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

Sijeh A. Asuk[1,2,3,4] | Joseph P. Wayman[1] | Jonathan P. Sadler[1,3] | Thomas A. M. Pugh[1,3,5] | Thomas J. Matthews[1,3,6] | Vincent T. Ebu[4] | Oliver L. Phillips[7] | Simon Lewis[7,8] | Bonaventure Sonké[9] | Joey Talbot[7,10] | James Comiskey[11] | Lise Zemagho[9] | Lucas Ojo[12] | Serge Begne[7,9] | Hermann Taedoumg[9] | Terry Sunderland[13,14] | Wannes Hubau[15,16] | Vincent Droissart[17,18] | Lan Qie[19] | Martin Gilpin[8] | Murielle Simo-Droissart[9] | Ted Feldpausch[20] | Kelvin S. H. Peh[21] | Lindsay F. Banin[22] | Marie Noel Djuikouo Kamdem[23] | Nicholas Kettridge[1]

[1]School of Geography Earth and Environmental Sciences, University of Birmingham, Birmingham, UK | [2]Department of Geography and Environment, School of Social Sciences and Humanities, Loughborough University, Loughborough, UK | [3]Birmingham Institute of Forest Research, University of Birmingham, Birmingham, UK | [4]Department of Forestry and Wildlife Resources Management, University of Calabar, Calabar, Nigeria | [5]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden | [6]CE3C—Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group/CHANGE—Global Change and Sustainability Institute and Universidade dos Açores—Faculty of Agricultural Sciences and Environment, Açores, Portugal | [7]School of Geography, University of Leeds, Leeds, UK | [8]Department of Geography, University College, London, UK | [9]Department of Biology, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon | [10]Institute for Transport Studies, University of Leeds, Leeds, UK | [11]National Park Service, Petersburg, Virginia, USA | [12]University of Abeokuta, Abeokuta, Nigeria | [13]Center for International Forestry Research, Bogor, Indonesia | [14]Faculty of Forestry, University of British Columbia, Vancouver, Canada | [15]Royal Museum for Central Africa, Tervuren, Belgium | [16]Department of Environment, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium | [17]Département Environnement et Ressources, Institut de Recherche Pour le Développement (IRD), Marseille, France | [18]Commission of Central African Forests (COMIFAC), Libreville, Gabon | [19]Department of Life Sciences, College of Science, University of Lincoln, Lincoln, UK | [20]Department of Geography, University of Exeter, Exeter, UK | [21]School of Biological Sciences, University of Southampton, Southampton, UK | [22]UK Centre of Ecology & Hydrology, Edinburgh, UK | [23]University of Buea, Buea, Cameroon

Correspondence: Sijeh A. Asuk (sijehasuk@gmail.com; n.kettridge@bham.ac.uk)

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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 66 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.

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 and Jetz 2018; 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 and 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 and 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; 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 (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; McMichael 2021). Historical low-intensity activities, such as deliberate planting and conservation of preferred tree species and selective logging, leave ecological legacies that 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; 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 and 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 and 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 being mainly focused on temperate forests, with less work focused solely on tropical forests (Aspin et al. 2018; Barnagaud et al. 2017; Biswas and Mallik 2010, 2011; Devictor et al. 2010; Fu et al. 2019; García-Navas et al. 2020; Herault et al. 2010; Jarzyna and 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. 2021a; Fotang, Bröring, Roos, Enoguanbhor, Dutton, et al. 2021b). 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. 2023; 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 and 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 16 villages with an estimated population of 1300 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 and 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 × 100 m except for one that measured 40 × 100 m (see Appendix S1, Table S2). The plots in Nigeria were smaller than those in Cameroon, measuring 40 m × 120 m (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°), almost flat (2°–5°), slightly sloping (5°–10°), moderately sloping (10°–20°) and steep (greater than 20°) 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 among the three adjacent plots were used as the centre point for the new plot. Filtering and joining the plots resulted in a dataset consisting of 66 plots across the study region (i.e., Cameroon and Nigeria), with an average size of 94.6 m (std. 17.4 m) by 101.5 m (std 5.3 m) and containing a total of 28,299 individual trees.

