

## RESEARCH ARTICLE

# Farmer selection of drought-tolerant enset landraces reduces trait diversity in drier environments

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## Societal Impact Statement

Drought stress poses a growing threat to food security worldwide. In this study, we investigated the putative drought tolerance traits of enset, a multipurpose staple crop endemic to Ethiopia that sustains over 20 million people. Our findings reveal that enset's domestication has reduced landrace diversity and trait variability, particularly in drier environments, potentially limiting the crop's adaptive potential. Farmers in arid areas preferentially selected landraces with drought tolerance traits, highlighting the vital role of indigenous knowledge in climate adaptation. By emphasizing the importance of preserving phenotypic and genetic diversity to enhance crop resilience, our study provides globally relevant insights for food security and sustainable agricultural systems under climate change.

## Summary

- Increasing drought stress driven by climate change presents a significant challenge to global food security, requiring crop adaptations. Indigenous knowledge and sustainable practices in drought-prone agricultural systems may offer effective climate adaptation strategies. This study investigates the functional traits associated with the reported drought tolerance of enset (*Ensete ventricosum*), a multipurpose Ethiopian staple crop providing food security to more than 20 million people.
- Through field surveys and farmer interviews along three aridity gradients in southwest Ethiopia, we determined how domestication and farmer cultivation choices have shaped enset trait and landrace diversity. We measured 12 morphological and physiological traits of 430 cultivated enset plants on farms and a subset of traits of 30 wild enset plants. We also conducted interviews on farmers' knowledge of drought and enset, and how it influenced their choice of landraces.
- We showed that domestication reduced trait variance in cultivated enset and lowered landrace diversity in drier environments. Farmers in drier areas chose landraces with drought tolerance traits, resulting in trait differentiation between wetter and drier farms. Cultivated enset exhibited lower stomatal density and a

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narrower aridity niche compared to wild enset, suggesting adaptation to reduce water loss. We also found increased leaf wax coverage, leaf number, leaf temperature differential and plant height growth rate and reduced stomatal conductance on drier farms.

- Our findings are globally relevant, highlighting that climate adaptation and farmer selection may reduce trait and genetic diversity in drier environments, potentially resulting in less adaptive capacity under climate change.

#### KEYWORDS

climate resilience, crop adaptation, *Ensete ventricosum*, Ethiopia, food security, functional traits, indigenous knowledge

## 1 | INTRODUCTION

Under future climate change scenarios, drought stress is projected to negatively impact food security (Jia et al., 2019; Marie Chimi et al., 2023; Sathyan et al., 2018). Globally, over 106 million people were affected by drought in 2022, with the most extreme episodes occurring in the Horn of Africa, which left 23 million people severely food insecure (EM-DAT, 2023; WFP, 2023). Moreover, drought disproportionately impacts rainfed smallholder farming systems. It is estimated that 77% of small-scale farms across low- and middle-income countries are located in water scarce regions, and only 37% have access to irrigation (FAO et al., 2021). Against the backdrop of increasing temperatures and more seasonable precipitation, the global population exposed to extreme drought is projected to more than double by 2100 (3% to 8%) (IPCC, 2022).

Many plants adapted to drought prone environments have evolved a suite of morphological, physiological, and biochemical responses to cope with water deficits (Farooq et al., 2009). These include reduced leaf area, a thick wax cuticle, high root to shoot ratio, prolonged stomatal closure, osmotic adjustment, and changes in phenology (Chaves et al., 2003; Farooq et al., 2009; Munns, 2011). In addition to species with specific drought tolerance adaptations, more generalist species may exhibit adaptive phenotypic plasticity in their traits, allowing them to respond to different environmental conditions (Nicotra & Davidson, 2010; Stotz et al., 2021; Sultan & Spencer, 2002). Plasticity in crops can be further influenced by farming techniques like seed selection, propagation, grafting, and optimized irrigation regimes (e.g., wheat [Mengistu et al., 2019], cucumber [Shehata et al., 2022], and olive [Gholami et al., 2022]). Distinguishing between canalized (i.e., fixed) and more plastic traits that emerged during crop domestication could help clarify the mechanisms underlying tolerance to climate change (Nicotra et al., 2010).

Plant trait adaptation and plasticity driven by climate can be identified by sampling along environmental gradients (Solé-Medina et al., 2022; Vilà-Cabrera et al., 2015). For example, McLean et al. (2014) demonstrated trait plasticity in leaf area and thickness in *Eucalyptus tricarpa* by comparing traits from sites along a rainfall gradient, while Anderegg et al. (2021) found that along two aridity gradients, drier conditions were associated with leaf and branch trait shifts in

seven Australian tree species. Interspecific variation also differs across trait scales, with organ-level traits, such as leaf pressure-volume traits, showing less variation than whole-plant traits, such as growth rates (Browne et al., 2023; Westerband et al., 2021).

Farmers offer valuable insights into adaptive plant traits, drawing on their deep, long-standing knowledge of local environments and crops to select varieties with beneficial characteristics that thrive under local conditions (Ford et al., 2020; Singh & Singh, 2017). Additionally, interviews with farmers, particularly in harsh environments, can provide useful traditional knowledge on important underutilized and climate resilient varieties that could be at risk of extirpation (van Zonneveld et al., 2020). For instance in Malawi, farmers chose to grow traditional crop varieties of sorghum and pearl millet because of their high tolerance to heat and drought (Zimba et al., 2023).

In this study, we investigated the trait variation and plasticity of the indigenous Ethiopian staple crop enset (*E. ventricosum* [Welw.] Cheesman) that may be linked to its putative drought tolerance. Cultivated enset is exclusively found in the southwest Ethiopian highlands, where hundreds of *E. ventricosum*-derived “landraces” (varieties) support over 20 million people (around 20% of the population) and have adapted to local environmental conditions and traditional management and uses (Borrell et al., 2020). Enset is part of a diverse mixed farming system of cereals, root and tuber crops, pulses, vegetables, fruits, and oilseeds, grown in close conjunction with livestock such as cows, sheep, and goats (Central Statistical Agency [CSA], 2020; Tsegaye & Struik, 2002). Figure 1 illustrates a typical enset garden plot located in the study area. Enset, known as ‘the Tree Against Hunger’, can be harvested at any stage of its life cycle and throughout the year, while its edible fermented pulp can be stored for extended periods and easily accessed when needed (Brandt et al., 1997). These characteristics, combined with its high yield per unit area and significant caloric and micronutrient content, make it crucial for the region's food security (Borrell et al., 2019; Morrow et al., 2023; Tamrat et al., 2020). During the main annual dry period in southwest Ethiopia (October–March), enset is reported to recover from the lack of rainfall better than other crops (Harrison et al., 2014; Mohammed et al., 2013; Quinlan et al., 2015). As farmers consider enset to be drought tolerant, they increase the production of enset in more drought-prone areas and after severe droughts when other crops fail (Chase et al., 2023).

