Review. *Current Landscape Ecology Reports 2023 8:2*, *8*(2), 62–72. https://doi.org/10.1007/S40823-023-00087-W

Asuk, S. A., Matthews, T. J., Sadler, J. P., Pugh, T. A. M., Ebu, V. T., Ifebueme, N. M., & Kettridge, N. (2023). Impact of human foraging on tree diversity, composition, and abundance in a tropical rainforest. *Biotropica*, *55*(1), 232–245. https://doi.org/10.1111/btp.13180

Asuk, S. A., Matthews, T. J., Sadler, J. P., Pugh, T. A. M., Ebu, V. T., & Kettridge, N. (2022). *Plot Data from Tree Species Inventory in a Nigerian Rainforest v1.1.0*. https://doi.org/10.5281/ZENODO.7082996

Auliz-Ortiz, D. M., Benítez-Malvido, J., Arroyo-Rodríguez, V., Dirzo, R., Pérez-Farrera, M. Á., Luna-Reyes, R., Mendoza, E., Álvarez-Añorve, M. Y., Álvarez-Sánchez, J., Arias-Ataide, D. M., Ávila-Cabadilla, L. D., Botello, F., Braasch, M., Casas, A., Campos-Villanueva, D. Á., Cedeño-Vázquez, J. R., Chávez-Tovar, J. C., Coates, R., Dechnik-Vázquez, Y., … Martínez-Ramos, M. (2024). Underlying and proximate drivers of biodiversity changes in Mesoamerican biosphere reserves. *Proceedings of the National Academy of Sciences*, *121*(6), e2305944121. https://doi.org/10.1073/PNAS.2305944121

Bailey, D., Schmidt-Entling, M. H., Eberhart, P., Herrmann, J. D., Hofer, G., Kormann, U., & Herzog, F. (2010). Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology*, *47*(5), 1003–1013. https://doi.org/10.1111/j.1365-2664.2010.01858.x

Barnagaud, J. Y., Kissling, W. D., Tsirogiannis, C., Fisikopoulos, V., Villéger, S., Sekercioglu, C. H., & Svenning, J. C. (2017). Biogeographical, environmental and anthropogenic determinants of global patterns in bird taxonomic and trait turnover. *Global Ecology and Biogeography*, *26*(10), 1190–1200. https://doi.org/10.1111/GEB.12629

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*(12), 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., & Henriques-Silva, R. (2018). *Package 'Betapart': Partitioning Beta Diversity into Turnover and Nestedness Components*. R Package 1.5.1. http://www.pwrc.usgs.gov/BBS/

Benchimol, M., & Peres, C. A. (2013). Anthropogenic modulators of species-area relationships in Neotropical primates: A continental-scale analysis of fragmented forest landscapes. *Diversity and Distributions*, *19*(11), 1339–1352. https://doi.org/10.1111/ddi.12111

Bennett, A. C., Dargie, G. C., Cuni-Sanchez, A., Mukendi, J. T., Hubau, W., Mukinzi, J. M., Phillips, O. L., Malhi, Y., Sullivan, M. J. P., Cooper, D. L. M., Adu-Bredu, S., Affum-Baffoe, K., Amani, C. A., Banin, L. F., Beeckman, H., Begne, S. K., Bocko, Y. E., Boeckx, P., Bogaert, J., … Lewis, S. L. (2021). Resistance of African tropical forests to an extreme climate anomaly. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(21). https://doi.org/10.1073/PNAS.2003169118/FORMAT/EPUB

Bennett, A. C., Rodrigues de Sousa, T., Monteagudo-Mendoza, A., Esquivel-Muelbert, A., Morandi, P. S., Coelho de Souza, F., Castro, W., Duque, L. F., Flores Llampazo, G., Manoel dos Santos, R., Ramos, E., Vilanova Torre, E., Alvarez-Davila, E., Baker, T. R., Costa, F. R. C., Lewis, S. L., Marimon, B. S., Schietti, J., Burban, B., … Phillips, O. L. (2023). Sensitivity of South American tropical forests to an extreme climate anomaly. *Nature Climate Change 2023 13:9*, *13*(9), 967–974. https://doi.org/10.1038/s41558-023-01776-4

Biswas, S. R., & Mallik, A. U. (2010). Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology*, *91*(1), 28–35. https://doi.org/10.1890/08-0887.1

Biswas, S. R., & Mallik, A. U. (2011). Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere*, *2*(4). https://doi.org/10.1890/ES10-00206.1

Bousfield, C. G., Massam, M. R., Peres, C. A., & Edwards, D. P. (2023). Large-scale impacts of selective logging on canopy tree beta-diversity in the Brazilian Amazon. *Journal of Applied Ecology*, *60*(6), 1181–1193. https://doi.org/10.1111/1365-2664.14403

Bush, M. B., Mcmichael, C. H., Piperno, D. R., Silman, M. R., Barlow, J., Peres, C. A., Power, M., & Palace, M. W. (2015). Anthropogenic influence on Amazonian forests in pre-history: An ecological perspective. *Journal of Biogeography*, *42*(12), 2277–2288. https://doi.org/10.1111/jbi.12638

Buzatti, R. S. de O., Pfeilsticker, T. R., Muniz, A. C., Ellis, V. A., Souza, R. P. de, Lemos-Filho, J. P., & Lovato, M. B. (2019). Disentangling the Environmental Factors That Shape Genetic and Phenotypic Leaf Trait Variation in the Tree Qualea grandiflora Across the Brazilian Savanna. *Frontiers in Plant Science*, *10*(December), 1–14. https://doi.org/10.3389/fpls.2019.01580

Chaturvedi, R. K., Raghubanshi, A. S., Tomlinson, K. W., & Singh, J. S. (2017). Impacts of human disturbance in tropical dry forests increase with soil moisture stress. *Journal of Vegetation Science*, *28*(5), 997–1007. https://doi.org/10.1111/jvs.12547

Choury, Z., Wujeska-Klause, A., Bourne, A., Bown, N. P., Tjoelker, M. G., Medlyn, B. E., & Crous, K. Y. (2022). Tropical rainforest species have larger increases in temperature optima with warming than warm-temperate rainforest trees. *New Phytologist*, *234*(4), 1220–1236. https://doi.org/10.1111/nph.18077

Clement, C. R., Denevan, W. M., Heckenberger, M. J., Junqueira, A. B., Neves, E. G., Teixeira, W. G., & Woods, W. I. (2015). The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1812), 20150813. https://doi.org/10.1098/rspb.2015.0813

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núñez, P. V., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H. C., Losos, E., & Hubbell, S. P. (2002). Beta-diversity in tropical forest trees. *Science*, *295*(5555), 666–669. https://doi.org/10.1126/science.1066854

de Lima Filho, J. A., Vieira, R. J. A. G., de Souza, C. A. M., Ferreira, F. F., & de Oliveira, V. M. (2021). Effects of habitat fragmentation on biodiversity patterns of ecosystems with resource competition. *Physica A: Statistical Mechanics and Its Applications*, *564*, 125497. https://doi.org/10.1016/j.physa.2020.125497

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*(8), 1030–1040. https://doi.org/10.1111/J.1461-0248.2010.01493.X

Diangha, M. N. (2015). *The effects of habitat heterogeneity and human influences on the diversity, abundance, and distribution of large mammals: the case of Deng Deng National Park, Cameroon*. Brandenburg University of Technology.

Didi Sacré Regis, M., Mouhamed, L., Kouakou, K., Adeline, B., Arona, D., Saint, C. H. J., Claude, K. K. A., Jean, C. T. H., Salomon, O., & Issiaka, S. (2020). Using the CHIRPS Dataset to Investigate Historical Changes in Precipitation Extremes in West Africa. *Climate 2020, Vol. 8, Page 84*, *8*(7), 84. https://doi.org/10.3390/CLI8070084

Dinku, T., Funk, C., Peterson, P., Maidment, R., Tadesse, T., Gadain, H., & Ceccato, P. (2018). Validation of the CHIRPS satellite rainfall estimates over eastern Africa. *Quarterly Journal of the Royal Meteorological Society*, *144*, 292–312. https://doi.org/10.1002/QJ.3244

Donoso, I., García, D., Martínez, D., Tylianakis, J. M., & Stouffer, D. B. (2017). Complementary effects of species abundances and ecological neighborhood on the occurrence of fruit-frugivore interactions. *Frontiers in Ecology and Evolution*, *5*(NOV), 1–12. https://doi.org/10.3389/fevo.2017.00133

Doughty, C. E., Keany, J. M., Wiebe, B. C., Rey-Sanchez, C., Carter, K. R., Middleby, K. B., Cheesman, A. W., Goulden, M. L., da Rocha, H. R., Miller, S. D., Malhi, Y., Fauset, S., Gloor, E., Slot, M., Oliveras Menor, I., Crous, K. Y., Goldsmith, G. R., & Fisher, J. B. (2023). Tropical forests are approaching critical temperature thresholds. *Nature 2023 621:7977*, *621*(7977), 105–111. https://doi.org/10.1038/s41586-023-06391-z

Ellis, E. C., Gauthier, N., Goldewijk, K. K., Bird, R. B., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Rebecca Shaw, M., Stephens, L., Svenning, J. C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(17). https://doi.org/10.1073/pnas.2023483118

Elo, M., Alahuhta, J., Kanninen, A., Meissner, K. K., Seppälä, K., & Mönkkönen, M. (2018). Environmental characteristics and anthropogenic impact jointly modify aquatic macrophyte species diversity. *Frontiers in Plant Science*, *9*(August), 1–15. https://doi.org/10.3389/fpls.2018.01001

Enuoh, O. O. O., & Ogogo, A. U. (2018). Cross River National Park and Communities: Is Authoritarian Park Protection the Answer? *Journal of Sustainable Development*, *11*(5), 212. https://doi.org/10.5539/jsd.v11n5p212

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Https://Doi.Org/10.1146/Annurev.Ecolsys.34.011802.132419*, *34*, 487–515. https://doi.org/10.1146/ANNUREV.ECOLSYS.34.011802.132419

