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RESEARCH ARTICLE

Variability in *Pterocarpus erinaceus* Poir. Traits Along an Aridity Gradient Provides Insights Into Its Adaptation to Dry Environmental Conditions

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ABSTRACT

Understanding species adaptation to environmental changes is crucial to guide conservation and habitat restoration. This study examined variability in *Pterocarpus erinaceus* Poir. traits along an environmental gradient in Benin, ranging from humid (Guinean), subhumid (Sudano-Guinean) to semi-arid (Sudanian) zones. Data on fourteen morphological and functional traits were collected from 120 trees along this gradient. Canonical discriminant analysis was used to identify traits that differentiate each climate zone, while redundancy analysis was employed to explore relationships between discriminative traits and environmental variables. Both univariate and multivariate (MVPi) plasticity indices were further computed to assess trait variability. Petiolule length (PeL), petiole length (PEL), diameter at breast height (DBH), number of branches (NB), and leaf mass per area (LMA) were the most discriminative traits. PeL, PEL, and LMA significantly decreased from arid (0.7 ± 0.15 cm, 4.5 ± 0.67 cm, 69.44 ± 15.17 g/m^2, respectively) to humid zones (0.4 ± 0.08 cm, 3.8 ± 0.48 cm, 40.9 ± 10.90 g/m^2, respectively), whereas NB declined from humid (11.7 ± 4.68) to arid zones (6.68 ± 1.64). Temperature, rainfall, and aridity positively influenced PEL and PeL but negatively influenced NB. DBH, NB, and LMA were negatively related to soil type. Substantial plasticity (0.45–0.50) was observed at individual trait level. When aggregated over all traits (MVPi), trait plasticity was slightly higher for SGZ vs. SZ and SZ vs. GZ compared to that for SGZ vs. GZ. Our findings highlight the function trade-offs underlying the growth and local adaptation of the species across the climatic zones. These insights underscore the importance of conserving the species' subpopulation within their respective ecological zones. Future research should explore the species' genetic diversity and adaptation mechanisms to enhance its conservation strategies.

1 | Introduction

Climate change driven by global warming is responsible for rapid and profound alterations in forest ecosystems, leading to significant loss of biodiversity (Hansen et al. 2001; Román-Palacios and Wiens 2020). In West Africa, where communities heavily rely upon natural resources for their livelihoods, climate forecasts indicate a temperature rise of 1.5°C–3°C by the

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end of the 21st century (IPCC 2022). This warming is expected to increase aridity and the extinction risk of many species (Liu et al. 2023; Vicente-Serrano et al. 2020). In this context, species that are already vulnerable may only survive by successfully developing adaptive strategies to arid environmental conditions (Basu et al. 2016). Woody species are particularly vulnerable to environmental changes and must therefore extend their physiological tolerance limits to cope with shifting climatic conditions (Araújo et al. 2022; Nicotra et al. 2010).

Morphological and functional traits play a crucial role in plant adaptation by mediating their responses to climatic and edaphic constraints. These traits influence key physiological processes such as photosynthesis, transpiration, and resource allocation, thereby determining growth, reproduction, and survival (Xu et al. 2009; Yaripour et al. 2018). Thus, modifications in morphological traits of these perennial organisms in response to environmental changes are critical for their ability to mitigate extinction risks (Akalusi and Bourque 2018; Daï et al. 2024). Plant morphological traits (e.g., leaf traits, seed traits, plant height, etc.) influence plant fitness through their role in functional processes such as dispersal, growth, reproduction, and survival (Violle et al. 2007). Therefore, understanding how these morphological traits vary within species in response to environmental changes is important not only for predicting species' responses to climate change but also for enhancing our capacity to implement adaptive management practices that support biodiversity conservation (Liu et al. 2023).

Growing interests in trait-based ecology and the development of the TRY plant trait database (Kattge et al. 2011) have greatly expanded our understanding of trait diversity and variability along environmental gradients (e.g., Kattge et al. 2020). However, extant empirical knowledge largely relates to interspecific trait variation, while intraspecific trait variability—variation among individuals of a species—remains understudied, especially in tropical trees. Intraspecific trait variation often reflects genetic variation and is important for local adaptation and resilience (Albert et al. 2011; Siefert et al. 2015). For example, Ahmad et al. (2016) demonstrated that intraspecific morphological trait variation in *Cynodon dactylon* (L.) Pers. reflected ecotypic adaptation to altitudinal stress. The authors concluded that trait-based ecological insights on plant adaptation can emerge not only from interspecific variation but also from intraspecific variability. Therefore, evaluating intraspecific trait variability is critical to understanding the adaptive capacity of widespread species.

Variation in morphological traits can be assessed at multiple levels, including the individual tree level (i.e., growth traits such as diameter and height) and specific plant parts (e.g., fruit, seed, root, bark, and leaf). Recent research indicated that leaf morphological traits (e.g., leaflet length, leaflet width, number of leaflets) and growth-related morphological traits (e.g., diameter, number of branches) are useful traits to discriminate tree species population along an environmental gradient and infer adaptation mechanisms (e.g., Gandji et al. 2020; Hounkpèvi et al. 2020). For example, leaf traits have been used to understand species' ecological performance and adaptation strategies due to their prominent role in plants' physiological processes, such as photosynthesis, respiration, and transpiration (Amahowe et al. 2016; Araújo et al. 2022). Significant variations were reported in leaf size in response to environmental parameters such as rainfall (Wright et al. 2017), temperature (Royer 2012), and soil type (Duan et al. 2022).

Leaf functional traits, such as specific leaf area (SLA), stomatal density, leaf nitrogen content, leaf dry mass, leaf mass per area (LMA), and chlorophyll content determine plant's resource-use strategies, water-use efficiency, and stress tolerance (Amahowe et al. 2018; Araújo et al. 2022). For instance, a high LMA indicates thick, resistant leaves, reflecting an increased allocation of resources to defence rather than growth (Wright and Cannon 2001). These traits give the leaves greater robustness and a longer lifespan (Pérez-Harguindeguy et al. 2016), making them less vulnerable to damage by herbivory (Wright and Westoby 2002). SLA is a key leaf trait, reflecting trade-offs between biomass production (Bond-Lamberty et al. 2023), light interception and resource conservation (Grady et al. 2024). SLA is essential for modelling plant growth and understanding plant adaptation strategies (Adhikari et al. 2018; Ahmed et al. 2021). It is linked to plant mortality and influenced by soil pH (Maire et al. 2015), nutrients (Donhouedé et al. 2023; Pandey et al. 2021), and environmental conditions (Adhikari et al. 2018). Several studies showed that SLA decreases under water stress (Ward et al. 2022). These observations suggest that understanding the plant functional traits across varying gradients of aridity and soil types could offer deeper insights into the complex mechanisms driving plant adaptation to variations in environmental conditions.