**FIGURE 1** Typical enset garden plot in the highlands of Gurage zone, at an altitude of 3000 m.a.s.l. Photo credit: R. Chase.



Despite its narrow distribution, cultivated enset has high genetic and phenotypic diversity (Gerura et al., 2019; Olango et al., 2015; Yemataw et al., 2018). White et al. (2023) showed that enset underwent a domestication bottleneck with sexual recombination of inedible wild genotypes, followed by clonal propagation by farmers to multiply preferred genotypes. The authors also detected strong phylogenetic signals in the diverse domestic gene pool for useful traits such as food quality, fiber quality, medicinal value, and disease resistance. Enset has a lifespan of 4 to 8 years, and its cultivation involves multiple stages—such as sucker propagation and successive transplantation—during which it adapts to environmental variations (Brandt et al., 1997; Hunduma & Ashenafi, 2011). Wild enset, which occurs from southwest Ethiopia to northern South Africa in forest and riverine habitats, differs from cultivated enset in its morphology and habitat niche (Borrell et al., 2019; Hildebrand, 2001). During its domestication, as farmers presumably expanded enset cultivation from wetter habitats into the drier and more seasonal environments of its current cultivation range, selection for more drought tolerant landraces may have occurred, resulting in distinctive diversity patterns on farms between different environments.

Previous analyses of enset's drought tolerance are limited. In a study of two enset landraces, Zewdie et al. (2007) showed early stomatal closure and increased underground biomass in response to drought. More extensive research on the closely related crop banana (*Musa* spp.) revealed that during drought stomata closed early to maintain water potential for cell functioning; however, the resulting reduction of photosynthesis slowed vegetative growth and delayed flowering and maturity, negatively affecting yield in the long-term (Israeli & Lahav, 2019; Uwimana et al., 2020; van Asten et al., 2011). The whole-plant process of transpiration efficiency (dry matter accumulated per unit of water transpired) increased in certain banana cultivars under drought conditions (Kissel et al., 2015). Genotypes derived from the wild ancestor *Musa balbisiana* reportedly have the highest tolerance to drought because of mechanisms related to root depth, stomatal regulation, and

leaf traits (Eyland et al., 2022; Thomas et al., 1998; van Wesemael et al., 2019).

To better understand how enset domestication has contributed to enset's putative drought tolerance, we first aimed to quantify any shifts in traits associated with drought tolerance that may have occurred during enset's domestication by comparing cultivated and wild enset trait data. Second, to determine how farmers' choices of landraces influenced traits currently observed on farms, we assessed cultivated trait values and diversity along three aridity gradients. In addition, we surveyed farmers about their knowledge on local drought history, enset's drought tolerance, and their landrace preferences. Our main study questions and hypotheses were therefore: (1) How did domestication influence the traits associated with drought tolerance and the diversity of cultivated enset? We posit that during domestication, the progressive expansion to drier habitats led to a reduced range of traits linked to drought tolerance in cultivated enset; (2) which traits help enset tolerate drought? We suggest that the trait values that are more frequent in landraces on drier compared to wetter farms may be linked to enset's putative drought tolerance; and (3) is drought tolerance associated with farmer selection of specific landraces or with trait plasticity within a landrace, or both? We hypothesize that farmers in more arid environments preferentially plant enset landraces with more plastic adaptations that respond more readily to drought.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

#### 2.1.1 | Study area and environmental data

We sampled cultivated enset on 43 smallholder farms along three steep aridity gradients in southwest Ethiopia. The three study zones