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

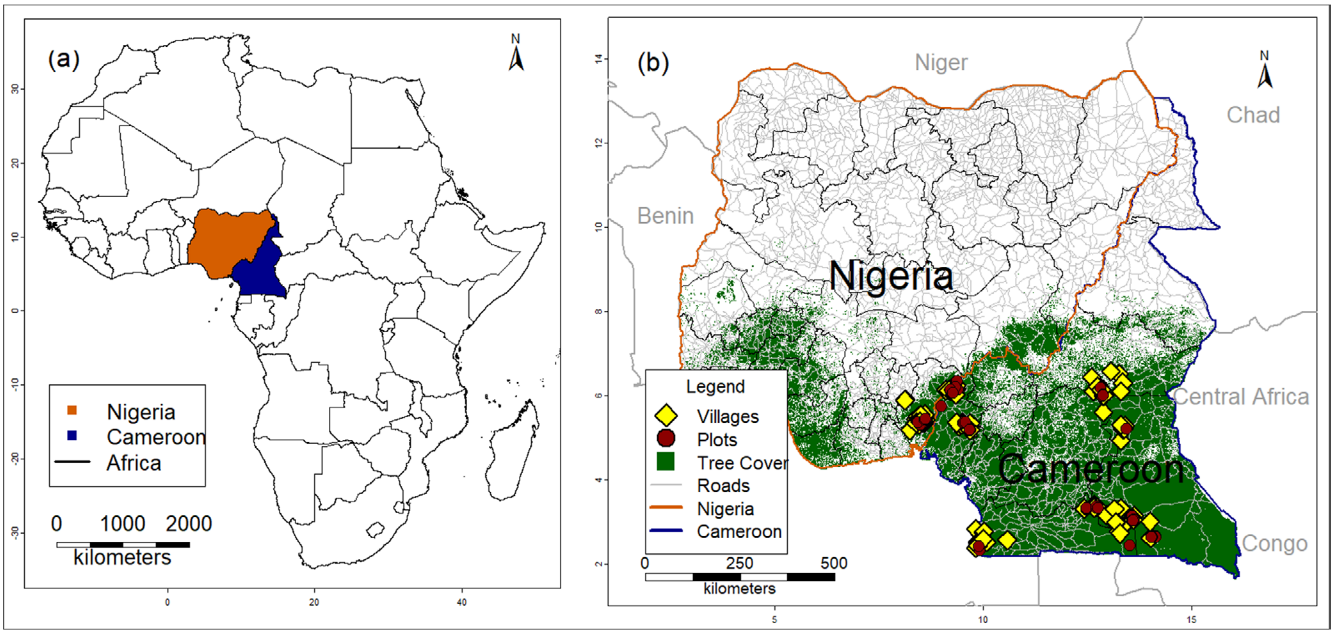

FIGURE 1 | Map of Africa showing the location of Nigeria and Cameroon (a) and tree cover map of Nigeria and Cameroon showing the location of the 66 plots used for the study (b).

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 S3):

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–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; Ferrier et al. 2007; Guerin et al. 2021; He et al. 2020). 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/ha), 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):

$$V_s = V_{full} - \left(V_{full} - V_g\right) - \left(V_{full} - V_e\right) \tag{1}$$

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. In total, 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; 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