Pterocarpus erinaceus Poir., a threatened tropical tree according to the International Union for Conservation of Nature (IUCN; status: Endangered) and listed in CITES Appendix II, is heavily exploited as timber, traditional medicine, and fodder for cattle in West Africa (Ouinsavi et al. 2021; Segla et al. 2020). As a result of the over-exploitation of its wood, logging was prohibited in Benin. However, the species continues to face local exploitation, posing significant threats to its remaining population and the surrounding environment (Biaou et al. 2023a, 2023b; Segla et al. 2020). Consequently, *P. erinaceus* population is declining and ageing, with few natural regenerations (Biaou et al. 2023a, 2023b). Moreover, silvicultural practices to safeguard the remaining population are poorly implemented. Previous research has reported morphological trait variability among populations of *P. erinaceus* in West Africa (e.g., Banla et al. 2019; Goba et al. 2021; Johnson et al. 2020). However, few studies have explored how environmental factors shape this variation or quantified the species' phenotypic plasticity. Assessing both morphological and functional intraspecific trait variation across environmental gradients could enhance our understanding of the adaptive capacity of *P. erinaceus*. Such knowledge can enhance the effectiveness of conservation initiatives and domestication programs by guiding the selection of genetic materials that are resilient to environmental changes.

In this study, we evaluated the variation in the morphological and functional traits of *P. erinaceus* in response to drought, elevation and soil type in Benin. *P. erinaceus* is distributed across the three climate zones of the country, including the Guinean zone (GZ, humid), Sudano-Guinean zone (SGZ, sub-humid),

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and Sudanian zone (SZ, semi-arid and arid), offering an appropriate context to study its response to environmental gradients (Adomou 2005). Specifically, we (1) assessed the variation in morphological and functional traits of the species along an aridity gradient, represented by a decrease in water availability from the GZ through SGZ to SZ, (2) identified the traits that best discriminate *P. erinaceus* populations across the climate zones, (3) evaluated the relationships between environmental variables and discriminating traits, and (4) quantified the plasticity of key traits across climate zones. Indeed, climatic gradients—determined by variations in factors such as temperature and precipitation—are recognised as major drivers of morphological and functional trait variation in tree species in tropical environments (Fyllas et al. 2017; Gallagher and Leishman 2012). Therefore, we hypothesised that morphological and functional traits would vary systematically along climatic gradients, but the direction of the change would depend on the specific trait considered. Specifically, we expect higher values of morphological (e.g., diameter at breast height—DBH, number of branches—NB, and leaflet size) and functional (e.g., SLA and chlorophyll content) traits in areas with more rainfall (Moles et al. 2009; Wright et al. 2004). Conversely, functional traits such as LMA are expected to be higher in drier and warmer conditions, reflecting adaptive strategies that improve water-use efficiency and stress resistance (Wright et al. 2017). We also assumed that soil texture would modulate the expression of morphological and functional traits in plants. Fine-textured soils (loamy or clayey), which retain more water and nutrients, would favour acquisitive strategies (more branches, larger leaflets, high SLA, low LMA, high chlorophyll content), as opposed to coarse soils (sandy), which are poorer in water and nutrients.

2 | Materials and Methods

2.1 | Study Species

P. erinaceus, a member of the Fabaceae family, is a leguminous plant with diverse uses (Rabiou et al. 2015; Segla et al. 2015; Habou et al. 2017). The tree can reach a height of 8–15 m and a diameter at breast height (DBH) of up to 1 m. It features a rounded, open crown shape. Its bark displays a blackish hue, characterised by cracks, and features a reddish-striped brown edge that releases a translucent reddish resin, which solidifies quickly (Arbonnier 2009). The leaves of *P. erinaceus* are compound-imparipinnate and arranged alternately. They consist of 9–11 elliptical to elliptical-oblong leaflets measuring 5–10 cm in length and 3–6 cm in width. These leaflets have a wedge-shaped to rounded base, while their apex is obtuse to slightly acuminate (Arbonnier 2009).

P. erinaceus is of great ecological and socio-economic importance in West Africa. Its dense and durable wood is highly prized in carpentry (Arbonnier 2009), while its stands are widely exploited for timber, firewood, and fodder (Habou et al. 2017; Ouinsavi et al. 2021). The species also has high medicinal value in traditional African pharmacopoeias (Louppe et al. 2008; Ouinsavi et al. 2021). Due to the high commercial value of its wood, it has been heavily traded internationally to Asia, particularly China, leading to a marked decline in its natural population (Dumenu 2019).

2.2 | Study Area

This study was conducted in the Republic of Benin, West Africa, and covered the entire climatic gradient from south to north. Benin is located in the intertropical zone, between latitude 6°30′ and 12°30′ North and longitude 1° and 3°40′ East (Figure 1). The country includes three climate zones, defined based on phytogeographic data and climatic gradient including the SZ, SGZ and GZ. The SZ (arid and semi-arid) is located in the north (9°45′–12°25′ N and 0°45′–3°50′ E) and characterised by a unimodal rainfall pattern, with annual precipitation ranging from 800 to 1000 mm, high temperatures (24°C–31°C), and high variability in relative humidity (18%–99%). The dominant soils are Luvisols, Arenosols, and Gleysols. The vegetation consists of savanna-grassland mosaic with patches of dry forests or woodlands (Adomou 2005; White 1983). The SGZ (sub-humid; 7°30′–9°45′ N and 1°30′–3°50′ E) represents a transition zone between the dry savannas of the north and the humid forests of the south. The rainfall pattern remains unimodal, with annual rainfall of 900 to 1110 mm and moderate temperatures (25°C–29°C). The most representative soils are Acrisols, Gleysols, and Vertisols. The vegetation is dominated by dense semi-deciduous forests, gallery forests and woodlands. The GZ (humid) covers the south Benin (6°25′–7°30′ N and 1°45′–2°50′ E). It benefits from an annual rainfall ranging between 1200 and 1300 mm, a temperature ranging between 25°C and 29°C, and a relative humidity ranging between 69% and 97%. The dominant soils are Acrisols and Gleysols (WRB 2006). The GZ vegetation is dominated by dense humid forests (White 1983).