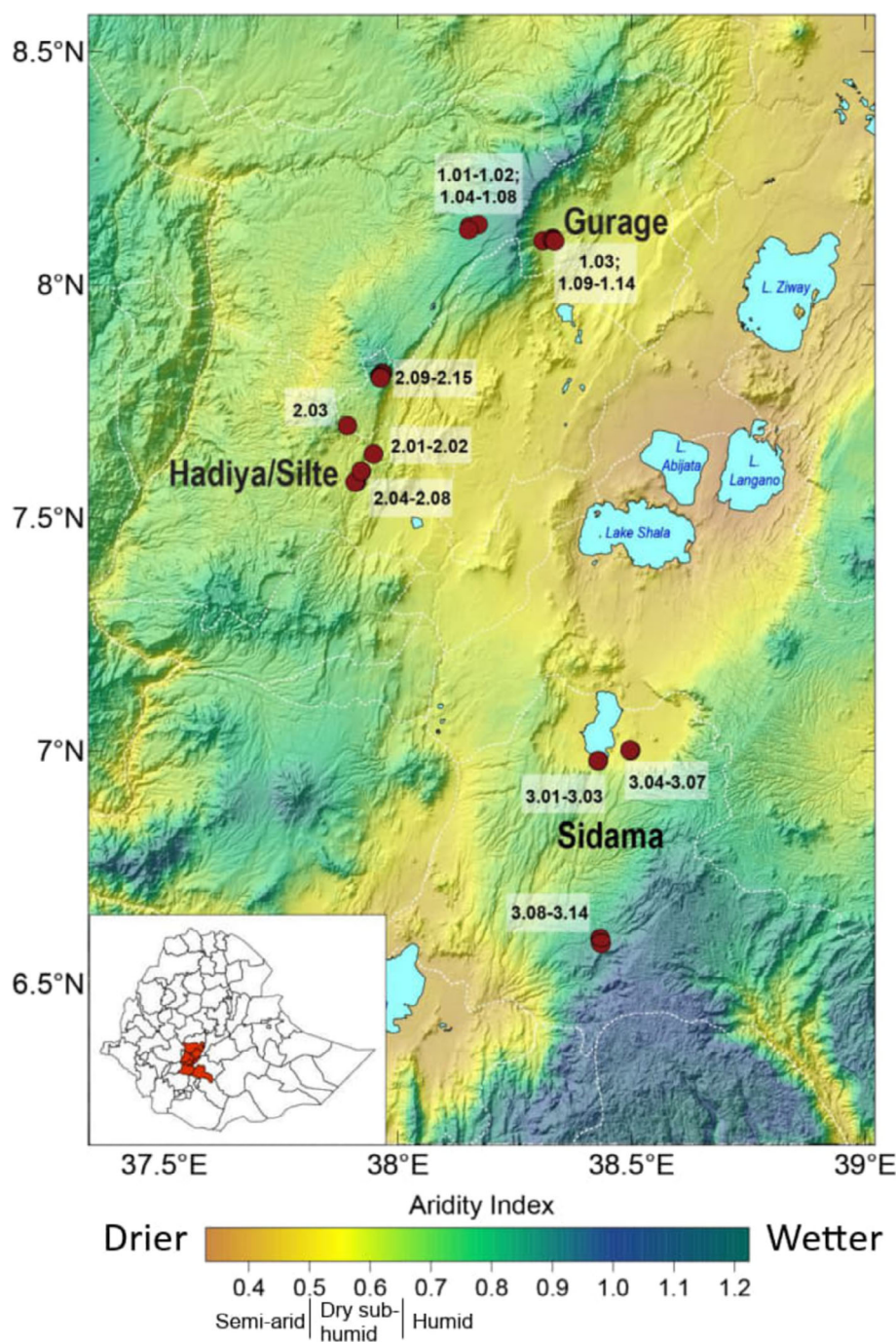


**FIGURE 2** Locations of the 43 sampled farms (red circles with corresponding study ID numbers) in three areas of Southwest Ethiopia: Gurage (Zone 1), Hadiya/Silte (Zone 2) and Sidama (Zone 3) (see inset). High aridity index (wetter) areas are shown in green/blue shades, and low aridity index (drier) areas in orange/yellow shades. Classification of aridity index values follows UNEP (1997).

were Gurage (Zone 1), Hadiye/Silte (Zone 2), and Sidama (Zone 3) (Figure 2). The farms were located between 1730 and 3200 m.a.s.l. in tropical highland subhumid/humid agroecological zones (FAO and IISA, 2020). We sought to minimize the distance between low and high aridity farms to mitigate other covariates in driving differences between sites. Farm locations are listed in Table S1.

Within each of the three study zones, seven or eight farms were selected from the upper and lower limits of the aridity scale using the Global Aridity Index GIS layer (Trabucco & Zomer, 2018). Aridity index is the ratio of precipitation to potential evapotranspiration and serves as a proxy to estimate drought conditions (Barrientos et al., 2023;

Nastos et al., 2013). Higher aridity index values indicate wetter conditions, while lower aridity index values indicate drier conditions.

To determine other environmental conditions at the sampled locations, we sourced mean annual gridded climate data from CHELSA (Karger et al., 2017). Using the R package “raster” (Hijmans, 2024), we extracted the 19 WorldClim variables and vapor pressure deficit data averaged from 1981 to 2010. In addition, solar radiation data (Global Horizontal Irradiation) was sourced from Global Solar Atlas 2.0 (The World Bank, 2019) and soil class data from SoilGrids (Poggio et al., 2021). The full list of environmental variables is found in Table S2.

## 2.1.2 | Phenotypic trait data

We performed phenotypic measurements of cultivated enset across aridity gradients to determine the effects of drought on functional traits. Ten mature plants were randomly sampled on each farm to capture community trait variation, for a total of 430 plants. We measured 10 morphological and two physiological traits per plant (Table 1) that have been associated with plant drought tolerance in other species (e.g., Bertolino et al., 2019; Solé-Medina et al., 2022; Wright et al., 2004) and particularly in the closely related crop, banana (e.g., Dhanyalakshmi et al., 2019; Sampangi-Ramaiah et al., 2016; Turner et al., 2007; Turner & Thomas, 1998). All data were recorded using ARCGIS Survey 123 (ESRI, 2023).

Selected morphological traits included plant height, pseudostem height, pseudostem volume, plant height growth rate, and pseudostem volume growth rate. We also measured the angle of phytotelma

(opening between leaf sheath and the base of the pseudostem), which creates a cavity where rainwater persists and thus could contribute to enset's drought tolerance. Leaf traits included leaf number, leaf wax coverage, and leaf area, which was leaf length  $\times$  width  $\times$  0.735 (enset leaf shape constant). The leaf shape constant was specifically derived for this study via a linear regression of actual leaf area and estimated leaf area (length  $\times$  width) of 30 different sized/aged leaves of wild and cultivated enset varieties collected in the field (see Methods S1). Leaf wax coverage was classified according to an interval scale based on the one used for characterizing banana (IPGRI, 1996), where a scale of 1–4 described the percentage of abaxial leaf area covered by wax: 1 = no wax, 2 = <25%, 3 = 25–50%, 4 = > 50%.

To measure stomatal area and density, a fresh leaf sample was collected from each plant from the middle of the third youngest leaf. A two-step procedure was followed: First, three photos were taken of different areas on the abaxial side of fresh leaves (where most

**TABLE 1** The 10 morphological and two physiological traits analyzed in the study, including their abbreviations used in the study, calculations and units, associations with drought tolerance in plants, and references for those associations.