Falconer, J. (1993). THE CULTURAL AND SYMBOLIC IMPORTANCE OF FOREST RESOURCES. In C. R. S. Koppell (Ed.), *The Major Significance of 'Minor' Forest Products: The Local Use and Value of Forests in the West African Humid Forest Zone*. FAO. https://www.fao.org/3/t9450e/t9450e00.htm

FAO. (1999). *NON-WOOD FOREST PRODUCTS OF CENTRAL AFRICA: CURRENT RESEARCH ISSUES AND PROSPECTS FOR CONSERVATION AND DEVELOPMENT*. https://www.fao.org/3/x2161e/x2161e.pdf

Ferenčík, M., Hofmeister, J., Mikoláš, M., Buechling, A., Gloor, R., Kozák, D., Topercer, J., Pavlin, J., Petriţan, I. C., Bače, R., Dúhová, D., Frankovič, M., Janda, P., Kameniar, O., Markuljaková, K., Mejstřík, M., Pardus, I., Wiezik, M., Wieziková, A., & Svoboda, M. (2024). Exploring the multiple drivers of alpha and beta-diversity dynamics in Europe's primary forests: Informing conservation strategies. *Forest Ecology and Management*, *571*, 122229. https://doi.org/10.1016/J.FORECO.2024.122229

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*(3), 252–264. https://doi.org/10.1111/J.1472-4642.2007.00341.X

Fongnzossie, E. F., Nyangono, C. F. B., Biwole, A. B., Ebai, P. N. B., Ndifongwa, N. B., Motove, J., & Dibong, S. D. (2020). Wild edible plants and mushrooms of the Bamenda Highlands in Cameroon: ethnobotanical assessment and potentials for enhancing food security. *Journal of Ethnobiology and Ethnomedicine*, *16*(1). https://doi.org/10.1186/S13002-020-00362-8

ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., Osinaga-Acosta, O., Bird, M., Bradford, M., Catchpole, D., Ford, A., Graham, A., Hilbert, D., Kemp, J., Laurance, S., Laurance, W., Ishida, F. Y., Marshall, A., Waite, C., … Tran, H. D. (2021). Taking the pulse of Earth's tropical forests using networks of highly distributed plots. *Biological Conservation*, *260*(October), 108849. https://doi.org/10.1016/j.biocon.2020.108849

Fotang, C., Bröring, U., Roos, C., Enoguanbhor, E. C., Abwe, E. E., Dutton, P., Schierack, P., Angwafo, T. E., & Birkhofer, K. (2021). Human Activity and Forest Degradation Threaten Populations of the Nigeria–Cameroon Chimpanzee (Pan troglodytes ellioti) in Western Cameroon. *International Journal of Primatology*, *42*(1), 105–129. https://doi.org/10.1007/S10764-020-00191-2/TABLES/3

Fotang, C., Bröring, U., Roos, C., Enoguanbhor, E. C., Dutton, P., Tédonzong, L. R. D., Willie, J., Yuh, Y. G., & Birkhofer, K. (2021). Environmental and anthropogenic effects on the nesting patterns of Nigeria–Cameroon chimpanzees in North-West Cameroon. *American Journal of Primatology*, *83*(9), e23312. https://doi.org/10.1002/AJP.23312

Fu, H., Yuan, G., Jeppesen, E., Ge, D., Li, W., Zou, D., & Huang, Z. (2019). Science of the Total Environment Local and regional drivers of turnover and nestedness components of species and functional beta diversity in lake macrophyte communities in China. *Science of the Total Environment*, *687*, 206–217. https://doi.org/10.1016/j.scitotenv.2019.06.092

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., & Michaelsen, J. (2015). The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. *Scientific Data 2015 2:1*, *2*(1), 1–21. https://doi.org/10.1038/sdata.2015.66

Funoh, K. N. (2014). *The impacts of artisanal gold mining on local livelihoods and the environment in the forested areas of Cameroon*.

Gallardo-Cruz, J. A., Pérez-García, E. A., & Meave, J. A. (2009). β-Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. In *Landscape Ecology* (Vol. 24, Issue 4, pp. 473–482). https://doi.org/10.1007/s10980-009-9332-1

García-Navas, V., Sattler, T., Schmid, H., & Ozgul, A. (2020). Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps. *Diversity and Distributions*, *October 2019*, 1–12. https://doi.org/10.1111/ddi.13076

Grinberger, A. Y., Minghini, M., Juhász, L., Yeboah, G., & Mooney, P. (2022). OSM Science—The Academic Study of the OpenStreetMap Project, Data, Contributors, Community, and Applications. In *ISPRS International Journal of Geo-Information* (Vol. 11, Issue 4). MDPI. https://doi.org/10.3390/ijgi11040230

Guerin, G. R., Biffin, E., & Lowe, A. J. (2013). Spatial modelling of species turnover identifies climate ecotones, climate change tipping points and vulnerable taxonomic groups. *Ecography*, *36*(10), 1086–1096. https://doi.org/10.1111/j.1600-0587.2013.00215.x

Guerin, G. R., Williams, K. J., Leitch, E., Lowe, A. J., & Sparrow, B. (2021). Using generalised dissimilarity modelling and targeted field surveys to gap-fill an ecosystem surveillance network. *Journal of Applied Ecology*, *58*(4), 766–776. https://doi.org/10.1111/1365-2664.13814

He, J., Lin, S., Kong, F., Yu, J., Zhu, H., & Jiang, H. (2020). Determinants of the beta diversity of tree species in tropical forests: Implications for biodiversity conservation. *Science of the Total Environment*, *704*, 135301. https://doi.org/10.1016/j.scitotenv.2019.135301

Heimpel, E., Ahrends, A., Dexter, K. G., Hall, J. S., Mamboueni, J., Medjibe, V. P., Morgan, D., Sanz, C., & Harris, D. J. (2024). Floristic and structural distinctness of monodominant

Gilbertiodendron dewevrei forest in the western Congo Basin. *Plant Ecology and Evolution 157(1): 55-74*, *157*(1), 55–74. https://doi.org/10.5091/PLECEVO.111539

Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*, *513*(7519), 543–546. https://doi.org/10.1038/nature13739

Herault, B., Ouallet, J., Blanc, L., Wagner, F., & Baraloto, C. (2010). Growth responses of neotropical trees to logging gaps. *Journal of Applied Ecology*, *47*(4), 821–831. https://doi.org/10.1111/j.1365-2664.2010.01826.x

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature 2020 579:7797*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Hundera, K. (2007). Traditional Forest Management Practices in Jimma Zone, South West Ethiopia. *Ethiopian Journal of Education and Sciences*, *2*(2), 1–10. https://doi.org/10.4314/EJESC.V2I2.41982

Hussein, A. (2023). Impacts of Land Use and Land Cover Change on Vegetation Diversity of Tropical Highland in Ethiopia. *Applied and Environmental Soil Science*, *2023*. https://doi.org/10.1155/2023/2531241

International Union for Conservation of Nature. (2017). *DJA FAUNAL RESERVE - World Heritage Datasheet*. http://world-heritage-datasheets.unep-wcmc.org/datasheet/output/site/dja-faunal-reserve/

Jaeger, R., Delagrange, S., Aubin, I., Joanisse, G., Raymond, P., & Rivest, D. (2022). Increasing the intensity of regeneration treatments decreased beta diversity of temperate hardwood forest understory 20 years after disturbance. *Annals of Forest Science*, *79*(1). https://doi.org/10.1186/s13595-022-01152-w

Jansen, M., Guariguata, M. R., Raneri, J. E., Ickowitz, A., Chiriboga-Arroyo, F., Quaedvlieg, J., & Kettle, C. J. (2020). Food for thought: The underutilized potential of tropical tree-sourced foods for 21st century sustainable food systems. *People and Nature*, *2*(4), 1006–1020. https://doi.org/10.1002/pan3.10159

Jarzyna, M. A., & Jetz, W. (2016). Detecting the Multiple Facets of Biodiversity. *Trends in Ecology and Evolution*, *31*(7), 527–538. https://doi.org/10.1016/j.tree.2016.04.002

Jarzyna, M. A., & Jetz, W. (2018). Taxonomic and functional diversity change is scale dependent. *Nature Communications*, *9*(1), 2565. https://doi.org/10.1038/s41467-018-04889-z

Jiang, L., Lv, G., Gong, Y., Li, Y., Wang, H., & Wu, D. (2021). Characteristics and driving mechanisms of species beta diversity in desert plant communities. *PLOS ONE*, *16*(1), e0245249. https://doi.org/10.1371/journal.pone.0245249

Jimoh, S., Adesoye, P., Adeyemi, A., & Ikyaagba, E. (2012). Forest Structure Analysis in the Oban Division of Cross River National Park, Nigeria - ProQuest. *Journal of Agricultural Science and Technology*, *2*(April), 510–518.

Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003). Pollination of Coffea canephora in relation to local and regional agroforestry management. *Journal of Applied Ecology*, *40*(5), 837–845. https://doi.org/10.1046/J.1365-2664.2003.00847.X

Levis, C., Costa, F. R. C., Bongers, F., Peña-Claros, M., Clement, C. R., Junqueira, A. B., Neves, E. G., Tamanaha, E. K., Figueiredo, F. O. G., Salomão, R. P., Castilho, C. V., Magnusson, W. E., Phillips, O. L., Guevara, J. E., Sabatier, D., Molino, J. F., Cárdenas López, D., Mendoza, A. M., Pitman, N. C. A., … Ter Steege, H. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, *355*(6328), 925–931. https://doi.org/10.1126/science.aal0157

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., Baker, T. R., & Phillips, O. L. (2009). *ForestPlots.net Database*. www.forestplots.net.