2.3 | Sampling and Data Collection

2.3.1 | Sampling

P. erinaceus is distributed over the three climate zones of Benin. One to three protected forests with *P. erinaceus* trees were identified as follows: one forest in the SZ (Ouénou-Bénou forest), three in the SGZ (Pénésoulou, Bassila, and Houin forests), and one forest in the GZ (Atakpamé forest). In each climate zone, the selected forests were located at least 30 km apart. In each forest, 22–27 trees of *P. erinaceus* were randomly sampled on either side of a transect strip (50 m wide and 3 km long), oriented north–south and east–west from a randomly selected starting point. On each transect strip, the distance between consecutive trees was at least 100 m (Daï et al. 2024). This was done to avoid selecting genetically closed trees and capture an important amount of the morphological and functional variation (Hounkpèvi et al. 2020).

We selected reproductive trees with a DBH ≥ 10 cm only to ensure that only mature and physiologically similar individuals were included in the analyses (Sokpon et al. 2006). This threshold is widely considered an indicator of reproductive maturity in tropical forest ecology because most woody species, and especially Fabaceae, begin flowering and fruiting at this DBH (Chave et al. 2003; Clark and Clark 1992; González-Melo et al. 2024). While the morphological and functional features of plants may differ with age, the sampling of actively reproductive trees minimised ontogenetic variation and allowed comparisons among climatic zones was

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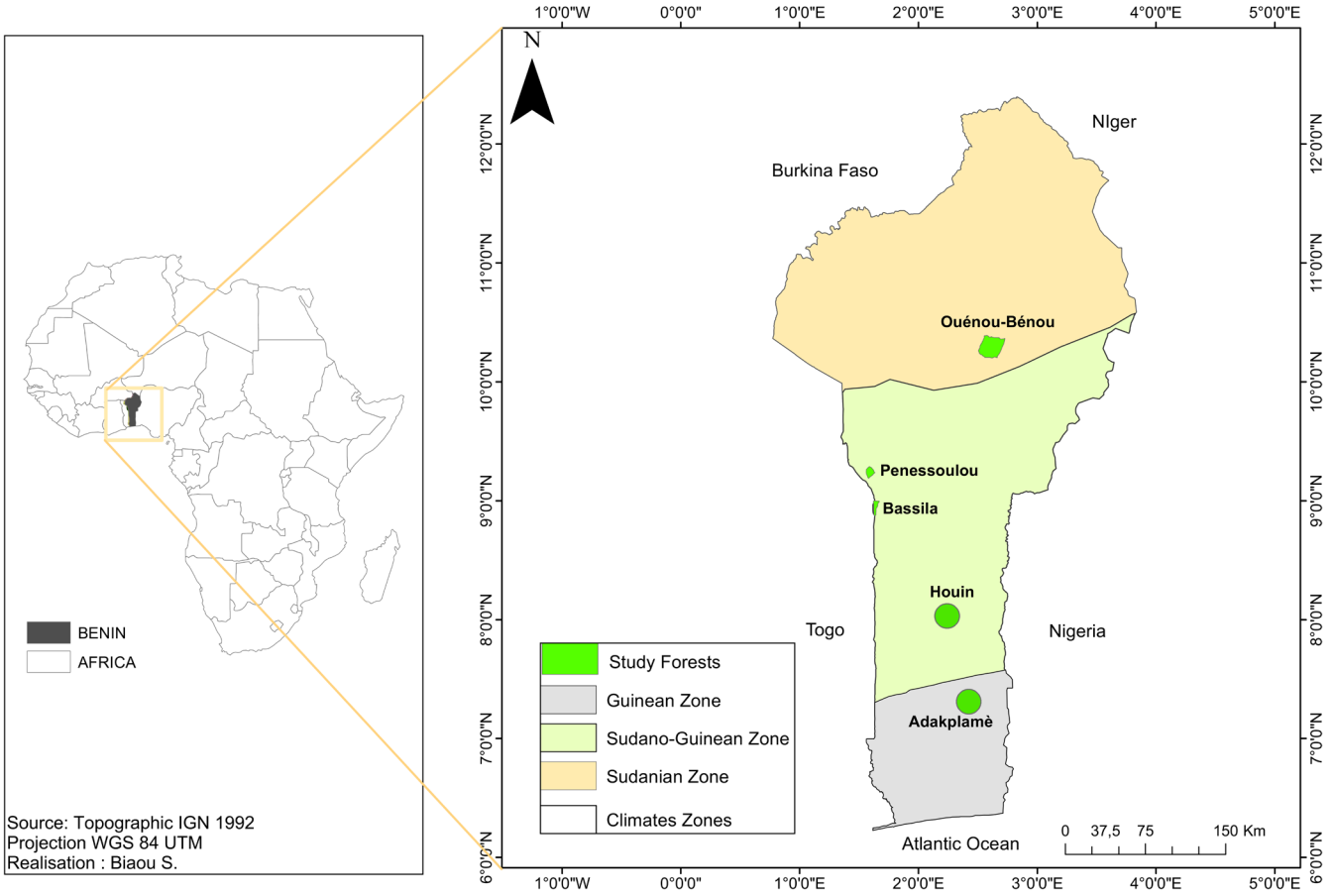


FIGURE 1 | Climate zones of Benin and location of the surveyed forests.

possible. In total, 120 individuals of *P. erinaceus* were inventoried in all the selected forests across the climate zones (Table S1).

2.3.2 | Data Collection

2.3.2.1 | Morphological Traits Data. For each tree, we recorded geographical coordinates, DBH, total height (TH), and NB. Coordinates were recorded using a Garmin 62 GPS. For each tree, four mature leaves—free of any pathogenic damage—were selected from the sun-exposed part of the crown and oriented in four directions to capture intra-individual variability. This selection ensured that all sampled leaves were physiologically active and representative of the tree's functional state. Fieldwork was carried out in accordance with national legislation, with the agreement of the Department of Water, Forests, and Hunting of Benin (DGEFC), considering ethical and environmental principles related to research work in forest ecosystems. Measured morphological traits included total leaf length (TLL; distance from the base of the petiole to the tip of the terminal leaflet), petiole length (PEL; distance from the base of the petiole to the first leaflet), number of leaflets (NL), leaflet length (LEL; from petiolule base to leaflet tip), leaflet width (LW; maximum diameter of the leaflet blade), and petiolule length (PeL). Functional traits were selected based on their ecological relevance to resource-use strategies and their established sensitivity to drought and aridity gradients in tropical environments. We focused on SLA, LMA, leaf mass (LM), leaf area (LA), and leaf relative chlorophyll content (LRCC). These functional traits capture essential components of the leaf economics spectrum and are key indicators of plant responses to water and nutrient availability (Pérez-Harguindeguy et al. 2013; Wright et al. 2004). Traits such as SLA, LMA, and LRCC serve as reliable proxies for photosynthetic capacity, resource-use strategy, and drought tolerance, enabling meaningful comparisons across environmental gradients (Hounkpevi et al. 2016; Poorter 2009).