| Traits                        | Abbr. | Calculation (units)                                                                          | Role in drought tolerance                                                                                                                                                                                  | References                                                                             |
|-------------------------------|-------|----------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|
| Size/form                     |       |                                                                                              |                                                                                                                                                                                                            |                                                                                        |
| Plant height                  | PH    | (cm)                                                                                         | Plants generally reduce growth in response to drought stress to conserve their water budget and allocate more resources to roots versus shoots to increase soil water uptake (i.e., biomass partitioning). | Chaves et al., 2003; Farooq et al., 2009; Olson et al, 2018; Schulze et al, 2019       |
| Pseudostem volume             | PSV   | 1/3 (π) (r1 <sup>2</sup> + r1r2 + r2 <sup>2</sup> ) x pseudostem height, (cm <sup>3</sup> )  |                                                                                                                                                                                                            |                                                                                        |
| Phytotelma                    | P     | Angle of bottom leaf sheath to pseudostem base                                               |                                                                                                                                                                                                            |                                                                                        |
| Growth rate                   |       |                                                                                              |                                                                                                                                                                                                            |                                                                                        |
| Plant height growth rate      | PHR   | PH/age, (cm/years)                                                                           |                                                                                                                                                                                                            |                                                                                        |
| Pseudostem volume growth rate | PSVR  | PSV/age, (cm <sup>3</sup> /years)                                                            |                                                                                                                                                                                                            |                                                                                        |
| Leaves                        |       |                                                                                              |                                                                                                                                                                                                            |                                                                                        |
| Leaf number                   | LN    | No. of healthy open leaves                                                                   | As conditions become drier, plants reduce their leaf area, including by leaf senescence, to minimize water loss.                                                                                           | Passioura, 1996; Farquhar et al., 2002; Díaz et al., 2016                              |
| Leaf area                     | LA    | Leaf length × leaf width × 0.735, (cm <sup>2</sup> )                                         |                                                                                                                                                                                                            |                                                                                        |
| Leaf wax                      | LW    | Percentage of epicuticular wax coverage on abaxial side of leaf                              | Wax blooms on leaves reduce water loss and help maintain high tissue water potential.                                                                                                                      | Farooq et al., 2009; Nicotra et al., 2010; Richards et al., 2010; Schulze et al., 2019 |
| Stomata                       |       |                                                                                              |                                                                                                                                                                                                            |                                                                                        |
| Stomatal density              | SD    | No. of stomata/circle of 0.03 mm <sup>2</sup>                                                | Reduced stomatal density and area have been linked to reduced water loss during drought.                                                                                                                   | Caine et al., 2019; Hughes et al., 2017; Kusvuran et al., 2010                         |
| Stomatal area                 | SA    | $\pi \times \left(\frac{\text{length}}{2}\right) \times \left(\frac{\text{width}}{2}\right)$ |                                                                                                                                                                                                            |                                                                                        |
| Physiology                    |       |                                                                                              |                                                                                                                                                                                                            |                                                                                        |
| Stomatal conductance          | SC    | (mmol/m <sup>2</sup> s)                                                                      | Reduced stomatal conductance prevents water loss and improves plant water-use efficiency.                                                                                                                  | Tardieu et al., 1996; Chaves et al., 2009; Farooq et al., 2009; Schulze et al., 2019   |
| Leaf temperature differential | LTD   | Abaxial–adaxial leaf temperature, (Celsius)                                                  | As there are more stomata on the abaxial side of the leaf, if stomata are open, the abaxial side is cooler than the adaxial side and the LTD is greater.                                                   | DeJonge et al., 2015; Huggins et al., 2018; Vantyghem et al., 2022                     |

stomata are located) with a smart phone (with 4X magnification) mounted on a Kruss optronic microscope with 10X lens and 10X eyepiece, resulting in 400X magnification. Any leaves that were too dry were rehydrated overnight in distilled water. Second, Image J software (Schneider et al., 2012) was used to measure the width and length of a typical stoma for each of the three photos. Measurements were calibrated from pixels using an image of a 1-mm micrometer taken at the same magnification as the analyzed images. Stomatal area was calculated as an ellipse (Table 1). Stomatal density was determined by counting stomata in a standard circle of area 0.03 mm<sup>2</sup>. Averages were made of the three measurements per plant.

The plant and leaf traits measured in this study are considered “soft” traits, which are practical for field measurements and are informative proxies to “hard” drought tolerance traits, such as physiological characteristics (e.g., photosynthesis) (Hodgson et al., 1999). However, we also measured the physiological traits stomatal conductance and leaf temperature differential. Using a handheld leaf porometer in the field (SC-1 leaf porometer, METER), we took three readings per plant from the middle lamina of the third youngest leaf to measure gas exchange (stomatal conductance) and the temperature of the bottom and top of the leaf (of which the difference is the leaf temperature differential). Porometer readings were taken at midday (between 11 a.m. and 1 p.m.), when environmental conditions were most stable. We also collected a subset of traits for wild onset that were sampled from the Southern Nations, Nationalities, and Peoples' Region and Amhara Region from 2018 to 2023 (see Table S3). Where wild plants were accessible, we measured pseudostem height and circumference (30 plants) and collected leaf samples (92 plants) to subsequently take stomatal measurements. Dried leaves were rehydrated overnight in distilled water, and stomatal area and density were measured following the same protocol described earlier for the cultivated leaf samples.

## 2.2 | Data analysis

### 2.2.1 | Comparison of wild and cultivated onset functional traits

To test our hypothesis on the shift in trait means during the domestication of wild onset, we compared four factors common to our wild and cultivated onset datasets: Aridity Index (using the geographical coordinates of plant records from this study and Koch et al. [2022]), the ratio of the pseudostem height to pseudostem volume, stomatal area, and stomatal density. Significance was determined using the Welch two sample *t*-test, and effect size (Hedge's *G*) was calculated using R package “*esvis*” (Anderson, 2020). To determine the relative degree of ecological specialization for wild and cultivated onset, we measured Levin's niche breadth for aridity index using the R package “*dplyr*” (Wickham et al., 2023). Data were visualized using R package “*ggplot2*” (Wickham, 2016). All data processing and statistical analyses were carried out using R (4.3.2) and R Studio (Posit Team, 2024; R Core Team, 2024).

### 2.2.2 | Patterns of landrace diversity at different scales

To test if there was a bottleneck of onset diversity resulting from the expansion of onset into more arid environments, we calculated diversity indices (i) within groups of farms of the same aridity level, (ii) between low and high aridity farms, and (iii) between zones. Diversity indices comprised alpha diversity, represented by the number of landraces per farm; gamma diversity, the total number of landraces recorded in all farms per zone; and beta diversity (Jaccard's Distance), calculated within groups of drier or wetter farms in each zone, between drier and wetter farms in each zone and between zones.

### 2.2.3 | Trait variance and associations with the environment

To first examine the trait variance, we calculated coefficients of variation for each trait. We then partitioned the trait variation of all plants by fitting a linear mixed-effects model with a fixed intercept and nested random effects of farm, zone, and aridity level (drier or wetter) following the methods of Bates (2010). Thus, the nested random effect variance parameters represented the between-farms, between-zones, and between-aridity level variation, while residual variance represented the within-farm variation.

To test how environmental variables, including aridity, were associated with traits, we used redundancy analysis from the R package “*vegan*” (Oksanen et al., 2024), with farm-level trait means as the response matrix and aridity index plus 22 other environmental predictors as the explanatory matrix (Table S2). Following the methodology of Borcard et al. (2011), we removed multicollinear variables and identified the environmental variables that best explained the trait variance. This analysis revealed that aridity index is an important predictor of trait variation. Next, we examined the relationship of traits with aridity index using multiple mixed-effects regression models. The response variables were farm-level means of the 12 functional traits as opposed to individual plant values, as we aimed to capture the effects of aridity at a “community” level. The fixed effect was aridity index and the random effect was “zone,” following the methods of Bates et al. (2015) and using the R package “*lmerTest*” (Kuznetsova et al., 2017). We then applied a Holm–Bonferroni correction.