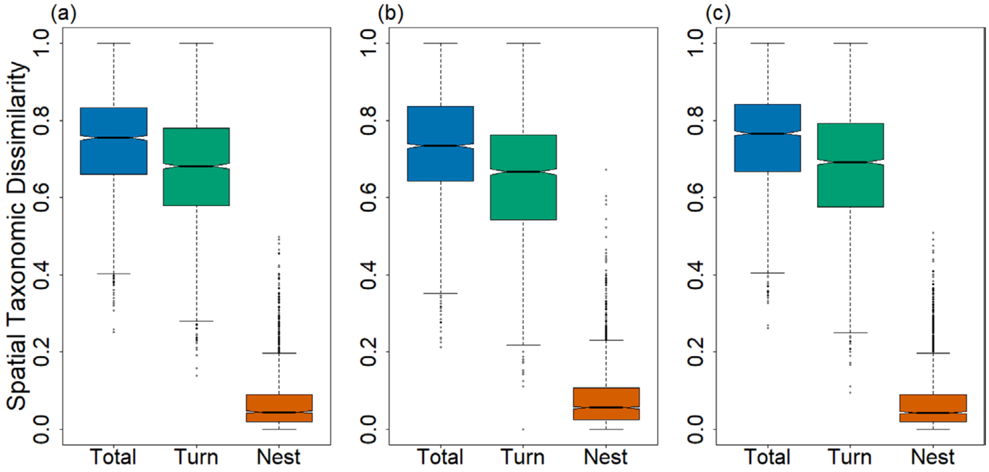

FIGURE 2 | Boxplots of pairwise spatial dissimilarity of all (a), edible (b) and inedible (c) tree species found in the region. Plots display total beta-diversity (Total) as well as the turnover (Turn) and nestedness (Nest) components.

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.

	All		Edible		Inedible	
Groups	**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

Note: '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, $p < 0.05$; see Table 2) was partitioned into Model 2 (only geographical distance), Model 3 (only significant environmental and human predictors from Model 1, $p < 0.05$) and Model 4 (only significant human predictors from Model 1, $p < 0.05$; 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. Significance of italic values represents the level of significance was $p < 0.05$.

TABLE 2 | Results from the GDMs showing variable importance from Model 1 (all significant predictor variables, $p < 0.05$) and Model 4 (only human predictors from Model 1).

	All		**Edible**		**Inedible**	
Groups	**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)*

Note: 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.

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).

3.2.1.1 | 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, Table 1, 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 Figures 3a and 4a,h, Figure S4).

3.2.1.2 | Edible Species Models.

For the edible species model (Figure 4e–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–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, Figure 4e–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