Each leaf was coded and stored in envelopes to prevent damage. LRCC was measured in the field using a portable chlorophyll meter (AtLeaf+; Novichonok et al. 2016). LA was determined using ImageJ software (Glozer 2008). LM was obtained after oven-drying leaves at 60°C for 72 h and weighing them to the nearest 0.001 g. SLA and LMA were calculated as the ratio of LA to LM and LM to LA, respectively (Pérez-Harguindeguy et al. 2013).

2.3.2.2 | Environmental Data. Environmental data included bioclimatic variables, aridity index, soil texture, and elevation. The bioclimatic data were downloaded from AfriClim database v.3.0 (Platts et al. 2015; available at: https://webfiles.york.ac.uk/KITE/Afri-Clim/ and accessed on 10 October 2025) at a spatial resolution of 1 km. These consist of 21 bioclimatic dimensional variables of biological significance, derived from mean annual temperature and precipitation (Fick and Hijmans 2017). We extracted the value of these 21 bioclimatic variables for each sampled tree based on their GPS coordinates using the "Raster" R package (Hijmans 2021). The De Martonne aridity index (De Martonne 1926) was calculated

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for each plot based on temperature and rainfall data, according to Equation (1):

$$I_{DM} = \frac{p}{T + 10} \quad (1)$$

where I_{DM} is De Martonne aridity index, P is the mean annual of rainfall (Bio 12, in mm) and T is the annual mean temperature (Bio 1, in degrees Celsius; Table S2). Soil texture and elevation variables were obtained from the FAO world database at a spatial resolution of 1 km (Jones and Thornton 2015).

2.4 | Data Analysis

All statistical analyses were performed in R statistical software, version 4.1.2 (R Core Team 2021). Descriptive statistics, including arithmetic mean, standard error of the mean, and coefficient of variation (CV; standard deviation/mean), were estimated for each climate zone for an initial diagnosis of the morphological and functional traits. Linear mixed-effects models were used to assess the variation in measured traits according to "climate zone", "subpopulation", and "tree". Individual trees from the same forest were considered as a subpopulation. The linear mixed-effects models were run using the "*nlme*" package (Pinheiro et al. 2023). In these models, "climate zone" was considered as a fixed factor, while the random term included "subpopulation" nested within climate zone and "tree" nested within subpopulation (1|climate zone/subpopulation/tree). We assumed that variability in the traits may result from differences between the climate zones and accounted for pseudo-replication at the levels of individual and population through the random factors. We performed Tuckey's post hoc tests on the outputs of the linear mixed-effect models for mean comparison using the function "*glht*" of the "*multcomp*" package (Hothorn et al. 2008). We identified the traits that best discriminated the trees according to the climate zones by performing a canonical discriminant analysis (CDA) on the traits of the 120 sampled individual trees using the "*candisc*" package (Friendly et al. 2017). This analysis ranks traits in their order of significance by discriminating trees according to the subpopulation and the climate zones. The most important morphological functional trait differentiating the species traits between the climate zones was identified using "*greedy.wilks*" function with the R package klaR (Weihs et al. 2005).

To examine the impact of environmental factors including bioclimatic variables, aridity index, and elevation on morphological and functional traits of *P. erinaceus* trees, we first used Spearman's correlation test to explore patterns of association between pairs of these variables. Considering the high correlations between the bioclimatic variables ($r \geq 0.9$; $p < 0.05$), we selected five of them for further analysis. These included annual mean temperature (BIO1), isothermality (BIO3), maximum temperature of warmest month (BIO5), annual moisture index (mi), and annual precipitation (BIO12). Elevation was added to the five bioclimatic variables because of its potential effect on morphological and functional traits (see Milla et al. 2008; Foll et al. 2014; Houehanou et al. 2019; Zhang et al. 2019). The discriminant morphological and functional traits from the CDA analysis, bioclimatic variables, aridity index, elevation, and type of soil were compiled for each tree to generate a matrix. The matrix was then submitted to a Redundancy Analysis (RDA) using the function "*rda*" of the "*vegan*" package (Jari Oksanen et al. 2019). Next, a stepwise regression analysis was performed to identify the most relevant environmental variables that discriminated the morphological and functional traits using the "*step*" function of the "*vegan*" package (Jari Oksanen et al. 2019). The most relevant variables were included in the finally selected model based on the lowest Akaike Information Criterion (AIC; Cameron and Trivedi 2005).

To assess plasticity in the discriminant morphological and functional traits, the index of phenotypic plasticity was calculated for each pair of climate zones (i.e., three pairs in total) following Valladares et al. (2000). This index ranges from 0 to 1 and was calculated for each trait (i.e., univariate plasticity index) as the difference between the minimum and the maximum mean values between the two climate zones being compared divided by the maximum mean value (Valladares et al. 2000). Given that phenotype emerges from complex genotype–environment interactions, we further calculated the Multivariate Phenotypic Plasticity Index (MVPi; Pennacchi et al. 2021) to quantify overall phenotypic shifts along the aridity gradient. The MVPi was derived from canonical variate analysis (CVA) scores obtained using the R package *Morpho* (Schlager et al. 2019). Each CVA axis summarises trait covariation, and the Euclidean distance (ED) between points in this multivariate space represents the magnitude of phenotypic divergence between environmental conditions (Equation (2)). The MVPi corresponds to the mean ED across all combinations of replicates and environments (Equation (3)), providing an integrated measure of multivariate plasticity (Figure 2).

$$\mathrm{ED}_{X-Y} = \left[\left(A_{\mathrm{CV}_1} - B_{\mathrm{CV}_1}\right)^2 + \left(A_{\mathrm{CV}_2} - B_{\mathrm{CV}_{12}}\right)^2 + \ldots + \left(A_{\mathrm{CV}_k} - B_{\mathrm{CV}_k}\right)^2 \right]^{\frac{1}{2}} \quad (2)$$

$$\mathrm{MVPi} = \left(\mathrm{ED}_{1-1} + \ldots + \mathrm{ED}_{1-m} + \mathrm{ED}_{2-1} + \ldots\right) + \left(\mathrm{ED}_{2-m} + \ldots + \mathrm{ED}_{n-1} + \ldots + \mathrm{ED}_{n-m} +\right) / (n.m) \quad (3)$$

where A and B are CV scores denoted as $A_{(\mathrm{CV1,CV2,...,CVk})}$ and $B_{(\mathrm{CV1,CV2,CV3,...,CVk})}$, representing environmental conditions; X and Y represent replicates within each environment; ED is the Euclidean distances; and MVPi represents the average distance of all combinations between X and Y with n and m replicates, respectively.