Finally, we ran a non-metric multidimensional scaling ordination (NMDS) using the R package “*vegan*” on all individual plant trait data to discern the difference in trait distribution between drier and wetter farms. NMDS was considered an appropriate ordination method for this analysis because it preserves among-sample relationships accurately in a low-dimensional picture (Clarke, 1993). We ran a Permutational Multivariate Analysis of Variance (PERMANOVA) to detect any significant difference between the mean and dispersion of trait data between the drier and wetter farms.

## 2.2.4 | Testing for plasticity in trait responses to drought

To differentiate traits with a plastic response, we applied a Genotype  $\times$  Environment approach using named landraces as genotypes. We applied two-way analyses of variance (ANOVAs) with the interaction of “aridity index” (low or high) and “landrace” on four enset landraces that were found in abundance on both low and high aridity farms (Ado, Badadet, Ganticha, and Gimbowe). Where the interaction of aridity and landrace was significant, we applied the Tukey's Honest Significant Differences post hoc test to determine how many landraces showed significant differences between low and high aridity farms for that trait.

## 2.2.5 | Farmer perceptions of drought tolerance traits

We interviewed 35 of the 43 farmers (those who were present during the surveys) to understand their perception of enset's drought tolerance and if/how knowledge and perception on this influences what they plant. Six questions were asked in the local language with the help of a translator: (1) Which enset landraces do you grow? (2) How much of each landrace do you grow? (3) What enset characteristics are important and why? (4) Which landraces tolerate drought the best and the worst? (5) Have you experienced any droughts, and if yes, how often in the last 40 years? (6) Did you grow more, less, or a similar area of enset after the drought(s) and with which landraces? Results were compiled by zone and aridity level (low or high) for comparison. We also calculated landrace abundance based on those answers and ordered landraces that were considered drought tolerant by their rank score.

# 3 | RESULTS

## 3.1 | Trait and niche differences between wild and cultivated enset

The current range of wild enset overlapped with the cultivated range; however, cultivated enset was grown in significantly more arid environments (lower aridity index) than wild enset ( $t$  [106.8] = 7.31,  $p$ -value < .001, effect size = 0.82) (Figure 3). Even though it has a smaller aridity index range, wild enset exhibited a higher niche breadth ( $B$  (wild) = 1.96 vs  $B$  (cultivated) = 1.64), because it was more evenly distributed across its aridity index range than cultivated enset. Cultivated enset also displayed significantly lower stomatal density compared to wild enset ( $t$  [63.2] = -16.37,  $p$ -value < .001, effect size = 2.25). However, pseudostem height to volume ratios ( $t$  [33.5] = -0.49,  $p$ -value = .63, effect size = 0.09) and stomatal area ( $t$  [192] = -1.12,  $p$ -value = .26, effect size = 0.1) did not significantly differ between wild and cultivated enset.

## 3.2 | Patterns of enset landrace diversity

We recorded 68 named landraces on 43 farms across the three study zones. The average number of landraces per farm was 5.3 (range 2–10). The average number of landraces (alpha diversity) was significantly higher on wetter farms (6) than on drier farms (4.6) ( $t$  [41] = 2.07,  $p$ -value = .045). The beta diversity between drier and wetter farms was 0.93, 0.68, and 0.75 for zones 1, 2, and 3, respectively. Between-zone beta diversity of landraces among the three zones was also very high, ranging from 0.85 to 1 (Figure 4).

## 3.3 | Environmental drivers of enset trait variation

Redundancy analysis identified three (out of 22) environmental variables that best explained the observed farm-level trait variation (with an adjusted  $R^2$  of 0.46). The significant predictors and corresponding percentage of trait variance explained were mean temperature of wettest quarter (Bio 8) – 14.9%; Aridity Index – 9.54% and precipitation of driest month (Bio 14) – 9.51%. The model was statistically significant ( $p$  < .001), and every variable included in this model and canonical axis resulting from the redundancy analysis was also statistically significant ( $p$  < .001). Bio 8 and Bio 14 were significantly correlated with aridity index at  $r(23) = -0.48$ ,  $p = .02$  and  $r(23) = 0.65$ ,  $p = .007$ , respectively. The redundancy analysis thus confirmed that aridity index is an important driver of trait variation. Furthermore, the clustering of the site scores (traits) toward increased aridity index indicates that wetter farms have more enset trait variation than drier farms (Figure S1).

The mixed-effects regression models revealed that five functional traits had significant relationships with aridity index ( $p$  < .05) (Figure 5, Plots a–l). Leaf wax coverage, leaf number, plant height growth rate, and leaf temperature differential were higher in drier farms, while stomatal conductance was higher in wetter farms. The NMDS plot clearly segregated plants on drier and wetter farms, driven primarily by the traits stomatal conductance, plant height growth rate, and leaf wax, with a stress value of 0.078, indicating a good model fit (Figure 6). PERMANOVA revealed a significant difference in data dispersion between drier and wetter farms ( $p = .001$ ). Comparison of the multidimensional trait space (ellipse area) showed slightly higher trait variance in drier farms (ellipse area =  $7.6 \times 10^{-3}$  and  $7.2 \times 10^{-3}$  for drier and wetter farms, respectively) (Figure 6). In landraces common to both drier and wetter farms (i.e., Ado, Badadet, Ganticha, and Gimbowe), there was a significant effect of aridity on stomatal conductance, leaf temperature differential, leaf wax, and leaf number for all four landraces (Tables 2 and S4).

## 3.4 | Farmers strategies for sustainable enset cultivation

A total of 35 farmers (80% of whom were male) were interviewed. Of those, 21 farmers (60%) had experienced severe drought in the last

