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RESEARCH ARTICLE

Mapping the Ecological Niche of a Key West African Species: *Terminalia leiocarpa*

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ABSTRACT

Terminalia leiocarpa (DC.) Baill is a tree species widely used in ethnoveterinary practices, human medicine, furniture and charcoal making. Our study aimed to (i) map the favourable areas for the species in Benin, both currently and in the future, and (ii) analyse the biotic and abiotic factors affecting the structure and availability of *T. leiocarpa*. To achieve this goal, a dendrometric inventory of 141 plots across the three climate zones of Benin was carried out. This included the collection of soil type and insect attack data at the plot level, as well as climate data downloaded from the WorldClim 2 platform. Dendrometry parameters, such as basal area, tree height and diameter, Lorey height and importance value index (IVI) were calculated, and generalised linear mixed models, were established to determine the effects of biotic (diameter of heterospecific trees, density and diameter of conspecific trees) and abiotic (mean of daily temperature variation (bio2) and annual precipitation (bio12)) factors on these parameters. The future distribution areas of *T. leiocarpa* in Benin were projected under SSP 2–4.5 and SSP 5–8.5 scenarios using Maximum Entropy (MaxEnt). The results predicted a decrease in the suitable areas of 22% and 33% under the SSP 2–4.5 and SSP 5–8.5 scenarios, respectively. Our results also showed that conspecific tree diameter ($\beta = 0.34$; $p = 0.000$) and conspecific tree density ($\beta = 0.02$; $p = 0.036$) were positively associated with the tree height, while bio2 ($\beta = -0.32$; $p = 0.039$) and bio12 ($\beta = -0.01$; $p = 0.004$) had a negative effect on *T. leiocarpa* diameter. These results should help us to understand the ecological niche and to take the necessary steps upstream to contribute to the conservation and sustainable use of *T. leiocarpa*. Future studies could focus on analysing the impact of environmental factors on juvenile growth and survival.

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1 | Introduction

Human activities and climate change are two major factors determining the geographical distribution of species (Mensah et al. 2014; Hounsou-Dindin et al. 2023). According to the sixth assessment report (AR6) of the Intergovernmental Panel on Climate Change (IPCC), global warming has induced the displacement of almost half of all species from their usual environment to a new ecosystem capable of providing them with optimal conditions for reproduction and growth (Calvin et al. 2023). The same report projects that the biological responses of species will no longer be sufficient to cope with the scale of heat extremes and predicts the loss of many species. Habitat modification due to climate change affects species survival and is a major threat when associated with anthropogenic actions (Stocker et al. 2013; Tiébré et al. 2016; Noulekoun et al. 2017; Krishnadas and Stump 2021). In such a context, it seems urgent and necessary to analyse the current and future distribution of multipurpose species that are under strong anthropic pressure due to their socio-economic importance. Understanding how climate change would affect the geographical distribution of species now and in the future has become a major concern in ecology and related sciences in recent years (Agbo et al. 2019; Biaou et al. 2023; Hounsou-Dindin et al. 2023).

Predicting the current and future geographical suitable habitats distribution of a species under several climate scenarios is a way of producing scientific data that should contribute to better species conservation and sustainable use. Several algorithms have been developed to predict the geographic distribution of a species and identify the factors influencing this distribution. Among these algorithms are species distribution models (SDMs), which predict the impact of climate change on species distribution using their occurrence records and bioclimatic variables provided by the WorldClim database (Booth et al. 2014; Cotrina Sanchez et al. 2021; Biaou et al. 2023; Hounsou-Dindin et al. 2023). Among the SDMs, Maximum Entropy (MaxEnt) remains the most widely used because it gives an excellent result when used in comparison with the others (Daï et al. 2023; Lokonon et al. 2023). To assess the effect of climate change on the future distribution of species, the Shared Socioeconomic Pathways (SSPs) scenarios are recommended because they take into account the socio-economic factors, which play a key role in climate change (Meinshausen et al. 2020; Ames-Martínez et al. 2022).

Many environmental factors affect the survival, growth, distribution and diversity of species within a community. The impact of abiotic (soil type, light, precipitation, temperature, etc.) and biotic (heterospecific and conspecific tree density, natural enemies, vegetation type, etc.) factors on plant structure has been extensively studied in recent years (Canham et al. 2004; Atanasso et al. 2019; Magee et al. 2021; Mensah et al. 2023). Diameter at Breast Height (DBH), tree density and height and basal area are among the structural parameters on which the impact of environmental factors is assessed (Atanasso et al. 2019; Mensah et al. 2023). The effect of biotic and abiotic factors has been evaluated on juvenile survival rate and/or structure of several species including *Tsuga heterophylla* (Raf.) Sarg, *Thuja plicata* Donn ex D. Don (Canham et al. 2004) and *Afzelia africana* Sm. (Atanasso et al. 2019, 2021; Mensah et al. 2023). It is well established that the presence or absence of a species in an environment, as well as its level of abundance, depends on a range of abiotic and biotic factors (Adomou et al. 2006; Atanasso et al. 2021; Liang et al. 2022). Understanding the impact of those factors on species is crucial for sustainable management and forest restoration.

Here we focus on *T. leiocarpa*, formerly known as *Anogeissus leiocarpa*, which belongs to the Combretaceae family. *T. leiocarpa* is a plant widely used in ethnoveterinary medicine (Kone et al. 2019; Traore et al. 2020; Tchetan et al. 2021). Its leaves are used to treat digestive disorders in small ruminants (Tchetan et al. 2022) and cough in cattle (Kone et al. 2019). *T. leiocarpa* wood is also widely used in the furniture and charcoal industries. Several scientific studies have focused on the ecological characteristics of *T. leiocarpa* in West Africa (Assogbadjo et al. 2009; Ouédraogo et al. 2013; Tchetan et al. 2024). For example, Ouédraogo et al. (2013) showed that the climate gradient did not influence the structural traits and parameters of *T. leiocarpa*. However, the impact of specific abiotic and biotic factors on the structural parameters of *T. leiocarpa* has not been documented. Furthermore, the literature reveals that *T. leiocarpa* is highly resistant to anthropogenic pressure and has the ability to reproduce both sexually and asexually (Assogbadjo et al. 2009; Bognounou et al. 2010). Moreover, Tchetan et al. (2024) have shown that *T. leiocarpa* is distributed in the three climate zones of Benin; however, the impact of climate change on this distribution in the future has not been predicted, and the factors that could affect this distribution have not been identified.

As revealed by some largely distributed tree species, climate change has reduced their suitable areas distribution (Fandohan et al. 2013; Ayihouenou et al. 2016). In addition, several studies have shown that the density and diameter of conspecific trees affect structure, particularly tree height and juvenile survival (Johnson et al. 2017; Atanasso et al. 2019; Magee et al. 2021; Mensah et al. 2023). Similarly, the work of Johnson et al. (2017) has shown that abiotic factors such as temperature significantly affect the structure and survival of plant juveniles in a plant community. In that case, we expect the same scenario for *T. leiocarpa*, a species that occurs from humid to dry zones.