3 | Results

3.1 | Variation of the Morphological and Functional Traits of *P. erinaceus* Between the Climate Zones

P. erinaceus showed a wide range of variation in morphological and functional traits (Figure 3; Table S3, Supporting Information). The amplitude of variation in both morphological and functional traits varied among the climate zones. The most significant variation was observed within the GZ (CV > 40%, Table S3) for traits such as SLA and LM (Table S3). Within the SGZ, traits such as SLA, NB, and LMA also displayed substantial

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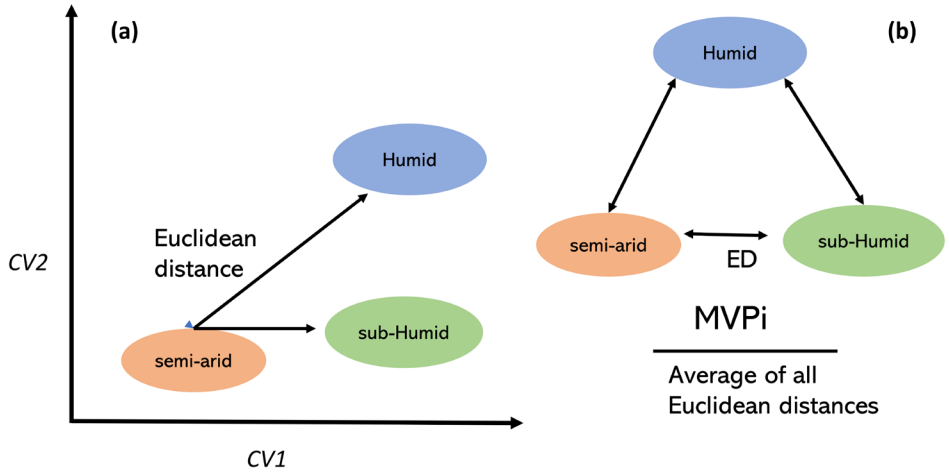


FIGURE 2 | Conceptual framework illustrating the calculation of the multivariate phenotypic plasticity index (MVPi). (a) shows the mean values of phenotypes in a bivariate space defined by the axes of canonical variability (CV1 and CV2). The coloured ellipses represent environmental conditions (semi-arid, sub-humid, and humid), and the arrows indicate the Euclidean distances (ED) between these conditions, reflecting the magnitude of phenotypic changes. (b) illustrates the relationship between these distances and the calculation of the MVPi, obtained as the average of all Euclidean distances between environments, thus representing the overall degree of phenotypic plasticity.

variation, with CV values higher than 30% (Figure 3, Table S3). However, in the SZ, a high CV was primarily observed in traits such as NB and SLA (Table S3).

All the growth-related morphological traits varied significantly between the climate zones (*p-value* <0.001, Figure 3, Table S3). The mean NB was the lowest in the SZ (Figure 3). The mean DBH was higher in the SGZ compared to SZ and GZ (Figure 3). Among the leaf- and leaflet-related morphological and functional traits, SLA significantly declined from the humid zone to the arid zone. NL, TLL, PeL, and PEL values were highest in the SGZ, while LEL and LMA values were the highest in the SZ (Figure 3, Table S3).

3.2 | Discriminant Morphological and Functional Traits According to the Climate Zone

According to the CDA results, the morphological and functional traits that significantly discriminated various *P. erinaceus* trees included PeL, DBH, NB, NL, PEL, and LMA (Figure 4; Table S4, Supporting Information). These traits significantly discriminated trees based on their climate zones of provenance (first function $\lambda_{Wilks}=0.58$, second function $\lambda_{Wilks}=0.77$, Prob <0.001, Figure 4 and Table S5). The two canonical axes explained 100% of the total variability in the morphological and functional traits (Figure 4). DBH, NL, PEL, and PeL showed higher values in the SGZ compared to GZ and SZ. However, the trees from SZ exhibited distinct traits from those in GZ, particularly evident in LMA. NB best discriminated GZ individuals against the other two (Figure 4, Table S5).

3.3 | Relationships Between Environmental Variables and Discriminant Traits of *P. erinaceus* Trees

RDA results showed that BIO1, BIO5, and soil texture were the environmental variables that influenced the discriminant traits of the trees from each climate zone (*p-value* <0.05, Table 1). RDA showed that the two redundancy axes were significant (*p-value* <0.05, Table 1) and explained 85.26% of the total variation in the discriminant morphological and functional traits. On the first axis (RDA1), BIO1 and BIO3 were negatively related to the discriminant morphological traits such as DBH, PEL, and PeL (Table 2). In contrast, they were positively associated with NB (Table 2, Figure S1). The second axis (RDA2) was associated with soil type and BIO5 (Table 2, Figure S1). RDA2 included discriminant morphological traits such as DBH, NB, NL, and LMA. DBH, NB, and NL were significantly and negatively related to soil type and BIO5 (Table 2, Figure S1). In contrast, they were positively associated with LMA.

3.4 | Phenotypic Plasticity of *P. erinaceus* Trees

The results showed differences in leaf MVPi values of *P. erinaceus* tree between the climate zones. In particular, the MVPi value was slightly higher for SGZ vs. SZ and SZ vs. GZ compared to that for SGZ vs. GZ (Figure 5). We also observed that leaf morphological and functional traits related to resource acquisition (PEL) and growth traits (NB and DBH) exhibited the highest phenotypic plasticity (>0.2). Conversely, LMA and NL were the least plastic. Plasticity varied across climate zones. The largest differences in NB and PEL were observed between SZ and GZ. DBH and PeL showed pronounced plasticity between the SGZ and GZ zones. The lowest plasticity values were generally observed between SZ and SGZ, except for NB, PeL, NL, and LMA (Figure 5).