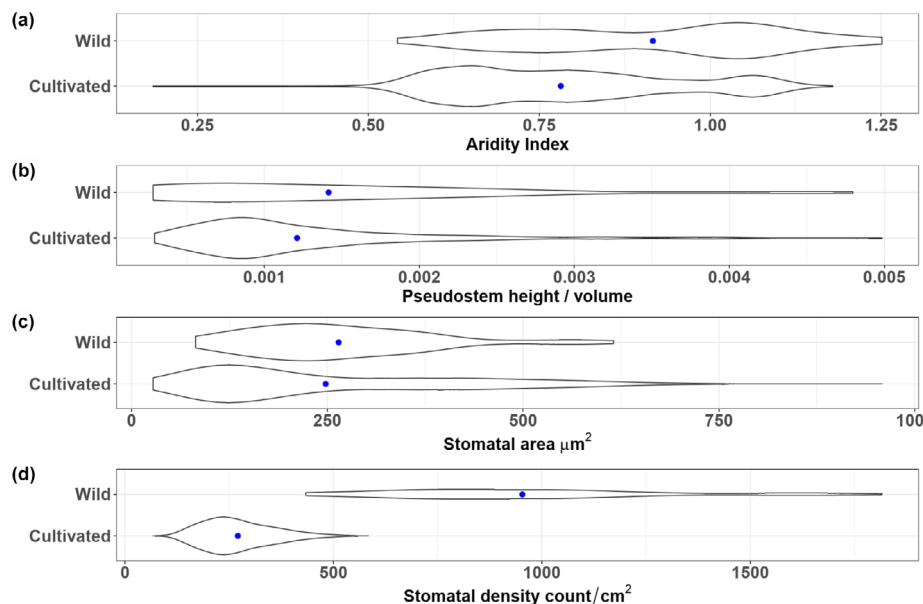


**FIGURE 3** Differences between wild and cultivated enset data for (a) aridity index, (b) the ratio of pseudostem height to volume, (c) stomatal area, and (d) stomatal density. Mean values are shown by blue circles. T-test *p*-values are significant for aridity index and stomatal density.

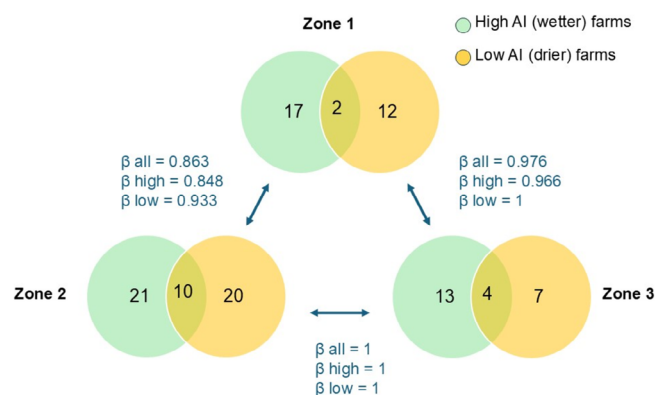


**FIGURE 4** Numbers of unique and shared landraces per groups of drier and wetter farms per zone, showing that alpha diversity is higher in groups of wetter farms in all zones. Total (gamma) diversity and shared number of landraces is highest in zone 2. Also shown in blue text is the dissimilarity (beta diversity) of landraces among the three zones, which is very high.

40 years, predominately in 1984 and 2007. Of the farmers that reported severe drought, 66% were from drier farms and 33% were from wetter farms. Farmers in drier areas reported that drought tolerance was an important criterion in choosing which landrace to plant. Other common criteria for landrace selection were “fits the local agroecology,” a concept possibly promoted by agricultural extensive agents, and “diversity of use,” meaning that a mix of landraces provides a variety of enset products. The most common landraces (recorded at more than 10 farms) in order of frequency were Agade, Gimbowe, and Ado. The four landraces most often cited by farmers as being drought tolerant in order of frequency were Ganticha, Badadet, Ado, and Gimbowe. Three farmers from drier farms indicated they planted more Badadet in response to previous severe droughts.

A decomposition of trait variance showed that leaf wax coverage, stomatal conductance, and leaf temperature differential had high

variance between aridity levels (Figure 7). Stomatal area primarily differed between zones, whereas other traits showed little difference between zones. The majority of trait variance, except for the traits stomatal area and leaf wax, occurred within individual farms.

## 4 | DISCUSSION

### 4.1 | Enset's domestication led to trait adaptations

The observed differences between wild and cultivated enset in our study suggest that domestication has driven specific trait adaptations to enhance drought tolerance, such as reduced stomatal density. Although unlikely to be selected by farmers, reduced stomatal density is likely present in the more drought tolerant landraces, as it has been shown to improve water use efficiency in other crops, such as wheat (Li et al., 2017), rice (Caine et al., 2019), and barley (Robertson et al., 2023). Stomatal area did not significantly differ between wild and cultivated plants; however, cultivated stomatal area data were highly skewed, with stomata in Zone 3 being more than twice the size of stomata in the other two zones. A plausible explanation is the presence of enset polyploidy in the region that includes Zone 3, which may account for the enlarged stomata—an effect also observed in other species such as banana (Auliya et al., 2019; Beaulieu et al., 2008; Vandenhout et al., 1995). Recent findings by Dussert et al. (2025) confirmed the existence of polyploid enset in the same region.

### 4.2 | Environmental filtering in more arid regions reduced landrace diversity

In enset, a clonal perennial crop, we found greater landrace diversity in wetter environments, which more closely resemble the