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., & Phillips, O. L. (2011). ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science*, *22*(4), 610–613. https://doi.org/10.1111/J.1654-1103.2011.01312.X

Lueder, S., Narasimhan, K., Olivo, J., Cabrera, D., Jurado, J. G., Greenstein, L., & Karubian, J. (2022). Functional Traits, Species Diversity and Species Composition of a Neotropical Palm Community Vary in Relation to Forest Age. *Frontiers in Ecology and Evolution*, *10*, 335. https://doi.org/10.3389/fevo.2022.678125

McMichael, C. H., Feeley, K. J., Dick, C. W., Piperno, D. R., & Bush, M. B. (2017). Comment on 'Persistent effects of pre-Columbian plant domestication on Amazonian forest composition'. *Science (New York, N.Y.)*, *358*(6361), 925–931. https://doi.org/10.1126/science.aan8347

McMichael, C. N. H. (2021). Ecological legacies of past human activities in Amazonian forests. *The New Phytologist*, *229*(5), 2492–2496. https://doi.org/10.1111/nph.16888

Meinhold, K., & Darr, D. (2022). Keeping Up With Rising (Quality) Demands? The Transition of a Wild Food Resource to Mass Market, Using the Example of Baobab in Malawi. *Frontiers in Sustainable Food Systems*, *6*, 840760. https://doi.org/10.3389/FSUFS.2022.840760/BIBTEX

Mokany, K., Ware, C., Woolley, S. N. C., Ferrier, S., & Fitzpatrick, M. C. (2022). A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. *Global Ecology and Biogeography*, *31*(4), 802–821. https://doi.org/10.1111/geb.13459

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. B., Kent, J., Mittermeler, R. A., Mittermeler, C. G., da Fonseca, G. A. B. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Ndobe, S. N., & Mantzel, K. (2014). *Deforestation, REDD and Takamanda National Park in Cameroon-a Case Study*. http://www.umverteilen.de/

Nguiffo, S. (2001). *Cameroon-Dja Wildlife Reserve One forest and two dreams: the constraints imposed on the Baka in Miatta by the Dja Wildlife Reserve*.

Nigerian National Park Service. (2019). *CROSS RIVER NATIONAL PARK-OBAN DIVISION QUARTERLY REPORT : OCTOBER-DECEMBER 2019 Prepared : by EBRI Isa WCS Nigeria Program December 2019* (Issue December). https://nigeria.wcs.org/DesktopModules/Bring2mind/DMX/Download.aspx?EntryId=37194&PortalId=139&DownloadMethod=attachment

Núñez, C. L., Poulsen, J. R., White, L. J. T., Medjibe, V., & Clark, J. S. (2022). Distinct Community-Wide Responses to Forecasted Climate Change in Afrotropical Forests. *Frontiers in Ecology and Evolution*, *9*, 742626. https://doi.org/10.3389/FEVO.2021.742626/BIBTEX

Oates, J. F., Bergl, R. a., & Linder, J. M. (2004). Advances in Applied Biodiversity Science: Africa's Gulf of Guinea Forests: Biodiversity Patterns and Conservation Priorities. In *Advances in Applied Biodiversity Science* (Vol. 6). Conservation International. https://doi.org/10.1896/1-881173-82-8

Owono, J. C. (2001). Cameroon-Campo Ma'an The extent of Bagyeli Pygmy involvement in the development and Management Plan of the Campo Ma'an UTO (J. Nelson & L. Hossack, Trans.). In J. Nelson & L. Hossack (Eds.), *ndigenous Peoples and Protected Areas in Africa: From Principles to Practice* (pp. 243–268). Forest Peoples Programme.

Oyewole, S. O., Ishola, B. F., & Aina-Oduntan, O. A. (2019). Maximizing the role of African forest for climate change mitigation and socioeconomic development. *World News of Natural Sciences*, *27*. www.worldnewsnaturalsciences.com

Paredes-Trejo, F., Barbosa, H. A., Kumar, T. V. L., Thakur, M. K., Buriti, C. de O., Paredes-Trejo, F., Barbosa, H. A., Kumar, T. V. L., Thakur, M. K., & Buriti, C. de O. (2020). Assessment of the CHIRPS-Based Satellite Precipitation Estimates. *Inland Waters - Dynamics and Ecology*. https://doi.org/10.5772/INTECHOPEN.91472

Piperno, D. R., McMichael, C., & Bush, M. B. (2015). Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *Holocene*, *25*(10), 1588–1597. https://doi.org/10.1177/0959683615588374

Pound, K. L., Lawrence, G. B., & Passy, S. I. (2019). Beta diversity response to stress severity and heterogeneity in sensitive versus tolerant stream diatoms. *Diversity and Distributions*, *25*(3), 374–384. https://doi.org/10.1111/ddi.12865

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rainforest Foundation UK. (2016). *NGUTI COUNCIL, SOUTH-WEST REGION, REPUBLIC OF CAMEROON FOREST COMMUNITIES AND THEIR TRADITIONAL WAY OF LIFE*. https://www.yumpu.com/en/document/view/41067505/nguti-council-monographic-study-impact-monitoring-of-forest-/6

Raj, A., Jhariya, M. K., & Khan, N. (2022). The Importance of Forest for Soil, Food, and Climate Security in Asia. *Biodiversity, Conservation and Sustainability in Asia: Volume 2: Prospects and Challenges in South and Middle Asia*, *2*, 33–52. https://doi.org/10.1007/978-3-030-73943-0_3/COVER

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D. W., Slotow, R., & Hamer, M. (2014). Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution*, *5*(4), 320–328. https://doi.org/10.1111/2041-210X.12166

Roberts, P., Hamilton, R., & Piperno, D. R. (2021). Tropical forests as key sites of the "Anthropocene": Past and present perspectives. *Proceedings of the National Academy of Sciences*, *118*(40), e2109243118. https://doi.org/10.1073/pnas.2109243118

Scerri, E. M. L., Roberts, P., Maezumi, S. Y., & Malhi, Y. (2022). Tropical forests in the deep human past. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 377, Issue 1849). The Royal Society. https://doi.org/10.1098/rstb.2020.0500

Sehra, S. S., Singh, J., & Rai, H. S. (2013). Assessment of OpenStreetMap Data-A Review. In *International Journal of Computer Applications* (Vol. 76, Issue 16). http://www.gartner.com/newsroom/id/1622614,

Seifert, T., Teucher, M., Ulrich, W., Mwania, F., Gona, F., & Habel, J. C. (2022). Biodiversity and Ecosystem Functions Across an Afro-Tropical Forest Biodiversity Hotspot. *Frontiers in Ecology and Evolution*, *10*, 816163. https://doi.org/10.3389/FEVO.2022.816163/BIBTEX

Shiembo, P. N., Newton, A. C., & Leakey, R. R. B. (1996). vegetative propagation of Irvingia gabonensis, a West African fruit tree. *Forest Ecology and Management*, *87*(1–3), 185–192. https://doi.org/10.1016/S0378-1127(96)03781-4

Singh, P. K., Prajapati, S. K., Sunita, K., & Chaturvedi, R. K. (2022). Disturbance Induced Changes in Diversity of Medicinal Plants in a Dry Tropical Forest of India. *Frontiers in Forests and Global Change*, *4*(February), 1–12. https://doi.org/10.3389/ffgc.2021.718930

Stahl, P. W. (2015). Interpreting interfluvial landscape transformations in the pre-Columbian Amazon. *Holocene*, *25*(10), 1598–1603. https://doi.org/10.1177/0959683615588372

Steadman, D. W. (1993). Biogeography of Tongan birds before and after human impact. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(3), 818–822. https://doi.org/10.1073/pnas.90.3.818

Sullivan, M. J. P., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., Ewango, C. E. N., Hubau, W., Marimon, B., Monteagudo-Mendoza, A., Qie, L., Sonké, B., Martinez, R. V., Baker, T. R., Brienen, R. J. W., Feldpausch, T. R., Galbraith, D., Gloor, M., Malhi, Y., … Phillips, O. L. (2020). Long-term thermal sensitivity of earth's tropical forests. *Science*, *368*(6493), 869–874. https://doi.org/10.1126/SCIENCE.AAW7578/ASSET/F902DD0D-DDF8-4B5A-B391-F5F41E476BB5/ASSETS/GRAPHIC/368_869_F4.JPEG

Swenson, N. G., Anglada-Cordero, P., & Barone, J. A. (2011). Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707), 877–884. https://doi.org/10.1098/rspb.2010.1369

ter Steege, H., Henkel, T. W., Helal, N., Marimon, B. S., Marimon-Junior, B. H., Huth, A., Groeneveld, J., Sabatier, D., Coelho, L. de S., Filho, D. de A. L., Salomão, R. P., Amaral, I. L., Matos, F. D. de A., Castilho, C. V., Phillips, O. L., Guevara, J. E., Carim, M. de J. V., Cárdenas López, D., Magnusson, W. E., … Melgaço, K. (2019). Rarity of monodominance in hyperdiverse Amazonian forests. *Scientific Reports*, *9*(1), 1–15. https://doi.org/10.1038/s41598-019-50323-9

UNESCO World Heritage Centre. (2020, June 4). *Cross River – Korup – Takamanda (CRIKOT) National Parks (Nigeria) - UNESCO World Heritage Centre*. https://whc.unesco.org/en/tentativelists/6204/

Vega, E., Martínez-Ramos, M., García-Oliva, F., & Oyama, K. (2020). Influence of environmental heterogeneity and geographic distance on beta-diversity of woody communities. *Plant Ecology*, *221*(7), 595–614. https://doi.org/10.1007/s11258-020-01036-x

Verrico, B. M., Weiland, J., Perkins, T. D., Beckage, B., & Keller, S. R. (2020). Long-term monitoring reveals forest tree community change driven by atmospheric sulphate pollution and contemporary climate change. *Diversity and Distributions*, *26*(3), 270–283. https://doi.org/10.1111/ddi.13017

Waddell, E. H., Chapman, D. S., Hill, J. K., Hughes, M., Bin Sailim, A., Tangah, J., & Banin, L. F. (2020). Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient. *Functional Ecology*, *34*(12), 2584–2597. https://doi.org/10.1111/1365-2435.13679/SUPPINFO