4 | Discussion

4.1 | Variation of Morphological and Functional Traits Along the Aridity Gradient: The Role of Climatic and Edaphic Factors

We found the differences in morphological and functional traits of *P. erinaceus* across climate zones may reflect adaptive responses of the species, resulting from the interaction

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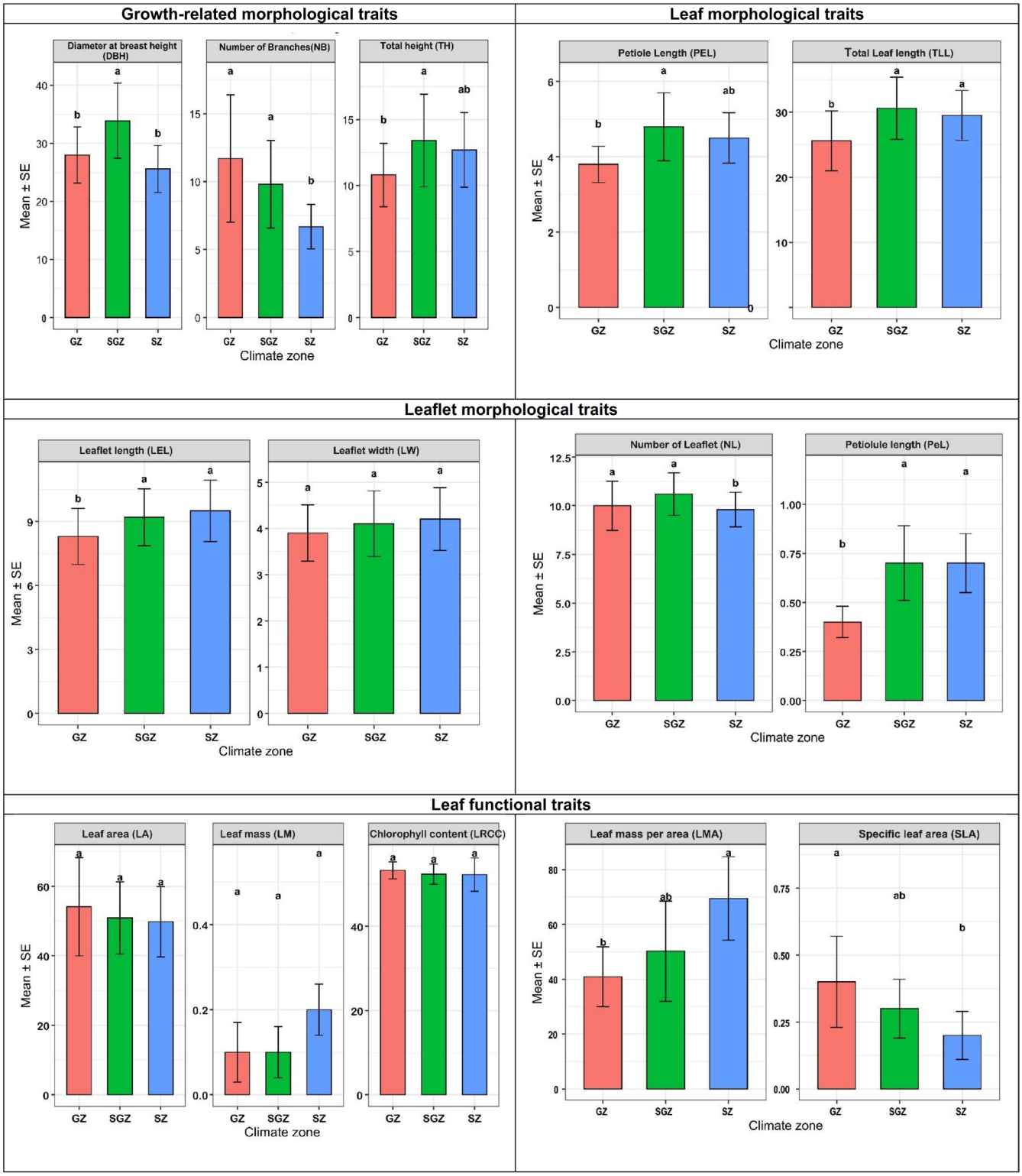


FIGURE 3 | Variation of the morphological and functional traits of *P. erinaceus* between the climate zones. For each trait, means and error bars followed by the same letters are not significantly different ($p\text{-value} > 0.05$) according to the Tukey's post hoc test. GZ, Guinean Zone; SGZ, Sudano-Guinean Zone; SZ, Sudanian Zone.

between genome and environmental factors (Aguirre-Liguori et al. 2019; Atkins and Travis 2010). Our results showed that growth-related traits like DBH and TH were higher in the sub-humid climate zone (SGZ) than in semi-arid (SZ) and the humid zone (GZ). These results suggest that *P. erinaceus* achieves optimal growth within the intermediate moisture range of its distribution. Although this result reflects a climatic regulation of stem growth, it is important to point out that ontogenetic variability may also influence these traits (Amahowe et al. 2016). Indeed, the age of a tree is correlated with its DBH, implying that the observed variation in DBH may reflect age differences rather than actual physiological limits imposed on growth by

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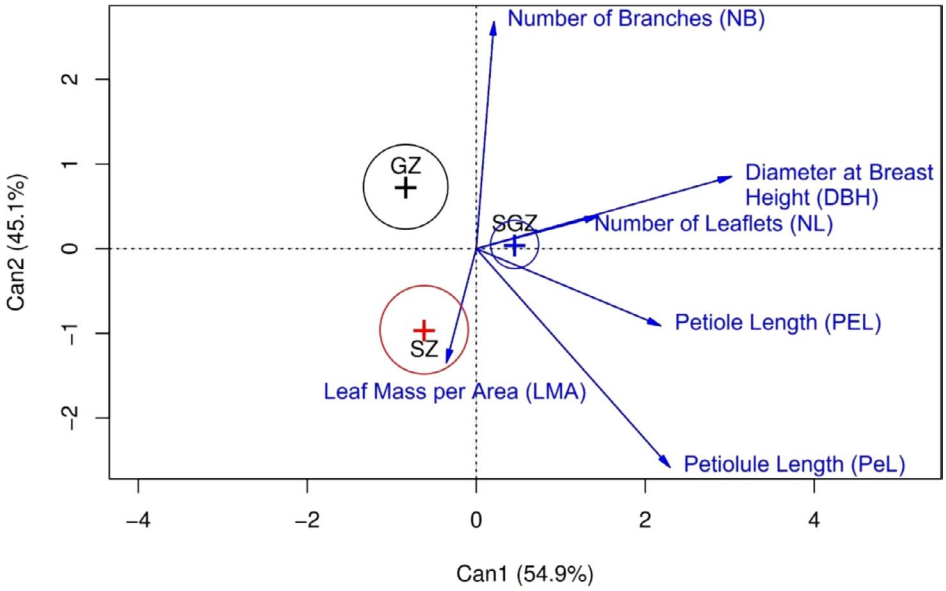


FIGURE 4 | Discrimination of the 120 individuals of *P. erinaceus* according to the climate zone of provenances based on the morphological and functional traits: Projection of the traits and climate zones into the system defined by the two first axes from the canonical discriminant analysis (CDA). Each climate zone is represented by the centroid of all trees of the climate zone. GZ, Guinean Zone; SGZ, Sudano-Guinean Zone; SZ, Sudanian Zone.