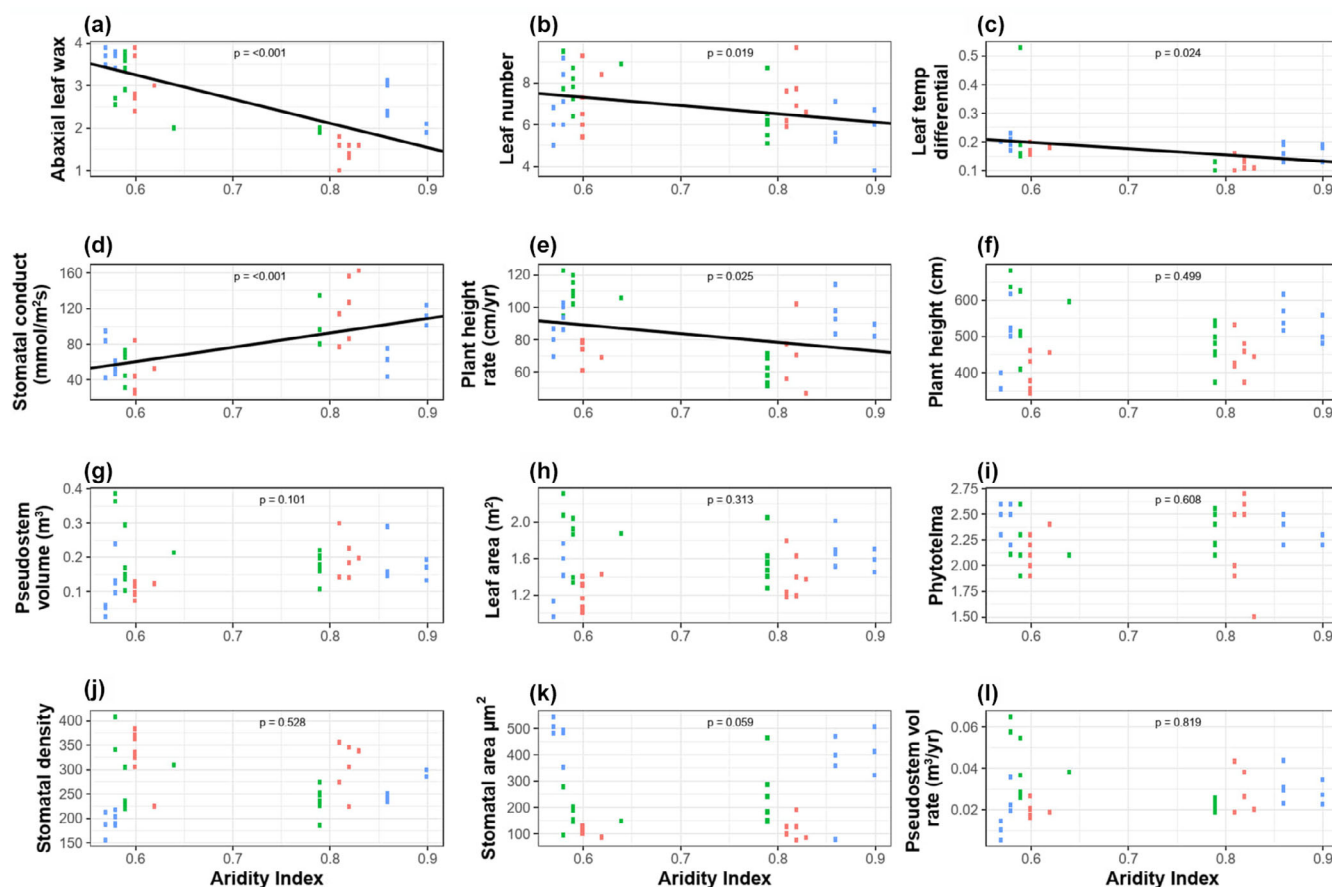


**FIGURE 5** (a–l) Mixed-effects model results of traits across the aridity index range (using farm means). Colors denote the three different study zones: Zone 1 = red, Zone 2 = green, Zone 3 = blue. *P*-values are given and significant models include a black regression line. High aridity index values correspond to wetter areas.

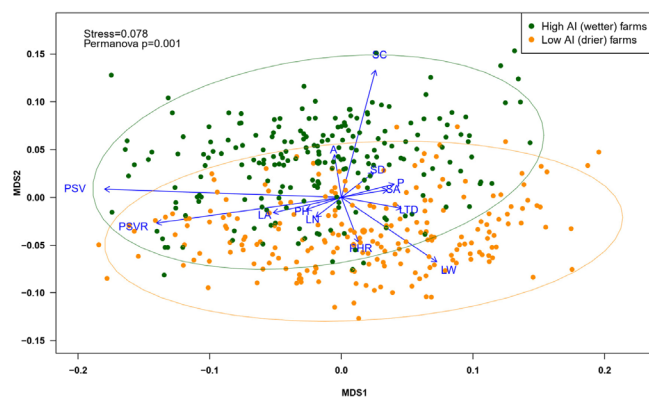


**FIGURE 6** Non-metric multidimensional scaling ordination (NMDS) of traits with ellipses showing 95% confidence interval of wetter and drier farms. The stress value of 0.078 indicates a good model fit, and PERMANOVA detected a significant difference in mean values and dispersion between drier and wetter farms ( $p = .001$ ). Trait abbreviations in blue text: PH = plant height, PS = pseudostem volume, P = phytotelma, PHR = plant height growth rate, PSVR = pseudostem volume growth rate, LN = leaf number, LA = leaf area, LW = leaf wax, SD = stomatal density, SA = stomatal area, SC = stomatal conductance, and LTD = leaf temperature differential.

natural habitat of wild enset than the drier areas where cultivated enset is also grown. The smaller landrace pool in drier climates may have resulted from environmental filtering during domestication. This continuous, long-term selection of adaptive traits has driven divergence between many crops and their wild ancestors (Stetter, 2020). Such “domestication bottlenecks” typically reduce genetic and phenotypic diversity, although this effect is often less severe in perennials because of their longer generation times compared to annuals (Alam & Purugganan, 2024).

In our study, drier farms had lower alpha diversity (landraces per farm) compared to wetter farms in all three study zones. The number of shared landraces between drier and wetter farms within each zone was also low, suggesting that most landraces could be specialists that have adapted traits for more arid conditions. Of particular interest are the landraces present at both wetter and drier farms, which may have a broader adaptive capacity or greater plasticity that allows them to readily adapt to changing environmental conditions. The number of shared landraces among zones was low to none, suggesting very little transfer of enset planting material over long distances.

### 4.3 | Aridity is associated with key drought tolerance traits

We found that leaf wax coverage, leaf number, plant height growth rate, and leaf temperature differential were higher on drier farms. Traits more frequently found in plants at the drier end of aridity gradients have been associated with drought tolerance in other crops. Epicuticular wax, in particular, has been shown to reduce water loss and

**TABLE 2** Two-way ANOVA results of the traits of four landraces common to both drier and wetter farms (Ado, Badadet, Ganticha, and Gimbowe), including *p*-values of relationships with aridity, landrace, and their interaction (aridity × landrace).

| Trait                         | <i>p</i> -values |          |             |
|-------------------------------|------------------|----------|-------------|
|                               | Aridity          | Landrace | Interaction |
| Stomatal conductance          | <.001**          | .19      | .111        |
| Leaf temperature differential | <.001**          | <.001**  | .524        |
| Leaf wax                      | <.001**          | <.001**  | .081        |
| Leaf number                   | .012*            | .019*    | .844        |
| Plant height                  | <.001**          | <.001**  | <.001**     |
| Leaf area                     | <.001**          | .002*    | <.001**     |
| Pseudostem volume             | <.001**          | .004*    | <.001**     |
| Pseudostem volume rate        | .005*            | .003*    | <.001**     |
| Stomatal area                 | .064             | <.001**  | .014*       |
| Stomatal density              | .128             | <.001**  | <.001**     |
| Phytotelma                    | .346             | <.001**  | <.001**     |
| Plant height rate             | .537             | <.001**  | <.001**     |

Note: Stomatal conductance, leaf temperature differential, leaf wax, and leaf number had a significant relationship with aridity for all four landraces (in bold). The other traits were significantly associated with aridity for fewer landraces. Full ANOVA results are found in Table S4.  
\**p* < .05, and \*\**p* < .001.

maintain turgor in banana (Sampangi-Ramaiah et al., 2016; N. C. Turner & Begg, 1981). Furthermore, we found leaf wax exclusively on the abaxial (lower) side of onset leaves, where in addition to water loss prevention, it reflects radiation and thereby reduces overheating. This likely contributed to the higher leaf temperature differential recorded on drier farms, where leaf wax coverage was highest.