Wayman, J. P., Sadler, J. P., Pugh, T. A. M., Martin, T. E., Tobias, J. A., & Matthews, T. J. (2021). Identifying the Drivers of Spatial Taxonomic and Functional Beta-Diversity of British Breeding Birds. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.620062

Wildlife Conservation Society. (2021). *Mbam Djerem National Park*. https://cameroon.wcs.org/Wild-Places/Mbam-Djerem-National-Park1.aspx

Williams, B. A., Venter, O., Allan, J. R., Atkinson, S. C., Rehbein, J. A., Ward, M., Di Marco, M., Grantham, H. S., Ervin, J., Goetz, S. J., Hansen, A. J., Jantz, P., Pillay, R., Rodríguez-Buriticá, S., Supples, C., Virnig, A. L. S., & Watson, J. E. M. (2020). Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems. *One Earth*, *3*(3), 371–382. https://doi.org/10.1016/j.oneear.2020.08.009

Yang, J., Swenson, N. G., Zhang, G., Ci, X., Cao, M., Sha, L., Li, J., Ferry Slik, J. W., & Lin, L. (2015). Local-scale Partitioning of Functional and Phylogenetic Beta Diversity in a Tropical Tree Assemblage. *Scientific Reports*, *5*(February), 1–10. https://doi.org/10.1038/srep12731

Zahawi, R. A., Werden, L. K., San-José, M., Rosales, J. A., Flores, J., Holl, K. D., San-José, M., Rosales, J. A., Flores, J., Holl, K. D., San-José, M., Rosales, J. A., Flores, J., & Holl, K. D. (2021). Proximity and abundance of mother trees affects recruitment patterns in a long-term tropical forest restoration study. *Ecography*, *44*(12), 1826–1837. https://doi.org/10.1111/ecog.05907

Zambrano, J., Cordeiro, N. J., Garzon-Lopez, C., Yeager, L., Fortunel, C., Ndangalasi, H. J., & Beckman, N. G. (2020). Investigating the direct and indirect effects of forest fragmentation on plant functional diversity. *PLoS ONE*, *15*(7). https://doi.org/10.1371/journal.pone.0235210

Zhou, Q., Wang, S., & Liu, Y. (2022). Exploring the accuracy and completeness patterns of global land-cover/land-use data in OpenStreetMap. *Applied Geography*, *145*, 102742. https://doi.org/10.1016/J.APGEOG.2022.102742

DATA ACCESSIBILITY STATEMENT

The data used for the study are available on request from the Forest Plots Database at https://forestplots.net/.

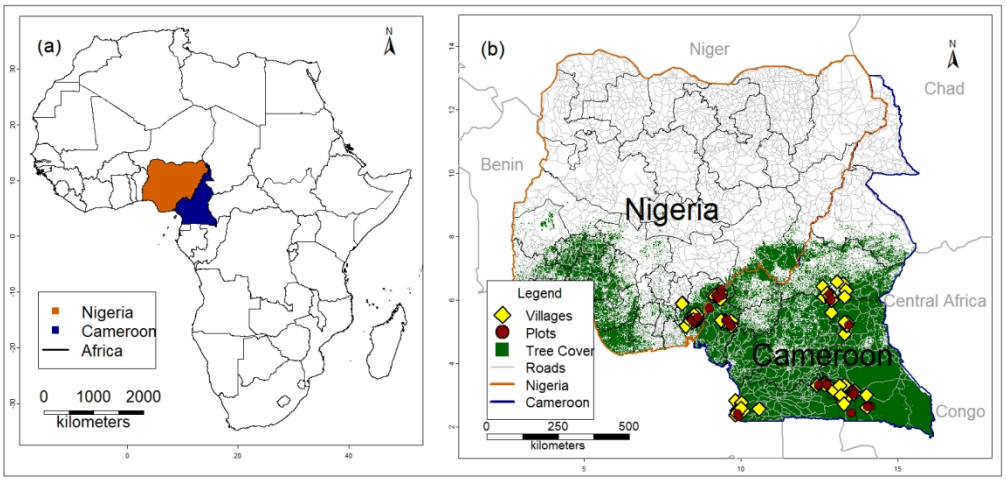

Figure 1. Map of Africa showing the location of Nigeria and Cameroon (a) and tree cover map of Nigeria and Cameroon showing the location of the 66 plots used for the study and villages around the plots (b).

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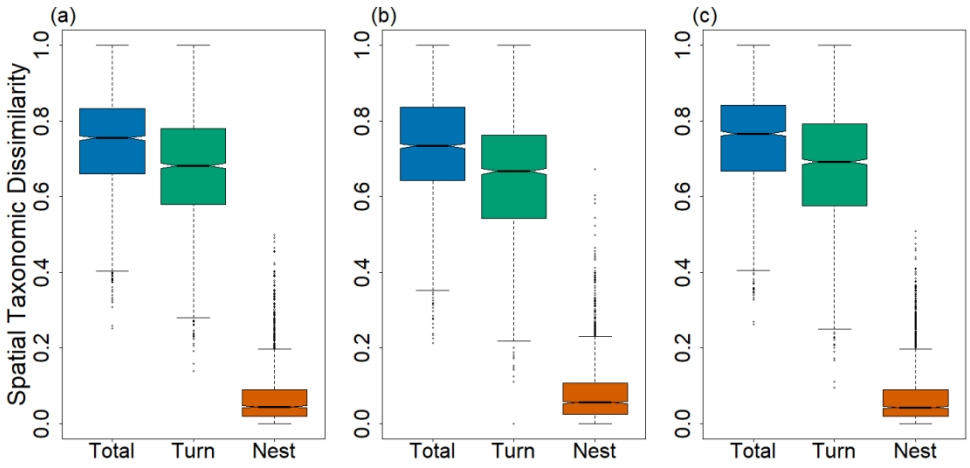

Figure 2. Boxplots of pairwise spatial dissimilarity of all (a), edible (b) and inedible (c) tree species found in the region. Plots display total beta-diversity (Total) as well as the turnover (Turn) and nestedness (Nest) components.

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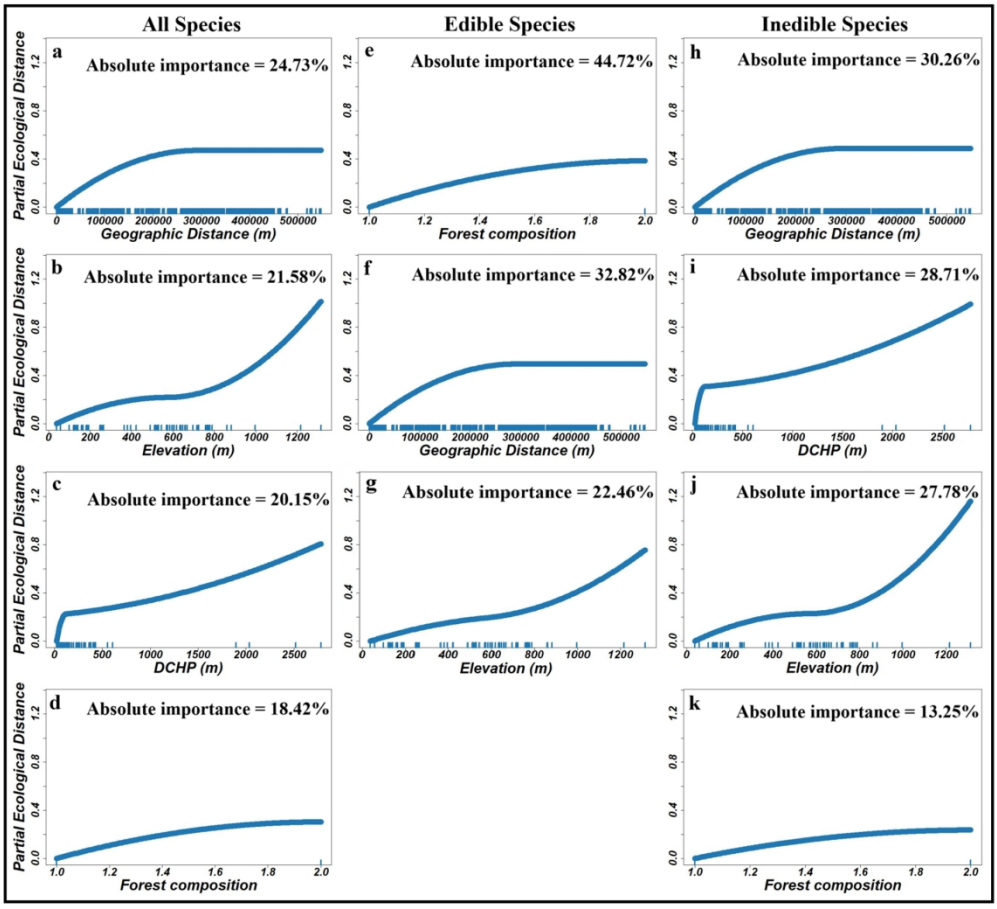

Figure 3. Plotted I-splines of the three variables with the highest importance scores from the GDMs analysing the spatial relationship between geographical gradients, environmental variables, and tree species composition. Plots are the Total Sørensen's beta-diversity for all the species in the region (a,b,c,d), for the edible species category (e,f,g), and for the inedible species (h,i,j,k). Plots are organised from top to bottom based on increasing absolute variable importance (percentage contribution by variable to the model outcome).