Our study aimed to (i) map the favourable area of distribution of *T. leiocarpa*, currently and in the future, and (ii) assess the biotic and abiotic factors affecting the structure and availability of *T. leiocarpa* in Benin.

We therefore projected that (1) the suitable area of distribution for *T. leiocarpa* in Benin will decrease under both climate scenarios and predicted that (2) diameter and density of conspecific trees will increase tree height, while (3) the annual temperature range (bio7) will negatively affect the basal area of *T. leiocarpa*.

2 | Materials and Methods

2.1 | Study Environment

The study was carried out in Benin (6°–12.25° N; 0.40°–3° E) between June and August 2023. It covered the three climate zones of the country: the Guinean zone, the Sudano-Guinean zone and the

Sudanian zone. *T. leiocarpa* is found in several forests distributed across these three climate zones (Akoègninou et al. 2006).

In the Guinean zone (1°00′–2°45′ E and 6°30′–7°30′ N), the study focused on the Lama and Dogo forests, as well as the surrounding fields and fallows (Figure 1). This climate zone is characterised by a bimodal rainfall regime, ranging from 900 to 1200 mm, and generally has ferralitic soils (Adomou et al. 2006). The average temperature is 27°C. The Lama forest covers an area of 16,250 ha and is located between the departments of Atlantique (9750 ha in Toffo) and Zou (6500 ha in Zogbodomey; Toyi et al. 2018). The Dogo forest covers 31,850 ha and is located in the northeast of the municipality of Kétou (Houndagba et al. 2007). The main ethnic groups around the Dogo and Lama forests are the Yoruba, Adja and Fon. Agriculture and trade are the main activities of the populations living around these forests (Adomou et al. 2006). The vegetation in this zone consists mainly of fallow land and dense forest dominated by *Chromolaena odorata* (L) King & H.E. Robins, *Afzelia africana* Sm, *Diospyros mespiliformis* Hocchst. Ex A. DC. and *Dialium guineense* Willd.

The Sudano-Guinean zone (1°55′–2°25′ E and 8°50′–9°10′ N) is characterised by a unimodal rainfall pattern (1100–1200 mm) and ferruginous soils (Adomou et al. 2006). Temperatures range from 21°C to 35°C. The vegetation in this climate zone is generally of the dry dense forest type. The study was conducted in the Ouémé Supérieur and Monts Kouffé forests and their surrounding fields and fallow land (Figure 1). The Ouémé Supérieur forest is located in the municipality of Djougou and covers 117,542 ha (Adjéran et al. 2020). The Monts Kouffé forest straddles the municipalities of Bantè and Bassila and covers 240,432 ha (Mouhamadou 2019). The main ethnic groups in this area are the Nagot, Dendi, Peulh and Holi. Agriculture, based on slash-and-burn cultivation, is the main activity of the local people (Adomou et al. 2006). This zone is characterised by forests and savannahs dominated by *Berlinia grandiflora* (Vahl) Hutch. & Dalziel, *Cola gigantea* A.Chev., *Vitex doniana* (Sweet), *Pterocarpus santalinoides* L'Hérit. ex-DC. and *Diospyros mespiliformis* Hocchst. Ex A. DC. (Adomou et al. 2006).

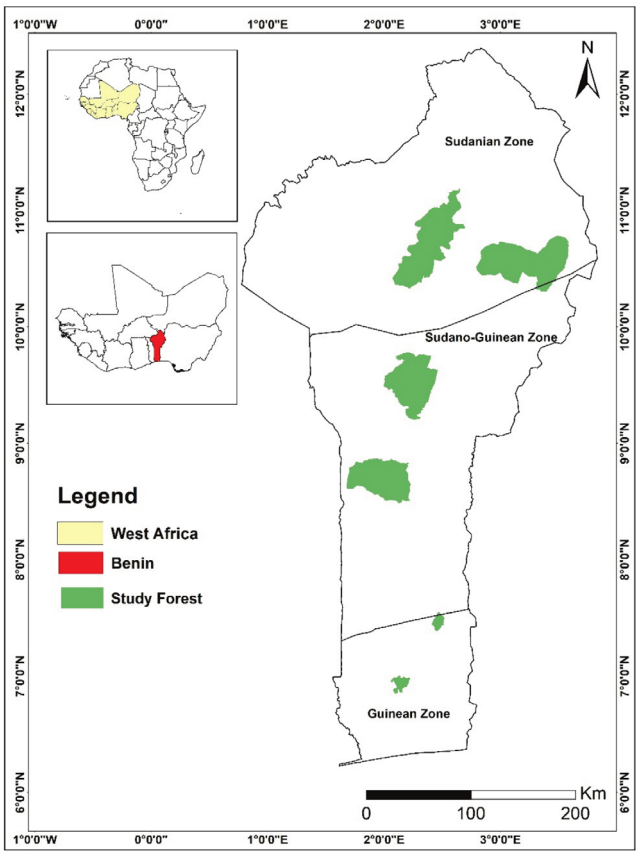


FIGURE 1 | Map of Benin showing the study sites by climate zone.

The Sudanian zone (2°25′–3°40′ E and 9°10′–12°30′ N) is located in the north of Benin and is characterised by savannahs, open forests and dense dry forests. This zone experiences unimodal rainfall (950–1000 mm) and has ferruginous soils (Adomou et al. 2006). Temperatures range from 17°C to 38°C. In this zone, we explored the Alibori Supérieur and Trois Rivières forests and their surrounding fields and fallow land (Figure 1). The Alibori Supérieur forest straddles the municipalities of Kandi, Banikoara and Kérou, covering 257,730 ha (Mama et al. 2020). The Trois Rivières forest lies between the municipalities of Bembèrèkè, Kalalé, Gogounou and Ségbana and covers 268,530 ha (Zakari et al. 2018). The main ethnic groups in this region are the Dendi, Peulh, Haoussa and Bariba. Their main activities are farming, raising ruminants and petty trading (Adomou et al. 2006). Savannah is the main vegetation type in this zone. *Parkia biglobosa* (Jacq) R.Br, *Anogeissus leiocarpa* Guill Perr. and *Acacia gourmaensis* A. Chev are among the dominant species in this zone (Houehanou et al. 2013).