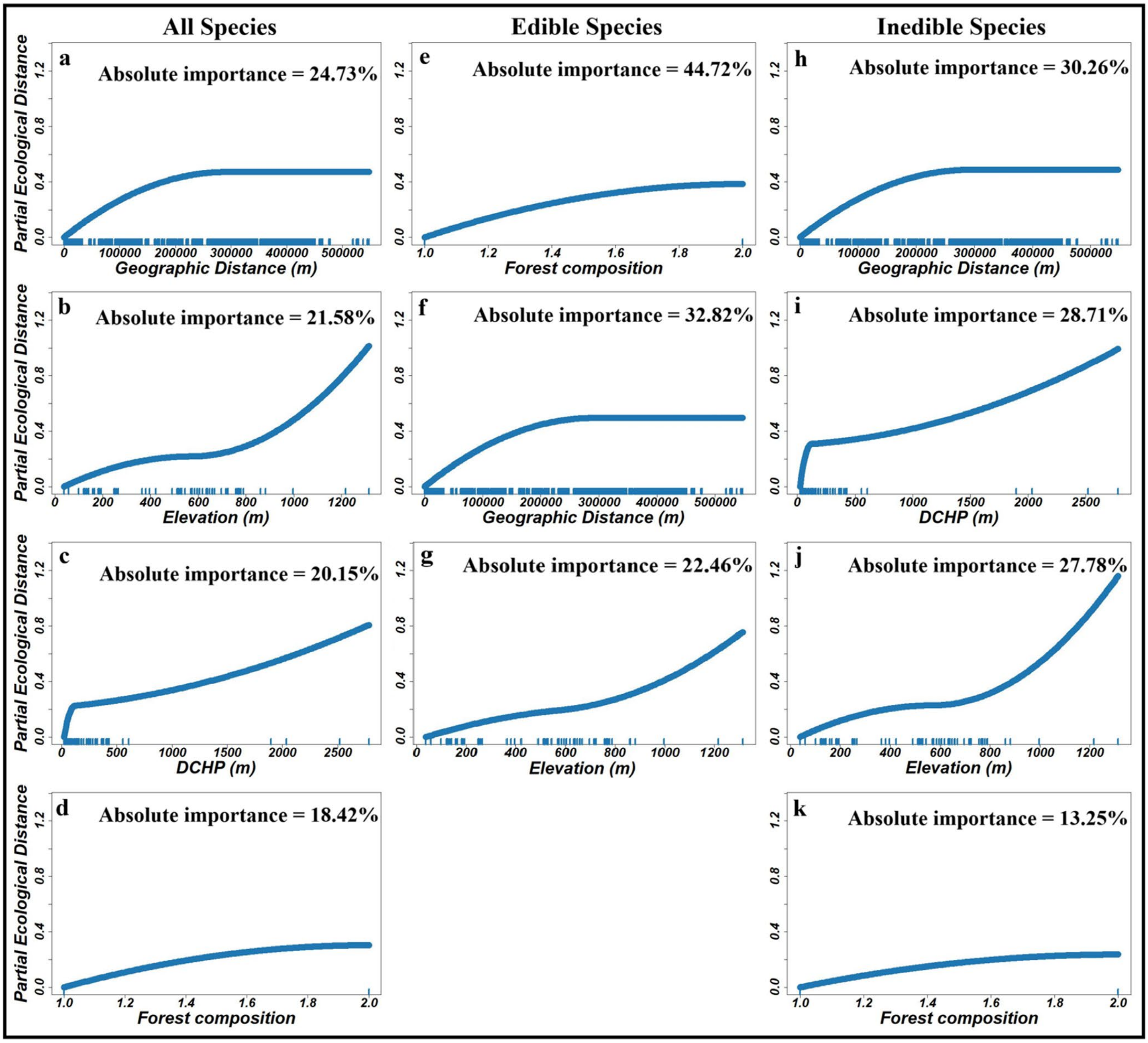

FIGURE 3 | Plotted I-splines of the three variables with the highest importance scores from the GDMs, analysing the spatial relationship between geographical gradients, environmental variables and tree species composition. Plots are the Total Sørensen's beta-diversity for all the species in the region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

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).

3.2.1.3 | **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 600 m 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.