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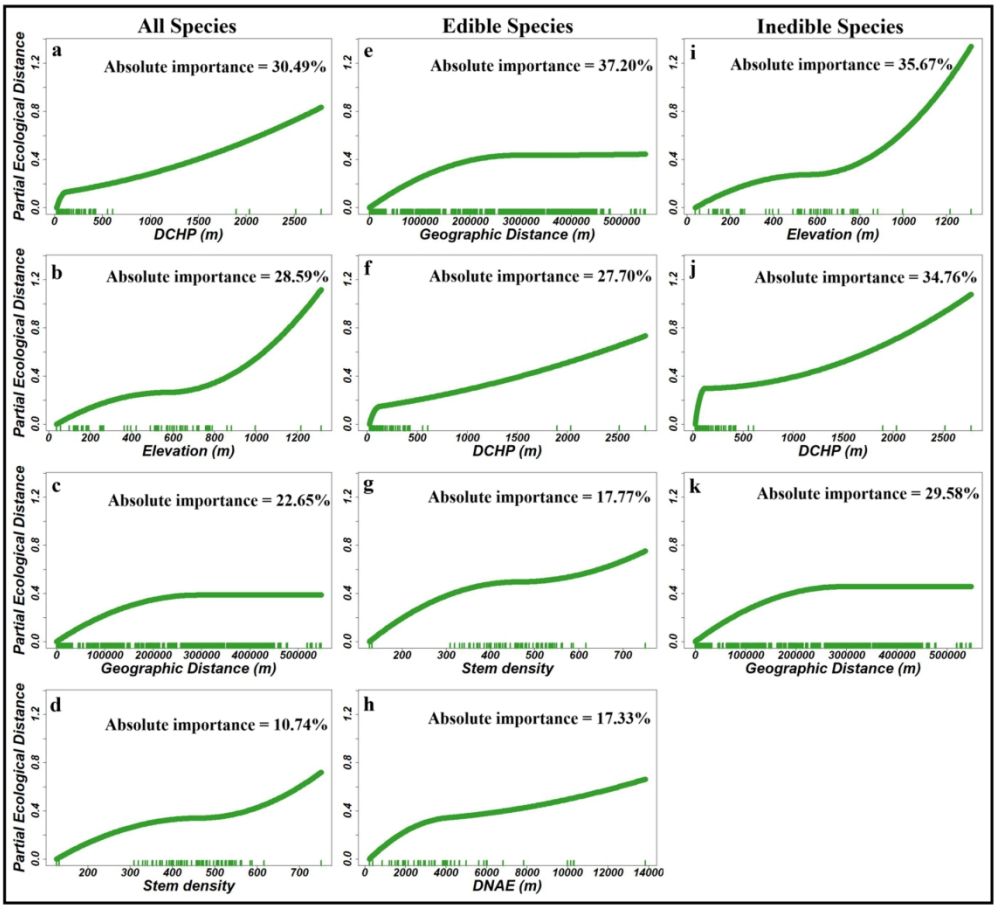

Figure 4. Plotted I-splines of the variables with the highest importance scores from the GDM, analysing the spatial relationship between the turnover component of Sørensen's beta-diversity and geographical gradients, environmental variables, and tree species categories. Plots columns are arranged from left to right with all species (a,b,c,d), edible species category (e,f,g,h), and inedible species category (i,j,k). Plots are organised from top to bottom based on increasing absolute variable importance (percentage contribution by variable to the model outcome).

254x230mm (200 x 200 DPI)

SUPPORTING INFORMATION

HUMAN AND ENVIRONMENTAL FACTORS SHAPE TREE SPECIES ASSEMBLAGE IN WEST AFRICAN TROPICAL FORESTS

Appendix S1. Information on the dimension, size, census year of plot establishment and plots located in different forest compositions

Table S1 Demographics of the villages around the forest used for the study

National Park or Reserve	Country	Date Established	Date further Management	Villages	Population of People	Source
Cross River National Park – Oban Division	Nigeria	1989	1989	39	40,000	(UNESCO World Heritage Centre, 2020; Asuk et al., 2023)
Takamanda National Park	Cameroon	1934 (reserve)	2008 (made a protected area)	32	28,000 (12000 within the park)	(Ndobe and Mantzel, 2014)
Campo Ma'an Reserve	Cameroon	1932;	1978 (area extended)	NA	300,000	(Owono, 2001)
Deng Deng National Park	Cameroon	2010	2010	16	1,300	(Diangha, 2015)
Dja Faunal Reserve	Cameroon	1950	1987 (UNESCO WHS)	37	25,500 (3000 within reserve)	(Nguiffo, 2001)
Mbam Djerem National Park	Cameroon	2000	2003 (WCS took over management)	74	30,000	(Wildlife Conservation Society, 2021)
Ngoyla-Mintom Forest	Cameroon	2010 (open to humans)	2012 (full management intervention)	NA	13,000	(Defo, 2023; Funoh, 2014)
Nguti Forest	Cameroon	1967		54	20,060	(Rainforest Foundation UK, 2016)

Table S2. Information on tree data from plots used for the study, including location of plot code, country of location, dimension, and year censused.

Plot Code	Country	Minimum Dimension (m)	Maximum Dimension (m)	Ground Area (sq. m)	Year Censused
AKG-01	Nigeria	40	120	4800	2019
AKG-02	Nigeria	40	120	4800	2019
BIS-01	Cameroon	100	100	10000	2013
BIS-02	Cameroon	100	100	10000	2013
BIS-03	Cameroon	100	100	10000	2013
BIS-04	Cameroon	100	100	10000	2013
BIS-05	Cameroon	100	100	10000	2013
BIS-06	Cameroon	100	100	10000	2013
CAM-01	Cameroon	100	100	10000	2012
CAM-02	Cameroon	100	100	10000	2012
CAM-03	Cameroon	100	100	10000	2002
DJK-01	Cameroon	100	100	10000	2019
DJK-02	Cameroon	100	100	10000	2019
DJK-03	Cameroon	100	100	10000	2019
DJK-04	Cameroon	100	100	10000	2019
DJK-05	Cameroon	100	100	10000	2019
DJK-06	Cameroon	100	100	10000	2019
DJL-01	Cameroon	100	100	10000	2016
DJL-02	Cameroon	100	100	10000	2016
DJL-03	Cameroon	100	100	10000	2016
DJL-04	Cameroon	100	100	10000	2016
DJL-05	Cameroon	100	100	10000	2016
DJL-06	Cameroon	100	100	10000	2016
DNG-01	Cameroon	100	100	10000	2016
DNG-02	Cameroon	100	100	10000	2016
EJA-04	Cameroon	100	100	10000	2011
EJA-05	Cameroon	100	100	10000	2011
ERK-01	Nigeria	40	120	4800	2019
MDJ-01	Cameroon	100	100	10000	2019
MDJ-03	Cameroon	100	100	10000	2019
MDJ-05	Cameroon	100	100	10000	2019
MDJ-07	Cameroon	100	100	10000	2019
MDJ-10	Cameroon	40	100	4000	2019
MIT-01	Cameroon	100	100	10000	2011
NGI-01	Cameroon	100	100	10000	2011
NGI-02	Cameroon	100	100	10000	2011
NGI-03	Cameroon	100	100	10000	2013
NGI-04	Cameroon	100	100	10000	2013
NGI-05	Cameroon	100	100	10000	2013
NGI-06	Cameroon	100	100	10000	2013
NGI-07	Cameroon	100	100	10000	2013
NGI-08	Cameroon	100	100	10000	2013
NGI-09	Cameroon	100	100	10000	2013

NGI-10	Cameroon	100	100	10000	2013
NGI-11	Cameroon	100	100	10000	2013
NGI-12	Cameroon	100	100	10000	2013
NGO-01	Cameroon	100	100	10000	2012
NGO-02	Cameroon	100	100	10000	2012
NGO-03	Cameroon	100	100	10000	2012
NGO-04	Cameroon	100	100	10000	2013
NGO-05	Cameroon	100	100	10000	2013
NGO-06	Cameroon	100	100	10000	2013
OBE-83	Nigeria	100	100	10000	2002
OBE-84	Nigeria	100	100	10000	2002
OSB-01	Nigeria	40	120	4800	2019
OSB-02	Nigeria	40	120	4800	2019
TNP-06	Cameroon	100	100	10000	2012
TNP-07	Cameroon	100	100	10000	2012
TNP-08	Cameroon	100	100	10000	2012
TNP-09	Cameroon	100	100	10000	2012
TNP-10	Cameroon	100	100	10000	2012
TNP-11	Cameroon	100	100	10000	2012
TNP-12	Cameroon	100	100	10000	2012
TNP-13	Cameroon	100	100	10000	2012
TNP-14	Cameroon	100	100	10000	2012
TNP-15	Cameroon	100	100	10000	2012

Table S3. Distribution of edible and inedible tree species found in mixed and monodominant forest plots

Plots	Mixed forest		Monodominant forest	
	edible	inedible	edible	inedible
AKG-01	111	107	-	-
AKG-02	118	109	-	-
BIS-01	-	-	87	260
BIS-02	208	261	-	-
BIS-03	-	-	36	293
BIS-04	155	284	-	-
BIS-05	-	-	41	286
BIS-06	206	240	-	-
CAM-01	95	299	-	-
CAM-02	119	226	-	-
CAM-03	112	279	-	-
DJK-01	-	-	43	264
DJK-02	185	179	-	-
DJK-03	-	-	39	301
DJK-04	244	222	-	-
DJK-05	-	-	28	332
DJK-06	192	254	-	-
DJL-01	-	-	27	322
DJL-02	159	245	-	-
DJL-03	-	-	31	401
DJL-04	202	378	-	-
DJL-05	-	-	50	259
DJL-06	189	273	-	-
DNG-01	328	250	-	-
DNG-02	255	273	-	-
EJA-04	385	153	-	-
EJA-05	330	200	-	-
ERK-01	131	88	-	-
MDJ-01	214	348	-	-
MDJ-03	187	247	-	-
MDJ-05	221	527	-	-
MDJ-07	314	146	-	-
MDJ-10	118	47	-	-
MIT-01	82	277	-	-
NGI-01	165	255	-	-
NGI-02	191	276	-	-
NGI-03	147	245	-	-
NGI-04	243	232	-	-
NGI-05	252	241	-	-
NGI-06	229	311	-	-
NGI-07	219	282	-	-