2.2 | Study Species

T. leiocarpa (formerly known as *A. leiocarpa/leiocarpus*) is a tree species native to tropical Africa and belongs to the Combretaceae family. It is commonly known as the "African birch". The tree is found in savannahs, dry forests, gallery forests and equatorial forests. It is a medium to large tree, reaching heights of up to 40 m, with a straight trunk and a spreading crown. Its leaves are alternate, simple, oblong and dark green in colour (Andary et al. 2005). The flowers are small, cream or white, and grouped in hanging clusters. The fruits are elliptical drupes, turning dark brown to black when ripe, and contain a single seed. It is prized for its durable, hard-wearing wood, which is used in construction, furniture-making, joinery and similar applications (Akoègninou et al. 2006). It is also widely used in traditional medicine to treat various ailments (Andary et al. 2005; Tchetan et al. 2021). *T. leiocarpa* has been identified in Djakotomey (Guinean zone), Borgou Sud (Sudano-Guinean zone) and Pendjari National Park (Sudanian zone). The structure of *T. leiocarpa* is negatively affected by anthropogenic actions, including fires, removal of leaves and other organs and grazing (Assogbadjo et al. 2009; Amoako and Gambiza 2021). The species tolerates drought and lack of light (Amoako and Gambiza 2021). The tree is also sensitive to several other climate and edaphic factors (Tchetan et al. 2024). Indeed, these authors showed that the values of the structural parameters of the plant varied significantly according to climate zones in Benin.

2.3 | Sampling Design

A total of 141 plots were established in six sites across the three climate zones. On average, 30 plots were established in each site:

15 plots in protected areas (forests) and 15 in their surrounding unprotected areas (fields and fallow land). In each area, plots of 0.1 ha (50 m × 20 m) were established where at least one individual of *T. leiocarpa* was present (Tchetan et al. 2024). A minimum spacing distance of 500 m was maintained between plots. Individuals with a diameter at breast height (DBH) ≤ 10 cm were considered as juveniles, and those with a DBH > 10 cm were considered to be in the tree layer (Sokpon et al. 2006; Moussilimi et al. 2022). Each plot was associated with four subplots of 100 m^2 (10 m × 10 m) established in the corners for regeneration enumeration (Hounsode et al. 2014).

2.4 | Data Collection

To predict the potential future distribution of *T. leiocarpa*, occurrence coordinates were downloaded from the Global Biodiversity Information Facility (GBIF) website (www.gbif.org) and enriched with field observation data (Fandohan et al. 2013). These data were cleaned to remove coordinates outside the range of the species and to eliminate duplicates. A total of 557 species occurrence data were used, of which 416 were downloaded from the GBIF website and 141 were recorded in the field. The spThin package (Aiello-Lammens et al. 2015) of the R software was used to refine the coordinates within a 1 km radius to avoid spatial sampling bias and align with the grid resolution, ensuring only one occurrence point per pixel (Ganglo 2023).

Bioclimatic variables (Table 1) were downloaded at a 1 km resolution from the WorldClim 2 (https://www.worldclim.org/data/worldclim21.html, accessed on 06 May 2025) for the current climate and for the SSPs projections (Fick and Hijmans 2017). Based on the Shared Socioeconomic Pathways (SSPs), future climate scenarios are organised in five main groups including SSP 2–4.5 and SSP 5–8.5 (Meinshausen et al. 2020). The first (SSP 2–4.5) projects average greenhouse gas emissions while the second (SSP 2–4.5) represents extreme greenhouse gas emissions. These two scenarios are widely used in plant habitat modelling (Ames-Martínez et al. 2022; Biaou et al. 2023).

The 1 km resolution soil variable, containing different soil types (Harmonised World Soil), was downloaded from the FAO world database (https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v20/en/; Fischer et al. 2008).

Information such as plot coordinates, DBH, total height of individuals with DBH ≥ 10 cm and the number of juveniles in sub-plots were collected in each plot. Anthropogenic pressure, which refers to all disturbances to the environment caused by human activities such as logging, grazing, late fires and agricultural activities, was recorded for each plot (Kagambega et al. 2019). A four-level codification was adopted based on the work of Kagambega et al. (2019): 0 for no trace of pressure, 1 for low pressure (< 10% of the plot), 2 for medium pressure (between 10% and 40% of the plot) and 3 for high pressure (> 40% of the plot). The activities of natural enemies such as insects and fungi were recorded as presence/absence according to Chanthorn et al. (2013). Any signs of decomposition of leaves, roots or trunks, insect attacks, galls or other signs of fungal diseases would indicate the presence of natural enemy activities (Mensah et al. 2020, 2023; Atanasso et al. 2021). Vegetation type was also recorded for each plot (Atanasso et al. 2021). Information on soil type in each plot, including the presence of clay, sand or rock (Houehanou et al. 2013; Mensah et al. 2023), was also collected.

TABLE 1 | Bioclimatic variables and descriptions.

Bioclimatic variables	Descriptions
Bio1	Annual mean temperature
Bio2	Mean diurnal range (mean of monthly (max temp − min temp))
Bio3	Isothermality (bio2/bio7) (×100)
Bio4	Temperature seasonality
Bio5	Maximum temperature of warmest month
Bio6	Minimum temperature of coldest month
Bio7	Annual temperature range (bio5–bio6)
Bio8	Mean temperature of wettest quarter
Bio9	Mean temperature of driest quarter
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of wettest month
Bio14	Precipitation of driest month
Bio15	Seasonality of precipitation (coefficient of variation)
Bio16	Precipitation of wettest quarter
Bio17	Precipitation of driest quarter
Bio18	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter

The bioclimatic variables downloaded from the WorldClim 2 for each climate zone were extracted at the centre of each plot using the GPS coordinates and the raster package extraction function of the R software (Table 1; Hijmans and Van Etten 2020; Akpovo et al. 2023).

2.5 | Data Analysis

2.5.1 | Model Development Process to Predict the Favourable Areas for *T. leiocarpa*

A correlation test was carried out using ENMTools 1.3 to select variables with low correlation coefficients. The five least correlated variables were then selected. MaxEnt 3.4.4 modelling

software (Phillips et al. 2006) was used to predict the favourable areas for *T. leiocarpa*. Future climate projections were made up to 1970–2000 currently, and 2041–2060 in the future, under the SSP 2–4.5 and SSP 5–8.5 (Meinshausen et al. 2020).

Part of the observations (75%) was used to build the model, and the remaining 25% was used for testing. The Jackknife test was performed on the selected bioclimatic variables to determine their contribution to the model, and the area under the curve (AUC) statistic was used to assess the performance of the model (Phillips et al. 2006; Fandohan et al. 2013). A model is considered powerful if the AUC value is greater than 0.90 (Swets 1988; Fandohan et al. 2013).