TABLE 1 | Redundancy analysis (RDA) and permutation ANOVA examining the potential influence of bioclimatic variables (BIO1: Mean annual temperature; BIO3: Isothermality; BIO5: Maximum temperature of the warmest month), aridity index and soil texture on discriminant morphological and functional traits of *P. erinaceus*. Correlation scores for each factor on the first two RDA axes (RDA1 and RDA2) are displayed. Bold values indicate the variables with the largest contribution to the RDA axes.

	Permutation ANOVA				Scores on axes	
Factors	**Df**	**Variance**	***F***	**Pr (>*F*)**	**RDA1 (64.02%)**	**RDA2 (21.24%)**
BIO1	1	0.73	17.68	0.001	**0.75**	−0.49
BIO3	1	0.06	1.42	0.215	**0.67**	−0.39
BIO5	1	0.20	4.90	0.002	0.33	**−0.49**
Aridity	1	0.07	1.79	0.133	−0.12	0.05
Soil	1	0.27	6.51	0.001	0.08	**−0.95**
Residual	114	4.67				
Axis						
RDA1	1	0.84	20.69	0.001	—	—
RDA2	1	0.28	6.86	0.007	—	—
Residual	114	4.67	—	—	—	—

Note: $R^2 = 0.22$; adjusted $R^2 = 0.18$.
Abbreviations: DF = degrees of freedom; *F* = Fisher statistics related to the test; Pr (>*F*) = probability of the significance; RDA = axes from the redundancy analysis.

water availability. However, in line with our hypothesis, NB was higher in the humid zone than in the other zones, indicating that higher humidity conditions stimulate vegetative growth, promoting the formation of primary branches. Previous studies have shown that increased humidity supports the allocation of resources to branching (Moles et al. 2009; Wright et al. 2004).

The variability patterns in morphological and functional leaf traits supported our hypothesis. We found that LMA increased with drier conditions, while SLA decreased. This observation reflects a shift towards a more conservative resource use strategy in response to increasing aridity. This finding was confirmed by the positive correlation of LMA with BIO5, suggesting that conservative traits allow plants to minimise water loss through transpiration and increase leaf residence time, thereby providing structural adaptation to water-constrained environments (Barbeta and Peñuelas 2016; Pérez-Harguindeguy et al. 2013).

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Soil type was also an influential factor of *P. erinaceus* traits. We found that sandy, low-clay, and infertile soils were associated with reduced growth traits (DBH, NB, NL), likely due to low water retention and limited nitrogen availability (Miatto et al. 2016). Overall, our results indicate that both water availability and soil properties act as powerful ecological filters, modulating the functional strategies of *P. erinaceus* and conditioning its resilience across wide environmental gradients.

TABLE 2 | Loadings of the discriminating morphological and functional traits on the axes of the redundancy analysis (RDA1 and RDA2). RDA1 and RDA2 explained 64.02% and 21.24% of the overall variance, respectively. Bold values indicate the traits that are highly correlated with the RDA axes.

Traits	RDA1 (68.75%)	RDA2 (25.52%)
Growth-related morphological traits		
Diameter at breast height (DBH)	−0.54	**−0.79**
Number of branches (NB)	**0.91**	**−0.55**
Leaf and leaflet morphological traits		
Petiole Length (PEL)	**−1.24**	−0.09
Petiolule length (PeL)	**−1.04**	0.05
Number of Leaflet (NL)	0.10	**−0.24**
Leaf functional traits		
Leaf mass per area (LMA)	0.07	**0.49**

4.2 | Plasticity in the Morphological and Functional Traits of *P. erinaceus*

The results show distinct trait plasticity patterns across the climate zones. The aggregate trait plasticity index (MVPi) was the highest between GZ and SZ populations and the lowest in the SZ and SGZ zones, highlighting the species' adaptability and potential to thrive under widely contrasting arid environmental conditions. When assessed at the trait level, discriminant traits of leaves related to resource acquisition (SLA and PEL) and growth traits (NB and DBH) showed the greatest phenotypic plasticity, while LMA and NL were the least plastic in all climate zones. This observation underscores that phenotypic plasticity in *P. erinaceus* is trait-dependent. High plasticity in resource acquisition and growth traits indicates the species' ability to optimise photosynthesis through light capture and modulate its growth architecture (i.e., investing more in vertical and lateral growth) under varying water availability conditions. Conversely, low plasticity in LMA and NL implies that these traits are more conserved in response to environmental constraints. These findings suggest that the functional tradeoff between plastic and non-plastic traits underlines *P. erinaceus* occurrence across a wider range of climates. Altogether, our results suggest that genetic diversity, physiological adaptations, and environmental conditions play a crucial role in shaping the observed variations in trait plasticity (Valladares et al. 2014; Yao et al. 2022). Further research into the molecular