NGI-08	192	257	-	-
NGI-09	286	254	-	-
NGI-10	237	307	-	-
NGI-11	301	274	-	-
NGI-12	228	290	-	-
NGO-01	75	367	-	-
NGO-02	158	355	-	-
NGO-03	152	210	-	-
NGO-04	-	-	75	333
NGO-05	-	-	29	373
NGO-06	-	-	19	354
OBE-83	45	85	-	-
OBE-84	43	80	-	-
OSB-01	138	110	-	-
OSB-02	98	136	-	-
TNP-06	225	236	-	-
TNP-07	268	201	-	-
TNP-08	199	333	-	-
TNP-09	243	269	-	-
TNP-10	174	280	-	-
TNP-11	195	213	-	-
TNP-12	172	249	-	-
TNP-13	220	261	-	-
TNP-14	231	182	-	-
TNP-15	217	200	-	-
Grand Total	10403	12903	505	3778

Table S4. Distribution and descriptive statistics of predictor variables included in the GDMs models

Variables	Elements within Variables	Count	Min	Max	Mean
Plots		66	-	-	-
Total tree stems		28299	-	-	-
Edible stems		11097	-	-	-
Inedible stems		17202	-	-	-
Forest composition	*Mixed forest plots*	54	-	-	-
	Mixed forest stems	23975	-	-	-
	Monodominant forest plots	12	-	-	-
	Monodominant forest stems	4324	-	-	-
Slope (number of plots)	*Almost Flat*	33	-	-	-
	Flat	17	-	-	-
	Moderately Sloping	8	-	-	-
	Slightly Sloping	5	-	-	-
	Steep	3	-	-	-
Elevation (masl)			38	1314	510.8
Stem density (stems/ha)	*All species*		126	751	452
	Edible species		19	385	181
	Inedible species		83	530	271
DNAE (m)			217	13840	4825.5
DCHP (m)			22.5	2782	306.5

Appendix S2. Qualitative data collection and structured questionnaire used for collection of data on forest tree species utilization in Oban Division, Cross River National Park

Structured questionnaire (see below) on utilization of fruit/seed/nuts from tree species for food were purposively administered to ten percent of the 39 forest-dependent enclave/buffer zone communities around Oban Division of the Cross River National Park, Nigeria, where all seven Nigerian plots are located. The purposive administration of questionnaires was done using a mixed method interview (Friant et al., 2019) based on the following criteria:

1. Individuals involved in the gathering of fruit/seeds/nuts and farmers
2. Individuals who are at least 30 years and likely to be knowledgeable about forest tree species utilization in the area
3. Individuals who had lived in the area for at least 15 years to give valid information on the study
4. The council of chiefs were interviewed as a group.
5. All gender who met criteria 1 to 4 above.

QUESTIONNAIRE USED FOR THE STUDY

Community Code: _____ Date of interview_____ Interviewers Name: _____

Demographic data

Q1. Type of interview

Individual [ ] Group [ ] Number of Respondent in Group: _____

Q2. Age group?

25-34 [ ] 35-44 [ ] Above 45 [ ]

Tree species utilization

Q3. What forest tree species and parts are utilized for food in your community?

Species name	Species part utilized for food					
	Fruit	Seed	Nut	Leaf	Flower	Others (specify)

Appendix S3. Methodology for assessing human impact on tree species composition using proximity measures

To evaluate the human influence on tree species composition within the study region, two distinct variables were employed as proxy measures. The categorisation and quantification of these variables are detailed as follows:

Distance to the Nearest Anthropogenic Edge (DNAE)

DNAE was computed as the Euclidean distance from the geographic coordinates of a given forest plot to the closest discernible anthropogenic edge at the time of the respective census (Figure 3.7.1 and 3.7.2). Anthropogenic edges often manifested as man-made alterations such as farms, settlements, or other types of human disturbance.

For forest plots within the Oban Division dataset, data on the nearest anthropogenic edge was readily available (Asuk et al, 2023). In cases where forest plots from the forestplots.net dataset did not contain this information, Open Street Map and Google Earth were consulted to measure the Euclidean distance from the plot's GPS coordinates to the closest identified anthropogenic edge. This metric acted as a gauge for potential high-impact human activities in areas surrounding the forest plots.

Distance to the Closest Human Presence (DCHP)

DCHP involved measuring the straight-line distance from the GPS centre point of each forest plot to the nearest identified human footpaths (Figure 1 and 2). These footpaths are often used for low-impact activities like foraging and hunting.

Spatial data for this variable was initially obtained from Open Street Map and subsequently validated on Google Earth. To accommodate for censuses conducted in different years, the satellite images on Google Earth were adjusted to match the year of each respective census.

DCHP typically exhibited shorter distances in comparison to DNAE, making it a potentially more precise indicator of low-impact human presence in the vicinity of the forest plots. Historical images were used on google earth engine to coincide with the year of plot census (Figure 3.7.2).

By utilizing these two proximity measures, this study offered an insight of the varying degrees of human impact on the tree species composition in the investigated region.

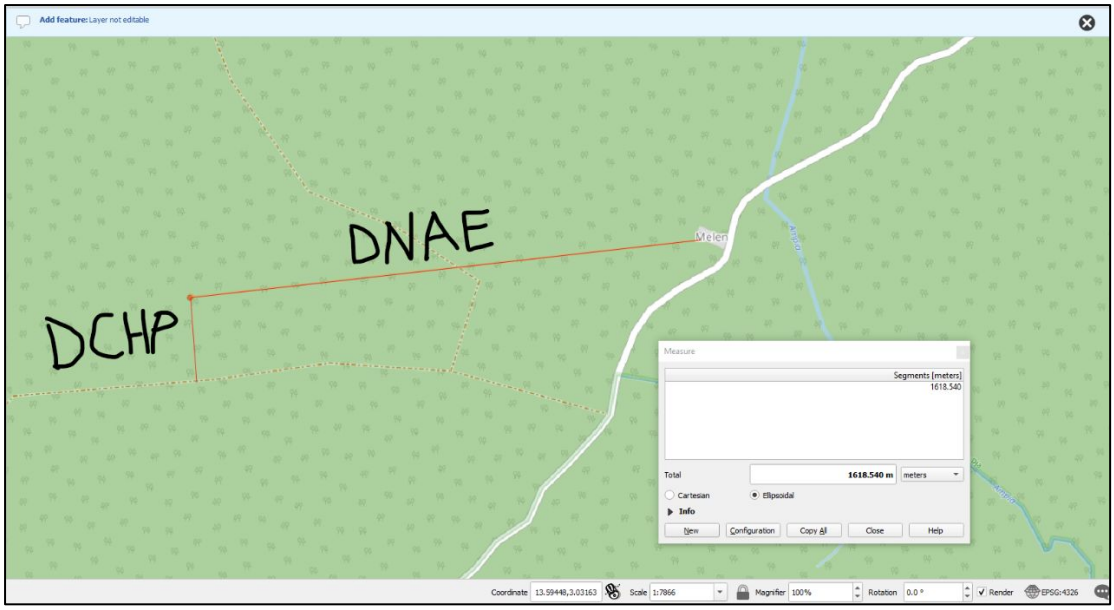

Figure S1. Open street map showing distance from plot to closes path representing distance to closest human presence (DCHP) and distance from plot to human settlement representing distance to nearest anthropogenic edge (DNAE).

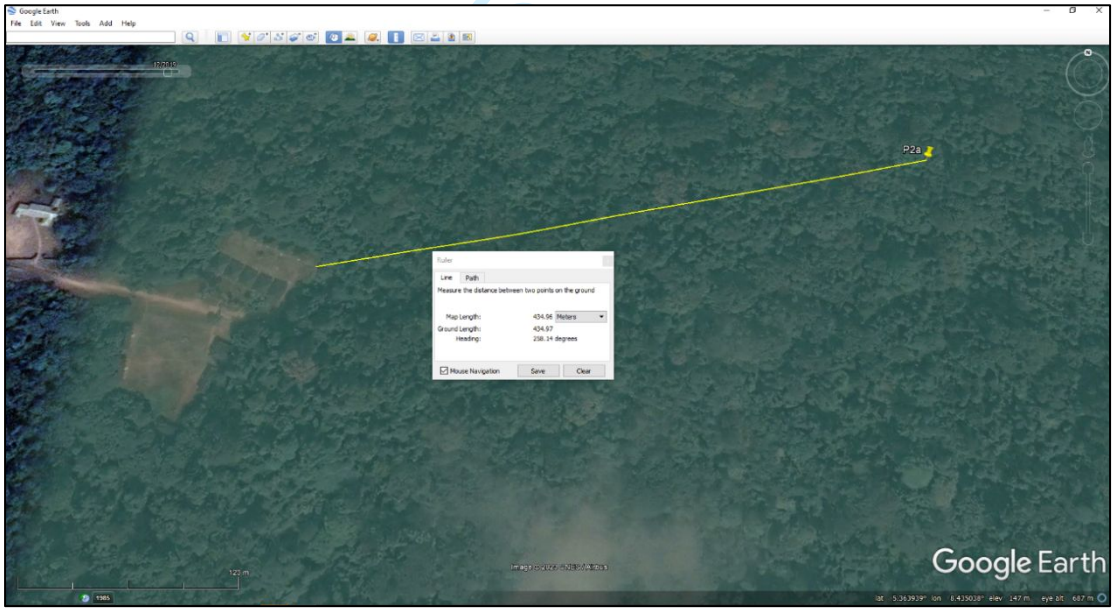

Figure S2. Map from Google Earth showing how distance from plot was measured based on historical images that coincided with date of plot census (see top left bar).