2.5.2 | Mapping and Spatial Analysis

The results of the models were transferred to ArcGIS 10.4 software to evaluate the different levels of favorability for *T. leiocarpa* based on logistic probability thresholds of presence, which vary from 0 to 1. Three habitat classifications were established for the study region: areas with a presence probability of less than 0.4 were considered not favourable, those between 0.4 and 0.7 as favourable and those between 0.7 and 1 as highly favourable for *T. leiocarpa* (Agbo et al. 2019). Using the spatial analysis functions of ArcGIS, we calculated the extent of each favourability level of habitat for both present and future conditions.

2.5.3 | Availability, Structural Parameters and Biotic Factors Calculated

Table 2 shows the calculated parameters.

2.5.4 | Effect of Anthropogenic, Biotic and Abiotic Factors on the Availability and Structural Parameters of *T. leiocarpa*

The effect of anthropogenic factor, biotic factors (heterospecific tree density, conspecific tree density, diameter of conspecific trees, diameter of heterospecific trees, natural enemies and vegetation type) and abiotic factors (soil type and climate variables) on availability and structural parameters was evaluated using two general linear mixed models (GLMMs) (Atanasso et al. 2021; Magee et al. 2021; Mensah et al. 2023). The first (Gaussian model) assessed the effect of anthropogenic, biotic and abiotic factors on availability, and the second lognormal model assessed the effect of these same factors on structural parameters of *T. leiocarpa*. The GLMMs were implemented using the GLMMTMB package (Brooks et al. 2023) in R software. We ran several linear models using tree density, height, diameter, basal area, Lorey height, importance value index (IVI), as response variables and anthropogenic factor, biotic factors (heterospecific tree density, conspecific tree density, diameter of conspecific trees, diameter of heterospecific trees, natural enemies and vegetation type), abiotic factors (soil type and climate variables, Table 1), as explanatory variables.

3 | Results

3.1 | Current and Future Distribution Areas of *T. leiocarpa*

3.1.1 | Contribution of Environmental Variables and Validation of the Model

A total of five variables were identified to be important in predicting the distribution of *T. leiocarpa*. These were soil, annual mean temperature (bio1), annual precipitation (bio12), temperature seasonality (bio4) and mean of daily temperature variation (bio2) (Table 3, Figure S1). Soil was the variable that contributed most to the model, with a contribution of 43.5%. The other variables made a similar contribution of around 15% (Table 3). The average AUC value (0.932) obtained shows that our models are of excellent quality and very robust (Figure S2). Similarly, the mean value of the TSS (0.68) indicates that our models have very good predictive power.

3.1.2 | Current Favourable Areas for *T. leiocarpa* in Benin

The current favourable areas for *T. leiocarpa* span the three climate zones but are more localised in the Sudano-Guinea zone (Figure 2). The current favourable areas cover 46,967 km^2 (41% of the surface area of Benin) compared to 9467 km^2 (8% of the surface area of Benin) for highly favourable areas (Table 4).

3.1.3 | Future Distribution of *T. leiocarpa* in Benin Under Climate Change

The projection of *T. leiocarpa* distribution under SSP 2–4.5 and SSP 5–8.5 showed a similar trend for both scenarios (Table 3, Figures 2 and S3). Similarly, both scenarios predicted that the favourable and highly favourable area for the distribution of the species would be concentrated in the Sudano-Guinean zone (Figure 2). In summary, the two scenarios projected a retraction of the suitable area (favourable plus highly favourable areas) for the distribution of *T. leiocarpa* of 22% (i.e., 12,530 km^2) and 33% (i.e., 18,396 km^2), for the SSP 2–4.5 and SSP 5–8.5 scenarios, respectively. Under these two climatic scenarios, retraction could be more pronounced in the Guinean and Sudanian zones, in contrast to the Sudano-Guinean zone, which remains largely suitable for the future distribution of the species (Figure 2).

3.2 | Effect of Anthropogenic, Biotic and Abiotic Factors on the Availability of *T. leiocarpa*

Several environmental factors significantly affected the availability of *T. leiocarpa* across the three climate zones. Anthropogenic factors were associated with *T. leiocarpa* availability (Figure 3a; Table S1). Biotic factors such as heterospecific tree diameter ($\beta = -0.45$; $p = 0.001$; Table S1) were negatively associated with *T. leiocarpa* availability. In fact, an increase in the heterospecific tree diameter leads to a decrease in the *T. leiocarpa* availability (Figure 3b). Vegetation type was also significantly associated with

TABLE 2 | Importance value index (IVI), dendrometric parameters and biotic factors calculated to characterise *T. leiocarpa* in Benin.

Parameters	Formulas	Descriptions	References
Importance value index (IVI)			
Importance value index (IVI)	$\mathrm{IVI} = \sum F_r + \mathrm{D_r} + \mathrm{G_r}$	F_r is the relative frequency of a species, D_r is its relative density, and G_r is its relative basal area. The IVI ranges from 0 to 300, with a higher value indicating greater ecological availability of the species	Curtis and McIntosh (1951)
Dendrometric parameters			
Density (D)	$D = \frac{n}{s}$	D is the density expressed as the number of individuals per hectare (trees/ha), n is the average number of individuals per plot and s is the area of the plot in hectares	Assogbadjo et al. (2009); Mensah et al. (2014)
Basal area (G)	$G = \frac{\pi}{4s} \sum_{i=1}^{n} d_i^2$	G is the basal area (m^2/ha), d_i is the DBH (m) of an individual of the species and s is the area of the plot (m^2)	
Average Lorey height (Hl)	$\mathrm{Hl} = \frac{\sum_{i=1}^{n} g_i h_i}{\sum_{1=1}^{n} g_i}$ with $g_i = \frac{\pi}{4} d_i^2$	g_i, h_i and d_i, respectively, are the basal area, total height and diameter of tree i	
Regeneration density (D_r)	$D_r = \frac{n}{s}$	$\mathrm{D_r}$ is the regeneration density expressed as the number of individuals per hectare (regeneration/ha), n is the average number of individuals per plot and s is the area of the plot in hectares	
Biotic factors calculated			
Average diameter of conspecific trees (DIAcons)	$\mathrm{DIAcons} = \frac{\sum d_i C}{N}$	DIAcons is the average diameter of conspecific trees, $d_i C$ is the diameter of conspecific tree i and N is the total number of conspecific trees	Johnson et al. (2017); Atanasso et al. (2019)
Density of conspecific trees (Dcons)	$D\mathrm{cons} = \frac{n}{s}$	Dcons is the density of conspecific trees, n is the number of individuals of the target species in each plot and s is the area of the plot in hectares	
Average diameter of heterospecific trees (DIAhetero)	$\mathrm{DIAhetero} = \frac{\sum d_i H}{N}$	DIAhetero is the average diameter of heterospecific trees, $d_i H$ is the diameter of heterospecific tree i and N is the total number of heterospecific trees in each plot	
Heterospecific tree density (Dhetero)	$D\mathrm{hetero} = \frac{n}{s}$	Dhetero is the density of heterospecific trees, n is the number of trees of non-target species in each plot and s is the area of the plot in hectares	

the IVI of *T. leiocarpa* (Figure S4). Other biotic factors, such as the mean diameter of conspecific trees, regeneration density, density of heterospecific trees, mean diameter of heterospecific trees, density of conspecific trees and activities of natural enemies, were not associated with the availability of *T. leiocarpa*.