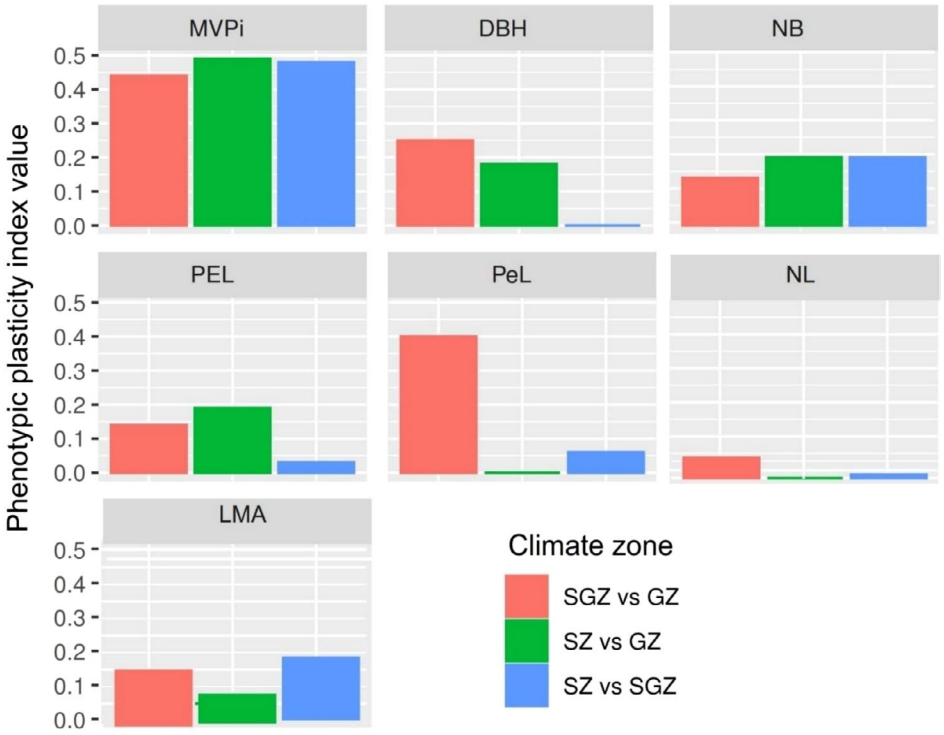


FIGURE 5 | Variation of the phenotypic plasticity of the discriminant morphological and functional traits of *P. erinaceus* among the climate zones in Benin. The index varies between 0 and 1, with values closer to 1 indicating greater phenotypic plasticity. DBH, Diameter at breast height; GZ, Guinean Zone; LM, Leaf mass; MVPi, Multivariate plasticity index; NB, Number of branches; NL, Number of Leaflet; PEL, Petiole Length; PeL, Petiolule length; SGZ, Sudano-Guinean Zone; SZ, Sudanian Zone.

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and physiological mechanisms underlying phenotypic plasticity may provide valuable insights into the species' resilience to aridity-related stresses.

4.3 | Implications for *P. erinaceus* Conservation and Domestication

Increasing anthropogenic pressures, the need to preserve local livelihoods, and the challenges of climate change heighten the need for the sustainable management and conservation of fodder and agroforestry trees (Houehanou et al. 2019; Lawin et al. 2021), including *P. erinaceus*. In the context of species conservation and domestication, trait plasticity allows for the selection of elite individuals adapted to ecological zones, ensuring optimal ecological resilience and economic potential for local communities. By integrating ecological knowledge into practical application, managers in West Africa, and particularly in Benin, can promote sustainable forest management and restoration in an environment of constant change. In this line, our study highlights variability in morphological and functional traits of *P. erinaceus* between climate zones, suggesting a local adaptation that should be considered in conservation efforts. This local adaptability also makes *P. erinaceus* an ecologically suitable species for the restoration of degraded landscapes in the face of increased climate variability.

Our findings on trait-specific plasticity suggest that subpopulations should be maintained and protected in their respective climate zones, as each may contain adaptive traits that contribute to the long-term resilience of the species (Lawin et al. 2021). Moreover, the relationships between traits and environmental factors indicated that *P. erinaceus* trait variability in Benin was not solely controlled by climatic conditions but also depended on edaphic factors, with nutrient-poor sandy soils limiting certain growth parameters. Furthermore, individuals in the SGZ showed higher values of DBH, NB, and NL, indicating that the subhumid zone is likely the most suitable for the survival and growth of the species. Therefore, soils with high nutrient and water retention capacity should be selected as priority areas for in situ conservation across the country while active restoration efforts involving the species may be implemented in the subhumid zone.

Beyond its practical value in ecology, the results on the phenotypic plasticity of *P. erinaceus* can inform ecological predictive models designed for species distribution modelling and restoration planning, as they offer valuable insights into the species' ability to establish and persist in modified habitats (Benito Garzón et al. 2019). This, in turn, could enhance predictions of the *P. erinaceus* responses to future climate change scenarios and guide adaptive strategies for its conservation and restoration across West African landscapes (Biaou et al. 2023b).

4.4 | Limitations and Perspectives

While our study advances our understanding of the adaptive ecology of *P. erinaceus*, acknowledging its limitations is essential for a more holistic view of the species' local adaptation. Indeed, the analysis focused on the morphological and functional traits along an aridity gradient without considering anthropogenic pressures (e.g., logging, grazing, and fires) and socio-ecological factors (e.g., land-use practices, local livelihood dependence, and cultural values), which often interact with climatic factors to influence these traits (Houehanou et al. 2019). Future research should consider anthropogenic and socio-ecological factors for enhanced understanding of the adaptive strategy of *P. erinaceus*. Although the potential confounding effect of tree age on traits such as DBH was accounted for by selecting mature, reproductive trees (DBH $\geq$ 10 cm), we recommend stratifying morphological and functional traits by diameter classes in future studies.

5 | Conclusions

This study assessed the variability of morphological and functional traits of *P. erinaceus* along the aridity gradient in Benin to explore interactions between the traits and environmental conditions. Several morphological and functional characteristics, namely PeL, DBH, NB, NL, PEL, and LMA, significantly distinguish different subpopulations of *P. erinaceus* along the aridity gradient. Trait variation and plasticity along the aridity gradient revealed trade-offs between plastic and non-plastic traits that determine species growth across wide environmental gradients. Besides climatic factors, soil type shaped the traits of the species, indicating that the selection of priority areas for in situ conservation should account for soil properties. Our findings highlight the need for additional insights on the species phenology and genetic diversity associated with its fruit and seed morphological and functional traits to design effective conservation and domestication strategies. We further argue that establishing common gardens and reciprocal transplant experiments would help distinguish phenotypic plasticity from local adaptation and quantify the heritability of key functional traits. Finally, future analyses of adaptive trait variation in African forests should consider not only the influence of climate and edaphic drivers but also the prominent roles of anthropogenic pressures such as overexploitation and land conversion.

Author Contributions

S.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, visualisation, writing – original draft. K.V.S.: conceptualization, data curation, formal analysis, methodology, software supervision, visualisation, writing original draft, writing – review and editing. F.N.: conceptualization, data curation, investigation, methodology, software, supervision, writing – review and editing. G.B.H.: data curation, writing – review and editing. K.A.F.S.: Data curation, writing – review and editing. T.D.H.: conceptualization, methodology, validation, writing – review and editing. C.O.: conceptualization, validation, writing – review and editing. G.N.G.: conceptualization, investigation, methodology, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available through Figshare (https://doi.org/10.6084/m9.figshare.25888225).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Summary of the number of transects and plots installed per forest in the climate zones. **Table S2:** Presentation of the bioclimatic (available online https://webfiles.york.ac.uk/KITE/AfriClim/) and environmental variables used in the analyses. **Table S3:** Variation of the morphological and functional traits of P. erinaceus between the climate zones. **Table S4:** Output of the redundancy analysis (RDA) showing the morphological and functional traits discriminating P. erinaceus tree against climatic zones. **Table S5:** Correlations between axes of the canonical discriminant analysis (CDA) and each discriminant morphological and functional trait of P. erinaceus. **Figure S1:** Projection of P. erinaceus trees in the redundancy analysis (RDA) correlation biplot defined by the two first axes.

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