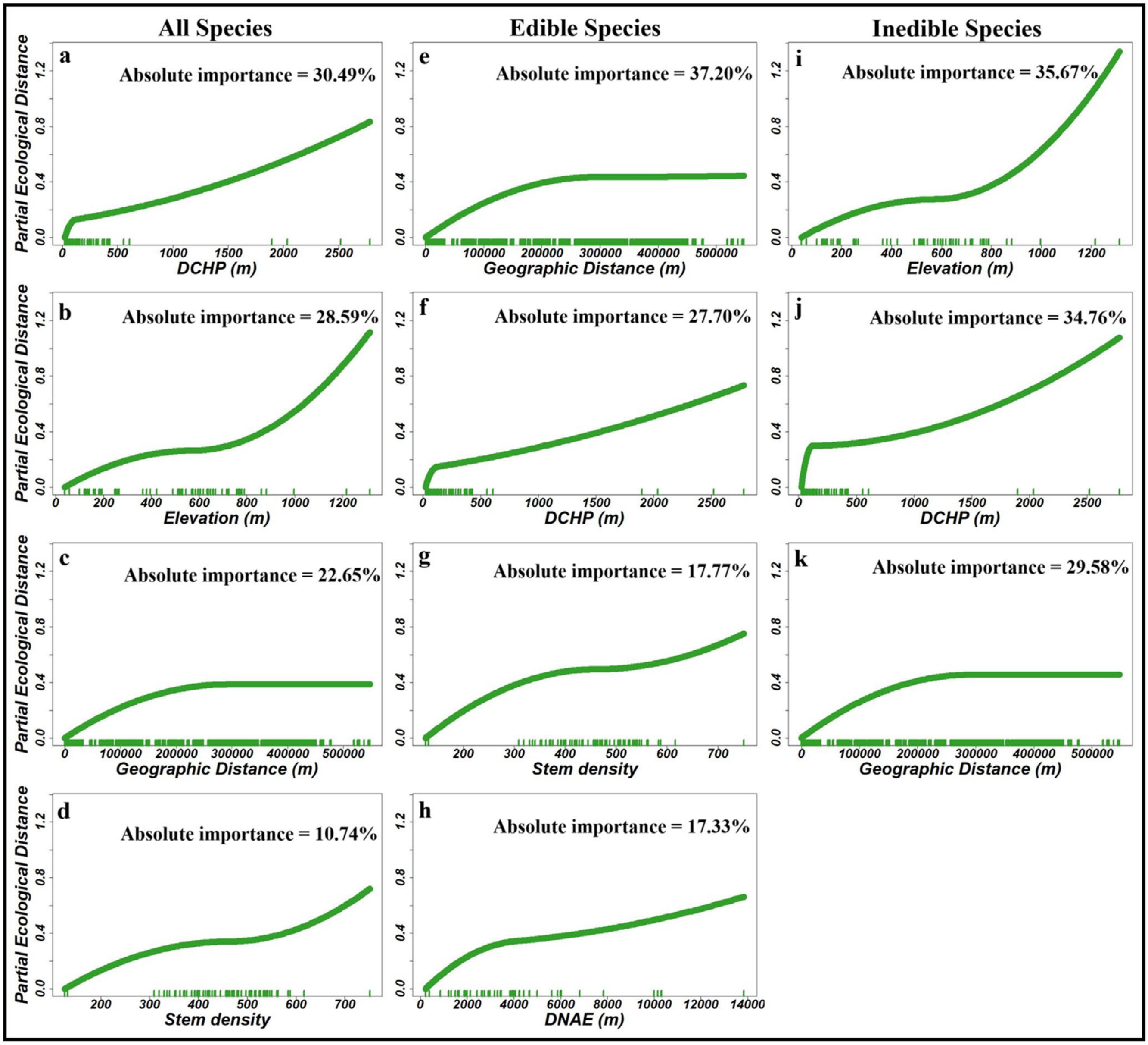

FIGURE 4 | Plotted I-splines of the variables with the highest importance scores from the GDM, analysing the spatial relationship between the turnover component of Sørensen's beta-diversity and geographical gradients, environmental variables and tree species categories. Plots columns are arranged from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

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. 2023; 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 (Adnan et al. 2015; Asuk et al. 2023), 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; 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. 2021a, 2021b; 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 were more important drivers 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 aligns 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; it 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 Amazonhave 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 occurred 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.

Author Contributions

S.A.A., J.P.W., N.K., J.P.S., T.A.M.P., and T.J.M. conceived the ideas. S.A.A. and V.T.E. collected the primary data. O.L.P., S.L., B.S., J.T., J.C., L.Z., L.O., S.B., H.T., T.S., W.H., V.D., L.Q., M.G., M.S.-D, T.F., K.S.H.P., L.F.B., and M.N.D.K. provided secondary data. S.A.A. and J.P.W. analysed the data. S.A.A. led the interpretation and drafted the first version of the manuscript, with input from J.P.W., N.K., J.P.S., T.A.M.P., T.J.M., K.S.H.P., and O.L.P. The manuscript was reviewed and edited by S.A.A., J.P.W., J.P.S., T.A.M.P., T.J.M., V.T.E., O.L.P., S.L., J.T., W.H., L.Q., T.F., K.S.H.P., L.F.B., and N.K. All authors approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings will be available in Dryad at https://doi.org/10.5061/dryad.4tmpg4fkq following an embargo from the date of publication to allow for commercialization of research findings. However, the full data that support the findings of this study are available from the Forest Plots Database. Restrictions apply to the availability of these data, which were used under license for this study. Data are available https://forestplots.net/ with the permission of the Forest Plots Database.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70075.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **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. **Table S2:** Information on tree data from plots used for the study, including location of plot code, country of location, dimension and year censuses. **Table S3:** Distribution of edible and inedible tree species found in mixed and monodominant forest plots. **Table S4:** Distribution and descriptive statistics of predictor variables included in the GDMs models. **Appendix S2:** Qualitative data collection and structured questionnaire used for collection of data on forest tree species utilisation in Oban Division, Cross River National Park. **Appendix S3:** Methodology for assessing human impact on tree species composition using proximity measures. **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. **Figure 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. **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–d,l), for the edible species category (e–g) and for the inedible species (h–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–d,l), edible species category (e–h) and inedible species category (i–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.