Among the abiotic factors, the annual mean temperature (bio1; $\beta = -330.86$, $p = 0.045$, Table S1) and the mean temperature of the coldest quarter (bio11; $\beta = 290.43$; $p = 0.019$; Table S1) were significantly associated with the availability of *T. leiocarpa*. In fact, an increase in bio1 led to a decrease in the availability of *T. leiocarpa*, and the opposite effect was observed with bio11 (Figure 3c). Other abiotic factors were not significantly associated with the availability of *T. leiocarpa* (Table S1).

3.3 | Effect of Anthropogenic, Biotic and Abiotic Factors on the Structural Parameters of *T. leiocarpa*

We analysed the effects of environmental factors (anthropogenic, abiotic and biotic) on each structural parameter of *T. leiocarpa*, separately. Table S2 summarises the effect of environmental

factors on the height of *T. leiocarpa*. Conspecific tree diameter ($\beta = 0.34$; $p = 0.000$; Table S2) and conspecific tree density ($\beta = 0.02$; $p = 0.036$; Table S2) were positively associated with the height of *T. leiocarpa*. An increase in the diameter and density of conspecific trees leads to an increase in the height of *T. leiocarpa* (Figure 4a,b). Vegetation type also significantly affected the height of *T. leiocarpa* (Figure S5). Other environmental factors were not significantly associated with *T. leiocarpa* height.

TABLE 3 | Contributions of the five selected variables to the model.

Selected variables	Contribution (%)	Permutation importance
Soil	43.5	25.9
Annual mean temperature (bio1)	15	6.5
Annual precipitation (bio12)	14.5	6.2
Temperature seasonality (bio4)	13.9	23.2
Mean of daily temperature variation (bio2)	13.2	38.2

Conspecific tree diameter ($\beta = 0.30$; $p = 0.000$; Table S3), conspecific tree density ($\beta = 0.04$; $p = 0.000$; Table S3) and precipitation of warmest quarter (bio18) ($\beta = 0.17$; $p = 0.004$; Table S3) were positively associated with the Lorey height of *T. leiocarpa*. In addition, the anthropogenic factor and the climate zone significantly affected the Lorey height of *T. leiocarpa* (Table S3 and Figure S5).

The basal area of *T. leiocarpa* was significantly associated with some environmental factors, including the diameter of conspecific trees ($\beta = 0.15$; $p = 0.000$; Table S4 and Figure S6), density of conspecific trees ($\beta = 0.06$; $p = 0.000$; Table S4 and Figure S6) and annual temperature range (bio7) ($\beta = -1.66$; $p = 0.001$; Figure 4c; Table S4). In addition, vegetation type and climate zone positively affected the basal area of *T. leiocarpa* (Figures 4d and S6).

3.4 | Effect of Ecological Niche Modelling Variables on the Availability and Structural Parameters of *T. leiocarpa*

As soil, annual mean temperature (bio1), annual precipitation (bio12), temperature seasonality (bio4) and mean of daily

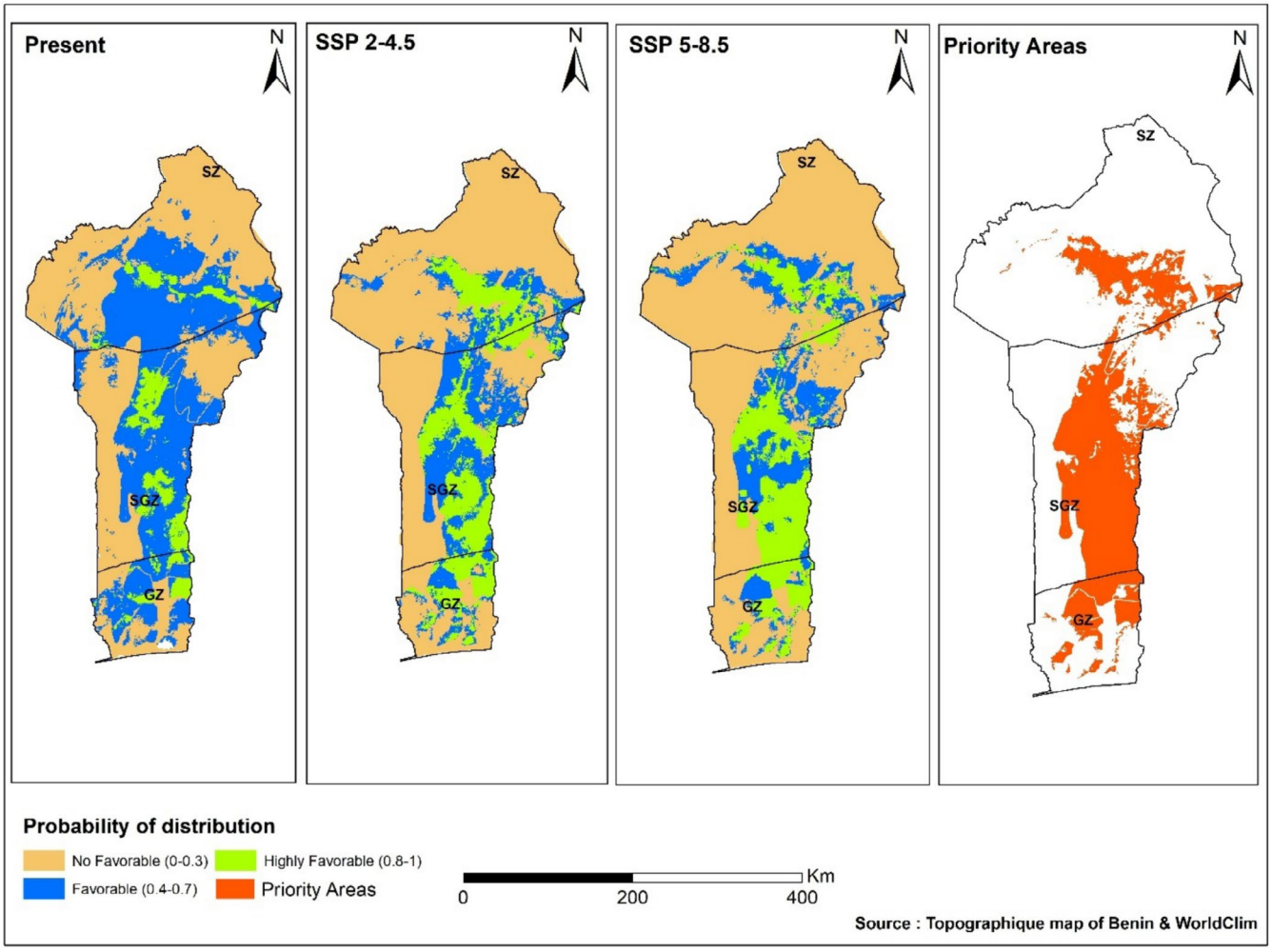


FIGURE 2 | Map of current and future distribution of *T. leiocarpa* in Benin (GZ, Guinean Zone; SGZ, Sudano-Guinean Zone; SZ, Sudanian Zone).