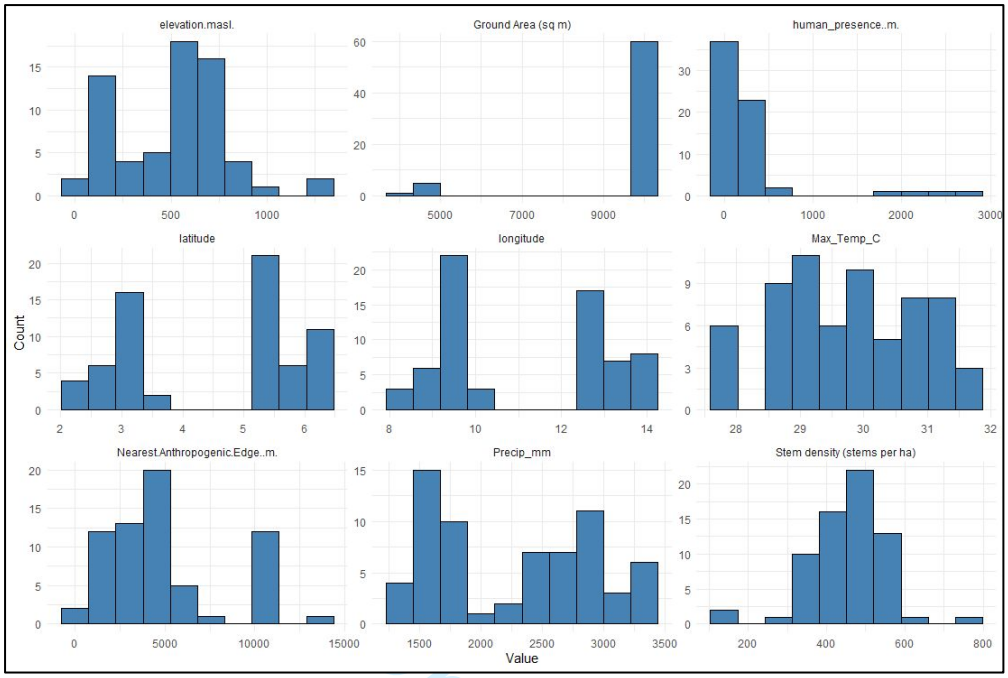

Figure S3. Distribution of predictor variables used in the study

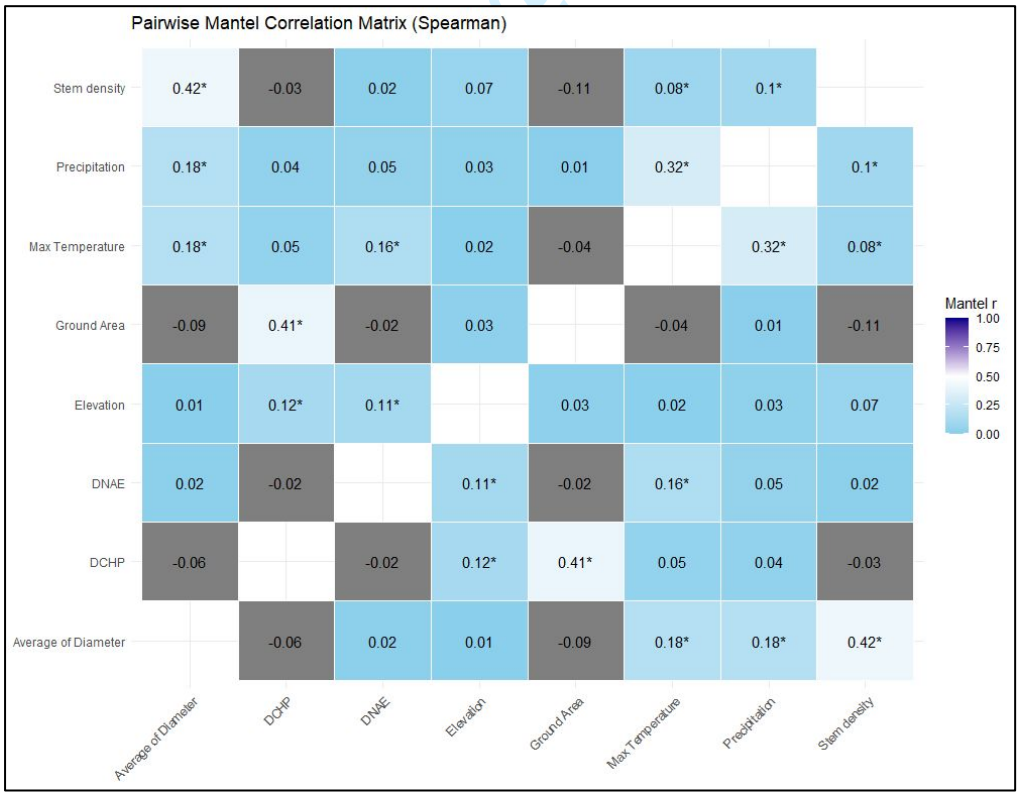

Figure S4. Plots showing correlation coefficient and non-significant correlations (at $p < 0.05$) of predictor variables included in the model

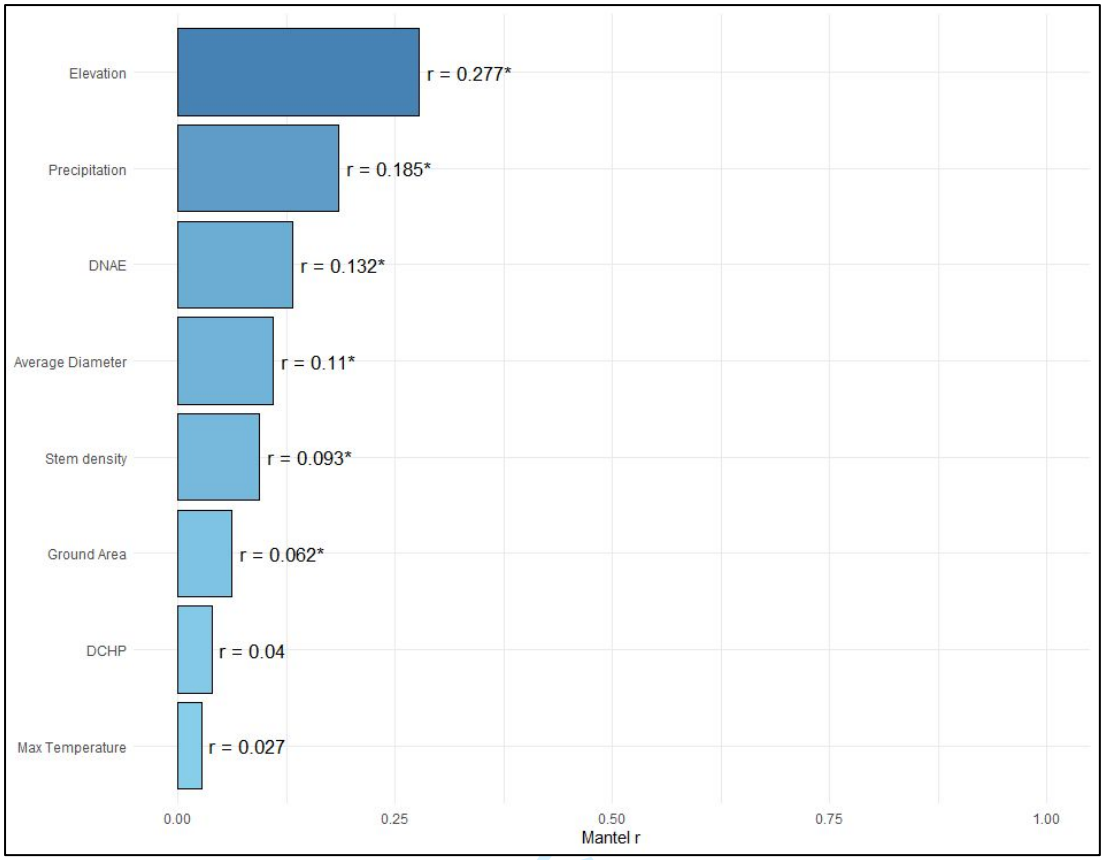

Table S5. Mantel's correlation of the geographical distance matrix generated from the plot longitude and latitude, against other environmental variables.

Appendix S4. Summary of alpha diversity and total tree stem count

Table S5. Alpha diversity of plots forest categorised as mix and mono dominant forests

Forest composition	Plots	Alpha diversity		
		edible	inedible	Total
Mixed forest	AKG-01	43	44	87
Mixed forest	AKG-02	43	37	80
Mixed forest	BIS-02	47	63	110
Mixed forest	BIS-04	50	67	117
Mixed forest	BIS-06	50	57	107
Mixed forest	CAM-01	31	51	82
Mixed forest	CAM-02	27	56	83
Mixed forest	CAM-03	30	44	74
Mixed forest	DJK-02	41	62	103
Mixed forest	DJK-04	55	70	125
Mixed forest	DJK-06	50	58	108
Mixed forest	DJL-02	35	54	89
Mixed forest	DJL-04	55	58	113
Mixed forest	DJL-06	44	58	102
Mixed forest	DNG-01	41	53	94
Mixed forest	DNG-02	48	50	98
Mixed forest	EJA-04	40	43	83
Mixed forest	EJA-05	37	52	89
Mixed forest	ERK-01	49	37	86
Mixed forest	MDJ-01	22	30	52
Mixed forest	MDJ-03	31	44	75
Mixed forest	MDJ-05	15	28	43
Mixed forest	MDJ-07	39	43	82
Mixed forest	MDJ-10	22	15	37
Mixed forest	MIT-01	21	52	73
Mixed forest	NGI-01	28	55	83
Mixed forest	NGI-02	27	49	76
Mixed forest	NGI-03	27	61	88
Mixed forest	NGI-04	34	64	98
Mixed forest	NGI-05	33	70	103
Mixed forest	NGI-06	42	60	102
Mixed forest	NGI-07	32	48	80
Mixed forest	NGI-08	37	42	79
Mixed forest	NGI-09	37	48	85
Mixed forest	NGI-10	31	37	68
Mixed forest	NGI-11	34	41	75
Mixed forest	NGI-12	32	38	70
Mixed forest	NGO-01	22	43	65
Mixed forest	NGO-02	38	53	91
Mixed forest	NGO-03	36	42	78
Mixed forest	OBE-83	23	30	53
Mixed forest	OBE-84	20	29	49

Mixed forest	OSB-01	40	42	82
Mixed forest	OSB-02	36	37	73
Mixed forest	TNP-06	43	57	100
Mixed forest	TNP-07	43	60	103
Mixed forest	TNP-08	17	50	67
Mixed forest	TNP-09	22	52	74
Mixed forest	TNP-10	36	65	101
Mixed forest	TNP-11	45	68	113
Mixed forest	TNP-12	37	55	92
Mixed forest	TNP-13	45	69	114
Mixed forest	TNP-14	31	53	84
Mixed forest	TNP-15	33	55	88
Total Alpha Diversity in Mixed		232	469	701
Monodominant	BIS-01	28	46	74
Monodominant	BIS-03	20	33	53
Monodominant	BIS-05	23	20	43
Monodominant	DJK-01	18	19	37
Monodominant	DJK-03	16	17	33
Monodominant	DJK-05	12	26	38
Monodominant	DJL-01	15	27	42
Monodominant	DJL-03	9	17	26
Monodominant	DJL-05	25	32	57
Monodominant	NGO-04	17	16	33
Monodominant	NGO-05	10	13	23
Monodominant	NGO-06	8	15	23
Total Alpha diversity in Monodominant		76	96	172
Total Alpha Diversity		236	472	708

The alpha diversity of edible and inedible species was higher in mix forest than in monodominant forest. Also, the difference in alpha diversity of edible and inedible trees in all plots was widder in mixed forest than in monodominant forest. Gilbertiodendron dewevrei, belonging to the inedible species category, was the most dominant species across all plots in the monodominant forest. A presence/absence metrics was used for computing the beta diversity thus reducing the effect of species dominance, however, stem density of each species as well as forest composition were added as variables within the model.