TABLE 4 | Dynamics of the current and future favourable areas for *T. leiocarpa*.

	No favourable areas		Favourable areas		Highly favourable areas		Suitable areas		Total areas
Projection	Extent (km^2)	Tendency (%)	Extent (km^2)	Tendency (%)	Extent (km^2)	Tendency (%)	Extent (km^2)	Tendency (%)	Extent (km^2)
Present	58,090	—	46,967	—	9467	—	56,434	—	114,524
SSP 2–4.5	70,619	+22	22,757	−52	21,147	+123	43,904	−22	114,524
SSP 5–8.5	76,485	+32	17,869	−62	20,169	+113	38,038	−33	114,524
Priority areas					2342				

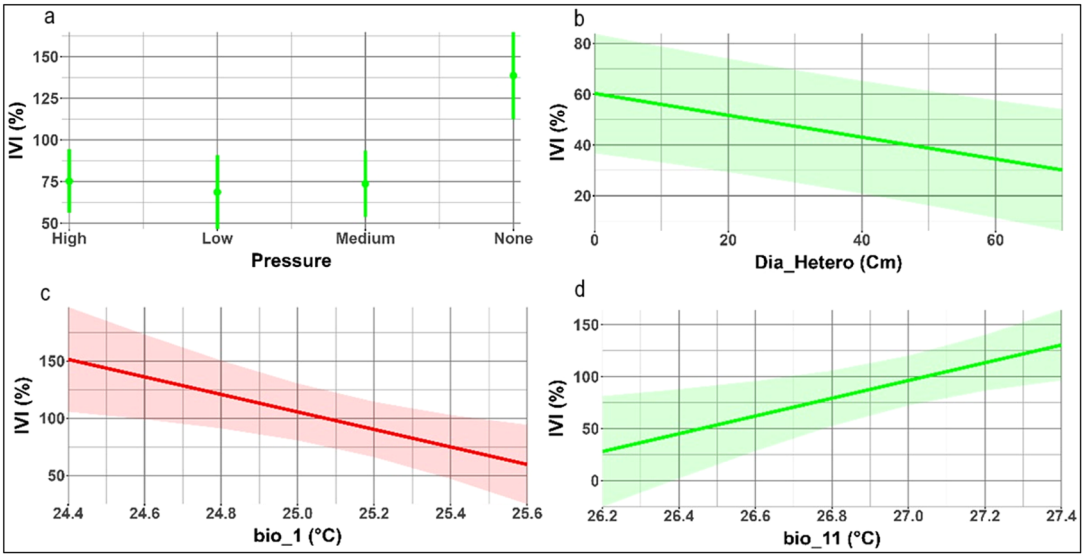


FIGURE 3 | Effects of anthropogenic factor (a), heterospecific tree diameter (b), annual mean temperature (bio1) (c) and mean temperature of coldest quarter (bio11) (d) on the importance value index (IVI) of *T. leiocarpa*.

temperature variation (bio2) were the five environmental variables that contributed most to the prediction of *T. leiocarpa* distribution areas, we decided to assess the effect of these variables on the availability and structure of *T. leiocarpa*.

Bio1 ($\beta = 95.48$; $p = 0.000$; Table S6; Figure 5a) and bio12 ($\beta = 0.49$; $p = 0.000$; Table S6; Figure 5b) were positively associated with the availability of *T. leiocarpa*. The other variables had no significant effect on the availability of *T. leiocarpa* (Table S6).

Bio2, bio12 and soil significantly affected the structure of *T. leiocarpa* (Table S7). For example, bio2 ($\beta = -0.32$; $p = 0.039$; Table S7; Figure 5c), soil ($\beta = 0.00$; $p = 0.047$; Table S7 and Figure S7) and bio12 ($\beta = -0.01$; $p = 0.004$; Table S7 and Figure S7) were significantly associated with the diameter of *T. leiocarpa*. Similarly, bio2 ($\beta = -0.47$; $p = 0.002$; Table S7; Figure 5d) has a negative effect on the Lorey height of *T. leiocarpa*.

4 | Discussion

The present study explored how environmental factors and climate change will impact the distribution and structure of *T. leiocarpa*, a tropical multipurpose plant. To achieve this, we used two approaches. The first is to implement the MaxEnt approach to predict the impact of climate change on the future distribution of *T. leiocarpa*. The second approach identifies the correlations between environmental factors (anthropogenic, abiotic and biotic) and the structure of *T. leiocarpa*. The results of both approaches remain predictive and cannot be considered experimental results. However, the results obtained are crucial and should help us to better understand the ecology of *T. leiocarpa* and prepare for its sustainable use.

4.1 | Current and Future Favourable Areas of *T. leiocarpa* in Benin

Our results show that temperature (bio1, bio2 and bio4), precipitation (bio12) and soil are the variables that most influence the distribution of *T. leiocarpa* in Benin. These results testify to the importance of climate and edaphic factors on the distribution of the species and corroborate those of Fandohan et al. (2013) on *Tamarindus indica* L., Agbo et al. (2019) on *Detarium microcarpum* and Daï et al. (2023) on *Uvaria chamae*. Soil was the variable that contributed most to the model, with a contribution of 43.5% (Table 3). The importance of the soil in the distribution of the

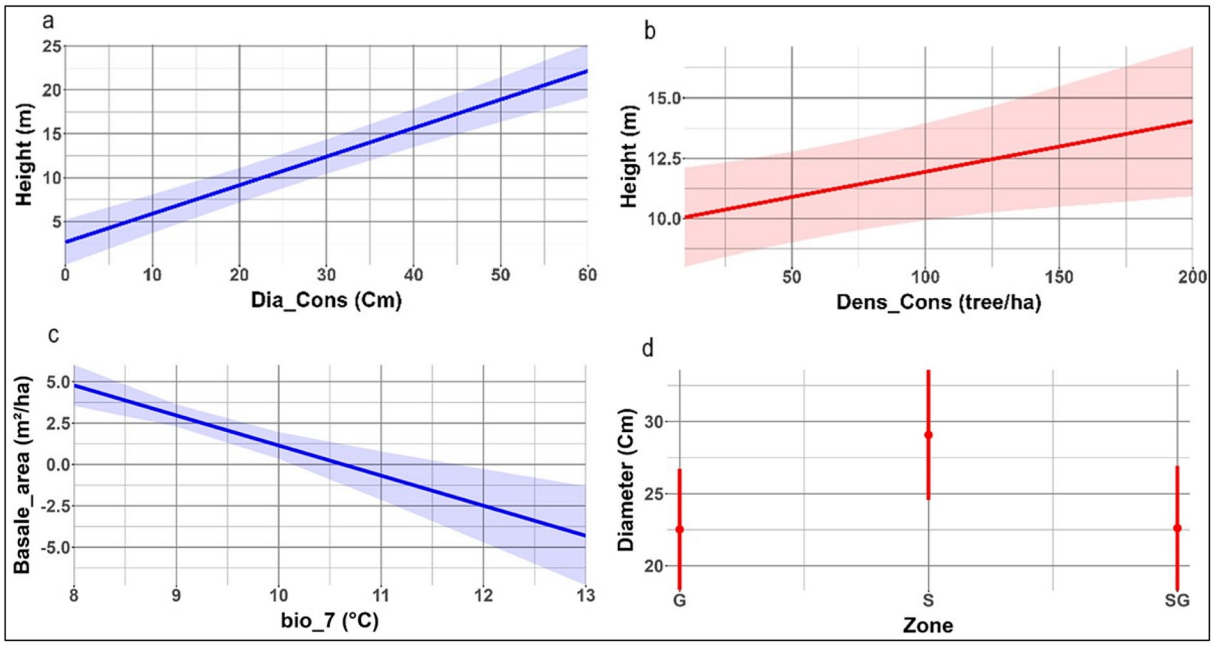


FIGURE 4 | Effects of selected biotic and abiotic factors on height and basal area of *T. leiocarpa*. bio-7, annual temperature range; Dens_Cons, conspecific tree density; Dia_Cons, conspecific tree diameter; G, Guinean zone; S, Sudanian zone; SG, Sudano-Guinean zone.

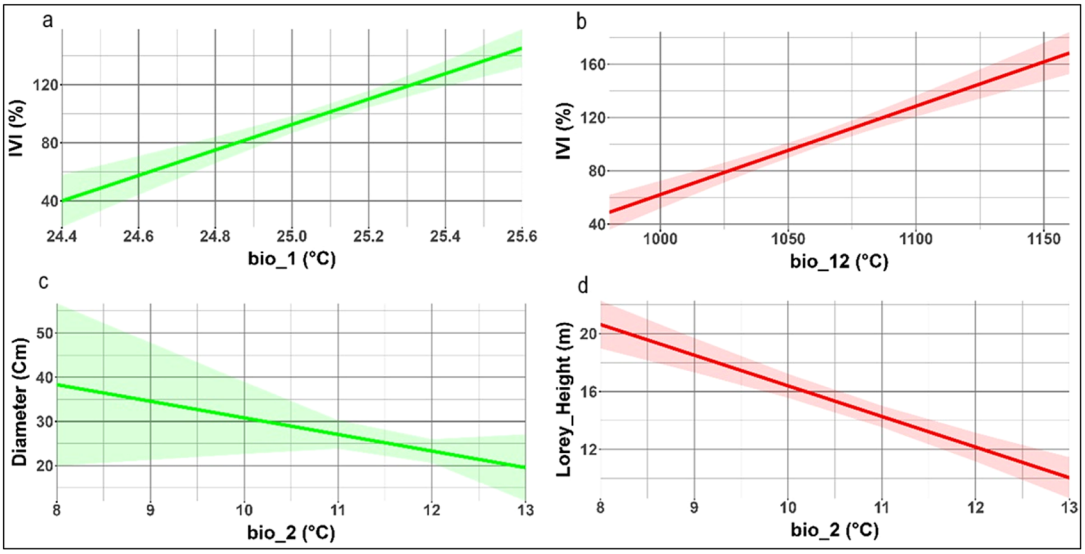


FIGURE 5 | Effects of some of the five factors that contributed most to habitat modelling on availability and some structural parameters of *T. leiocarpa*. Bio-1, annual mean temperature, bio_2, mean of daily temperature variation; bio_12, annual precipitation.

species can be justified by the fact that the soil is an important support that provides the nutrients necessary for plant growth. In fact, soil plays a part in the physiological processes of plants, providing the nutrients required for growth and reproduction.

The current favourable and very favourable areas cover 41% and 8% of the total surface area of Benin, respectively (Table 4). The current distribution of *T. leiocarpa* extends over the three climate zones of Benin (Figure 2). These results corroborate those of Akoègninou et al. (2006), who reported the presence of the species in all three climate zones of Benin. The impact of climate change on the future distribution of *T. leiocarpa* was analysed under scenarios SSP 2–4.5 and SSP 5–8.5, two scenarios often used in plant habitat modelling (Meinshausen et al. 2020; Ames-Martínez et al. 2022; Biaou et al. 2023). The results showed that climate change under the two scenarios negatively affected the distribution of *T. leiocarpa* in 2050 (Table 4; Figure 2). Indeed, the results predicted a decrease in the suitable area (favourable plus very favourable) for the distribution of the species of 22% and 33% under the SSP 2–4.5 and SSP 5–8.5 scenarios, respectively (Table 4). These results confirm our hypothesis (1), which states that the suitable area of distribution for *T. leiocarpa* in Benin will decrease under SSP 2–4.5 and SSP 5–8.5. In addition, these results are consistent with those obtained by Fandohan et al. (2013) on *T. indica*, Ayihouenou et al. (2016) on *Parkia biglobosa* but contrary to those of Agbo et al. (2019) on *D. microcarpum* and Lokonon et al. (2023) on *Caesalpinia bonduc* (L.) Roxb. The contraction of the distribution area for *T. leiocarpa*

in 2050 can be explained by climate forecasts, which predict an increase in temperature and irregular precipitation (Calvin et al. 2023). Indeed, with moderate (SSP 2–4.5) and high (SSP 5–8.5) greenhouse gas emissions under the scenarios considered, we can expect a considerable increase in temperature and a contraction in the distribution of *T. leiocarpa*, as temperature and precipitation are very important in the distribution of the species (Table 3). These results are in line with those of Lokonon et al. (2023) who showed that climate variables such as temperature and precipitation are very important in the shaping and the distribution of *C. bonduc*. The decrease in the distribution of the species can also be partly justified by the demographic and socio-economic growth forecasts taken into account by the scenarios considered (Meinshausen et al. 2020). In fact, as the population grows and demand for the species increases, given its socio-economic importance, the current distribution of *T. leiocarpa* may well decline. The results predicted that the Sudano-Guinean zone remains largely suitable for the distribution of *T. leiocarpa* compared with the other two zones (Figure 2). This could be justified by the fact that the Sudano-Guinean zone is a climate transition zone and offers moderate climate conditions for plants (Tchetan et al. 2024). Thus, plants adapt easily in such a zone, given the moderate climate conditions it offers.