Appendix S5. GDM Results

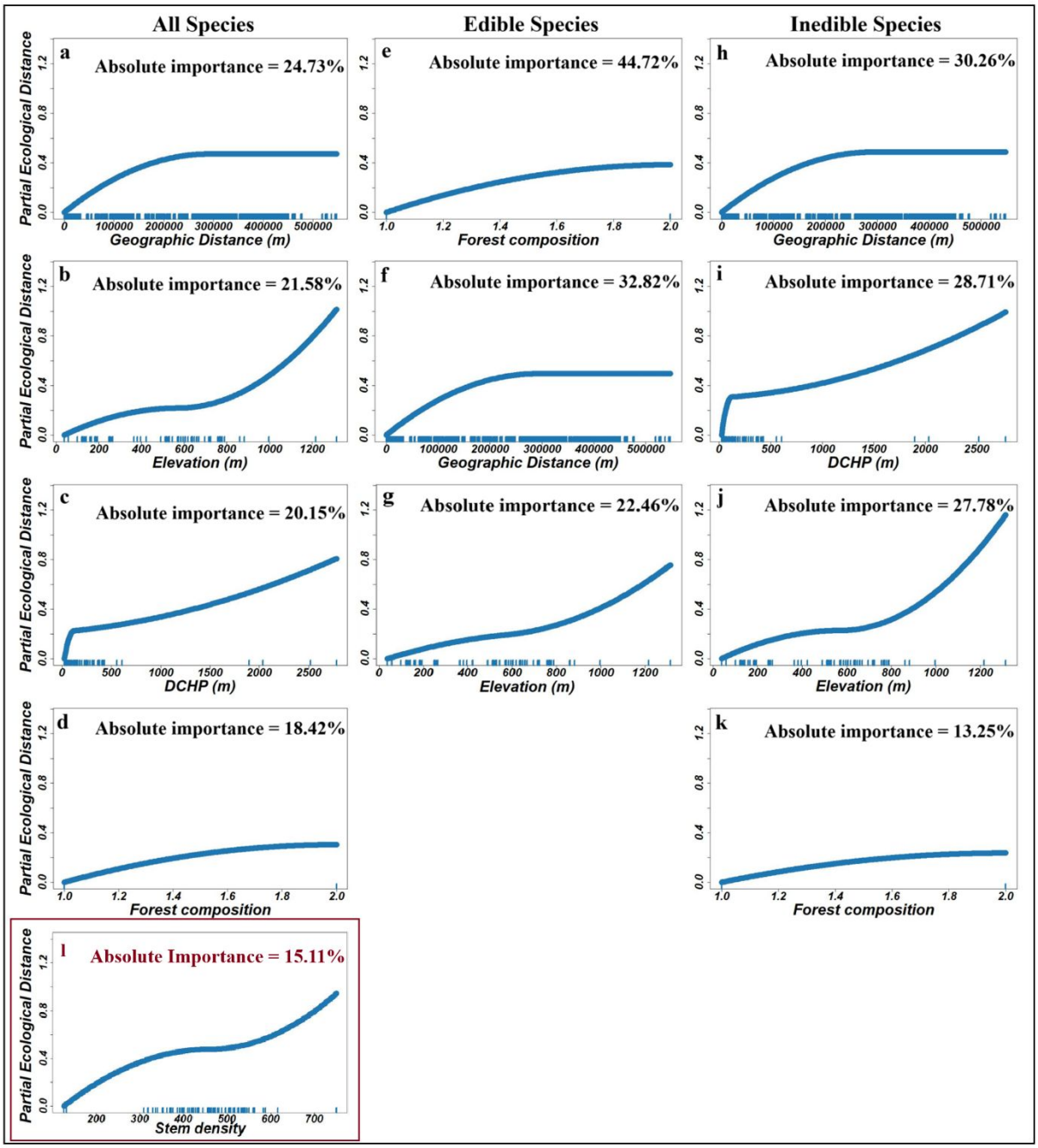

Table S6. Plotted I-splines of the three variables with the highest importance scores from the GDMs analysing the spatial relationship between geographical gradients, environmental variables, and tree species composition. Plots are the Total Sørensen's beta-diversity for all the species in the region (a,b,c,d,l), for the edible species category (e,f,g), and for the inedible species (h,i,j,k). Plots are organised from top to bottom based on increasing absolute variable importance (percentage contribution by variable to the model outcome). The red border represents the plot for I-splines that was not presented in the main manuscript.

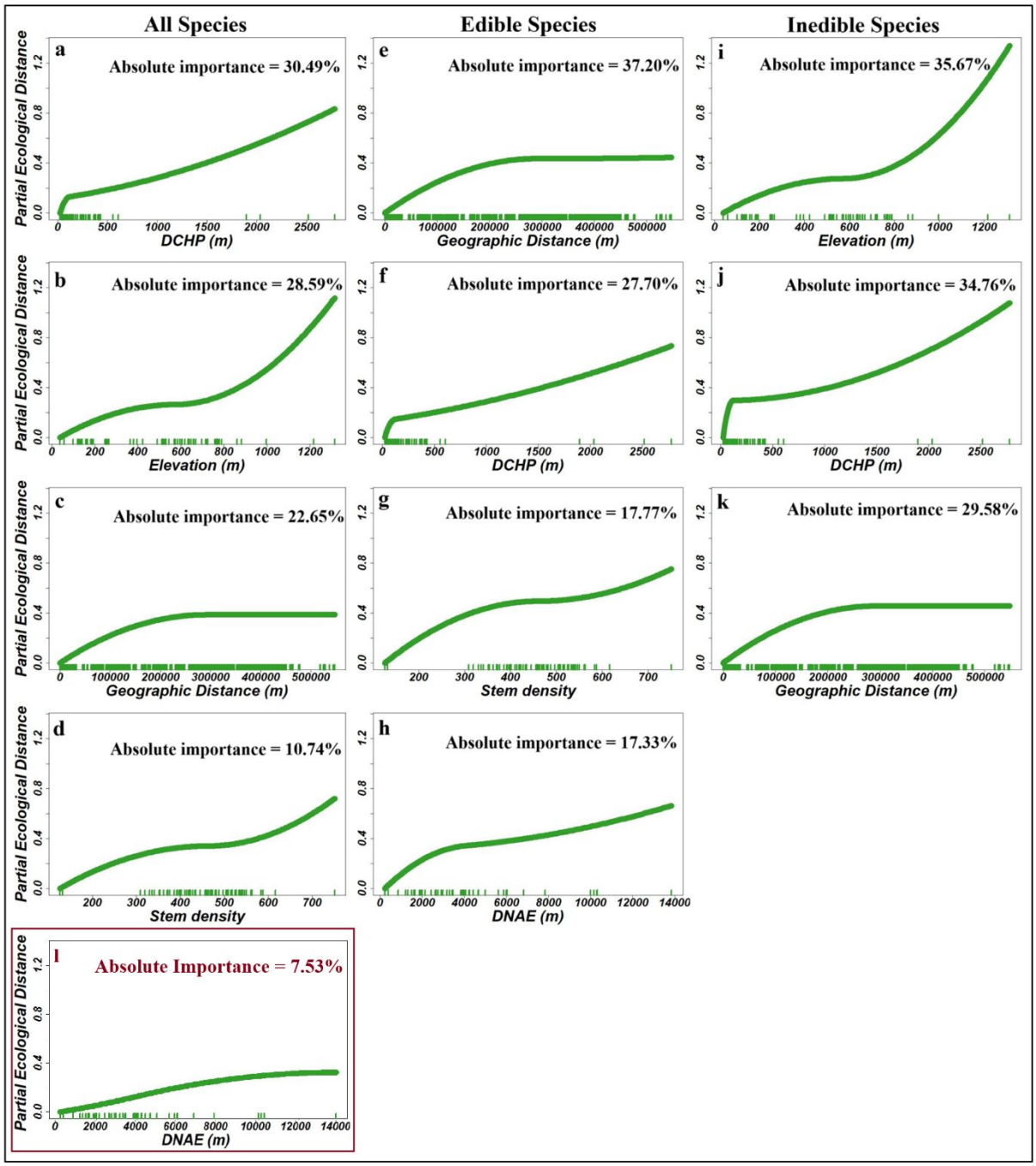

Table S7. Plotted I-splines of the variables with the highest importance scores from the GDM, analysing the spatial relationship between the turnover component of Sørensen's beta-diversity and geographical gradients, environmental variables, and tree species categories. Plots columns are arranged from left to right with all species (a,b,c,d,l), edible species category (e,f,g,h), and inedible species category (i,j,k). Plots are organised from top to bottom based on increasing absolute variable importance (percentage contribution by variable to the model outcome). The red border represents the plot for I-splines that was not presented in the main manuscript.