4.2 | Effect of Biotic and Abiotic Factors on the Availability of *T. leiocarpa*

Our results showed that the anthropogenic factor significantly affected the IVI of *T. leiocarpa*. Indeed, the IVI value in a stand with zero pressure was significantly higher than those obtained in stands under various pressures (low, medium; Figure 3a). These results corroborate those of Tchetan et al. (2024) and Taonda et al. (2024), but contradict those of Assogbadjo et al. (2009), who state that *T. leiocarpa* tolerates anthropic pressure well. Indeed, *T. leiocarpa* is a very important plant for the local population, who use it for medicine, animal feed, charcoal and furniture (Kone et al. 2019; Traore et al. 2020; Tchetan et al. 2021). Thus, uncontrolled harvesting of the plant in unprotected habitats inevitably leads to a reduction in the abundance of the species. Our results also showed that as the diameter of heterospecific trees increases, the IVI of *T. leiocarpa* decreases (Figure 3b). These results corroborate those of Canham et al. (2004), who showed that in a plant community, trees of the same species can be subject to two types of competition: shading and crowding effects. These effects adversely affect the abundance of the target species in the community. The annual mean temperature (bio1) negatively affected the IVI of the species, while the mean temperature of the coldest quarter (bio11) had the opposite effect on the IVI (Figure 3c,d). These results confirm the importance of temperature for *T. leiocarpa*. Furthermore, analysis of the results suggests that the studied species is sensitive to both high and low temperatures. These results also suggest that *T. leiocarpa* is suitable for moderate temperatures and may partly justify the fact that the Sudano-Guinean zone (a zone with moderate temperatures compared with the other two) is largely suitable for the distribution of the species (Figure 2).

4.3 | Effect of Biotic and Abiotic Factors on the Structural Parameters of *T. leiocarpa*

Our results showed that the diameter and density of conspecific trees positively affected the height of *T. leiocarpa* (Figure 4a,b). This confirms our second hypothesis, which states that the diameter and density of conspecific trees will increase *T. leiocarpa* height. These results are justified, on the one hand, by the strong positive correlation between tree diameter and height (Assogbadjo et al. 2009), and, on the other hand, by the effect of shading in the presence of high tree density (Canham et al. 2004). In a high-density community, trees tend to grow taller in search of light for photosynthesis. The diameter and density of conspecific trees had the same effect on the Lorey height and the basal area of *T. leiocarpa*. These results are in line with those of Johnson et al. (2017); Atanasso et al. (2019); Magee et al. (2021); Mensah et al. (2023), who showed that conspecific tree density and diameter significantly affect the structure of different plant species in a community. Furthermore, our results showed that climate zone as well as vegetation type significantly affected the structure of *T. leiocarpa*. For example, the mean diameter of trees in the Sudanian zone was significantly greater than those obtained in other climate zones. These results corroborate those of Mensah et al. (2014), who observed a positive effect of Sudanian and Sudano-Guinean zones on the structural parameters of *A. africana*. This result could be explained by the favourable effects that climate can have on plant growth. Taonda et al. (2024) have also shown the influence of climate zone on the structure of *Detarium microcarpum* Guill. & Perr. in Burkina Faso.

4.4 | Effect of Ecological Niche Modelling Variables on the Availability and Structure of *T. leiocarpa*

Analysing the effect of the factors that contributed most to habitat modelling on the IVI and structure of *T. leiocarpa*, we found that annual mean temperature (bio1) and annual precipitation (bio12) were positively associated with IVI (Figure 5a,b). These results confirm the importance of temperature and precipitation in the abundance of the species. In fact, precipitation provides the soil with water, which the plant will absorb along with nutrients to carry out photosynthesis, a physiological phenomenon necessary for the survival, growth and abundance of a plant (Lokonon et al. 2023). Like water, temperature plays an important role in plant physiological processes. Our results are, however, contrary to those of Taonda et al. (2024), who showed that temperature and precipitation negatively affected *D. microcarpum*. Furthermore, our results showed that variation in the mean of daily temperature variation (bio2), annual precipitation (bio12) and soil are associated with the diameter of *T. leiocarpa*. These results corroborate those of Agbo et al. (2019) on *D. microcarpum*, Lokonon et al. (2023) on *C. bonduc* and Taonda et al. (2024) on *D. microcarpum*. These authors have shown the importance of climate and edaphic variables on the structure of different plants. In addition, our previous work highlighted the importance of climate regimes on *T. leiocarpa* diameter in Benin (Tchetan et al. 2024).

5 | Conclusion and Implications for Sustainable Use

Our study aimed to map the favourable areas for the species in Benin, both currently and in the future, and analyse the biotic and abiotic factors affecting the structure and availability of *T. leiocarpa*. The results predicted a retraction of 22% and 33% in the suitable area for the distribution of the species under the SSP 2–4.5 and SSP 5–8.5 scenarios, respectively. The suitable area of the distribution of the species is mainly in the Sudano-Guinean zone. The results also showed that the distribution of *T. leiocarpa* is mainly influenced by climate variables such as temperature and rainfall, followed by edaphic variables such as soil. The results of habitat distribution modelling remain indicative, as this is based on a mathematical approach, and climate predictions may differ from field realities at the appropriate time. However, these results should help to take the necessary steps upstream to contribute to the conservation of the species.

Several abiotic, biotic and anthropogenic factors have significantly affected the abundance and structure of *T. leiocarpa*. For example, our results showed that high anthropogenic pressure led to a decrease in abundance, while the density and diameter of conspecific trees increased the height of *T. leiocarpa*. In addition, our results showed that the mean of daily temperature variation (bio2), annual precipitation (bio12) and soil are associated with the diameter of *T. leiocarpa*. These results represent a significant advance in our understanding of the ecology of *T. leiocarpa*, which will be useful in the future for the conservation and sustainable use of the species.

Author Contributions

Conceptualisation and methodology: E.T., T.D.H., S.I.A.Y., A.B.F. and P.A.O. Data collection: F.J.E.C.G., D.F.E.S., F.D.A. and P.K.N. Data analysis: F.J.E.C.G., E.T., D.F.E.S., F.D.A. and P.K.N. Writing – original draft: F.J.E.C.G. and E.T. Manuscript review: T.D.H., S.I.A.Y., A.B.F. and P.A.O. Funding acquisition: E.T., T.D.H., S.I.A.Y., A.B.F. and P.A.O. Project administration: E.T., T.D.H., S.I.A.Y., A.B.F. and P.A.O. All authors have read and approved the manuscript submission in its current version.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.