Plants on drier farms had more leaves and faster plant height growth rates than plants on wetter farms. These traits are not necessarily expected of plants subjected to drought. Our observation of more leaves on drier farms (although not greater leaf area) could be because of the plants' ability to adapt to drought conditions by abandoning older parts and renewing younger parts (Xu et al., 2010). We also found that plants on drier farms had lower stomatal conductance, but leaves were generally not wilted, suggesting that onset adheres to “isohydric” drought tolerance behavior, where leaf water status (and thus leaf number) is maintained regardless of soil water status (Skelton et al., 2015). This agrees with the findings of Zewdie et al. (2007), where onset stomatal conductance and net photosynthetic rate declined after 60 drought days, but there was little change in leaf water content. The faster plant height growth we observed on drier farms is likely driven by higher temperatures accelerating metabolic and enzymatic processes that influence growth rate (Nievola et al., 2017; Taiz & Zeiger, 2002). This idea is supported by the earlier harvest times of onset in low-altitude farms compared to high-altitude farms observed by Hunduma and Ashenafi (2011) and by our observation that plants were significantly older on higher altitude farms, indicating that they grow more slowly in cooler climates.

Aridity had a significant effect on four traits of the four landraces that were common on both drier and wetter farms: stomatal conductance, leaf temperature differential, leaf wax coverage and leaf number. These traits could be considered plastic, but we could not rule out the possibility that trait variation was because of intra-landrace genetic differentiation between drier and wetter farms. Furthermore,

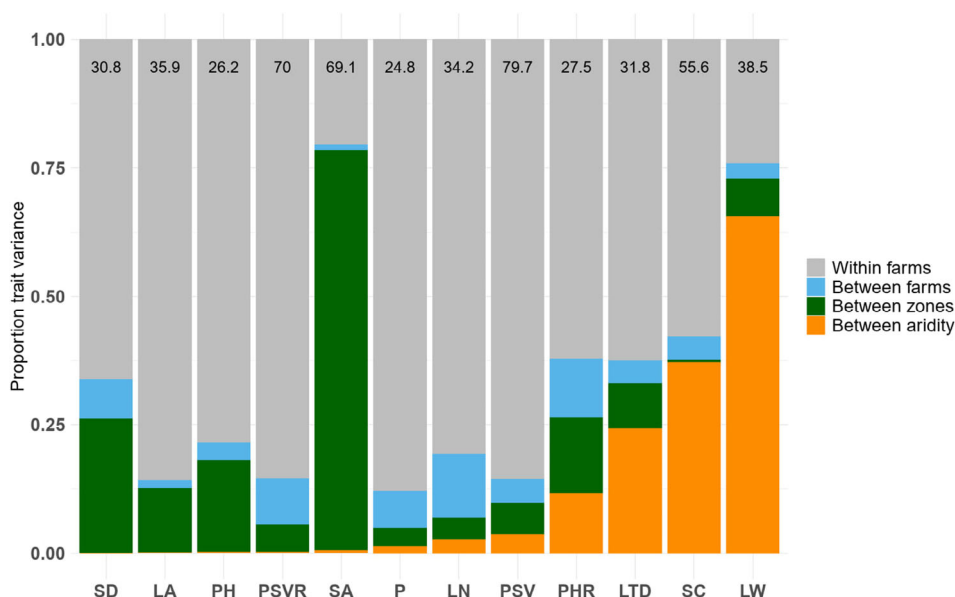


**FIGURE 7** The proportion of variance of traits occurring within farms, between farms, between zones, and between aridity index (AI) levels (drier and wetter), with coefficients of trait variation at the top of each column. Trait abbreviations: SD = stomatal density, LA = leaf area, PH = plant height, PSVR = pseudostem volume growth rate, SA = stomatal area, P = phytotelma, LN = leaf number, PSV = pseudostem volume, PHR = plant height growth rate, LTD = leaf temperature differential, SC = stomatal conductance, and LW = leaf wax.

even though the analyzed landraces between farms had the same name and phenotypic appearance, we did not genotype plants to confirm that all landraces with the same name were indeed genetically identical. Given enset's clonal means of propagation and the high beta diversity among zones (indicating little exchange of germplasm), we would expect named landrace lineages to be genetically similar, although this cannot be ruled out without genetic identification.

Enset's response to drought may affect its value for farmers. For instance, higher root to shoot ratios could result in more yield for the dish made of boiled corm (*amicho*) and less yield for the dishes made primarily from the pseudostem, *kocho* and *bullā*. Landraces with higher growth rates may allow quicker delivery of secondary products, such as rope fiber and other building materials. Changes in leaf area could also affect the availability of animal fodder during dry periods.

#### 4.4 | Farmers influenced the variance of drought tolerance traits

Farmers' preferences for drought-tolerant landraces, driven by their experiences with severe drought, have shaped enset trait distribution and landrace composition, which has reduced the landrace pool in arid environments. Most farmers who reported severe drought in the past 40 years were from drier farms. Based on their responses, we suggest that this experience increased their knowledge on which landraces and traits confer higher drought tolerance and led some of them to plant more of those landraces.

Although we found correlations between traits and aridity, the majority of trait variance occurred within farms, implying that factors other than environment (including aridity) are influencing traits. This aligns with similar studies that showed plant trait variance was not solely driven by the environment (e.g., Anderegg et al., 2021; de Oliveira et al., 2020). Enset diversity has been associated with non-climatic factors such as household wealth, farm size, number of livestock, and culture (e.g., the Gurage ethnic group are known as “the people of enset”) (Abebe, 2013; Shack, 1966; Tsegaye & Struik, 2002). The localized availability of planting material (corms or suckers) may also be a limiting factor in landrace diversity, as farmers propagate most new plants themselves, followed by exchange with neighbors, within informal farmer networks and at local markets (Egizabiher et al., 2020; Olango et al., 2014). Additionally, farmers in our survey revealed that there were biotic constraints in all three study zones, notably the deadly enset wilt disease (*Xanthomonas campestris* pv. *musacearum*), which is present in nearly all enset growing regions (Zerfu et al., 2018).

## 5 | CONCLUSION

During enset's domestication, Ethiopian smallholder farmers progressively selected enset landraces with beneficial traits. We demonstrated for the first time that the expansion of wild enset into drier

areas led to trait differentiation from their areas of origin. Following this selection process, climate adaptations such as reduced stomatal density have become more prominent in cultivated enset. Farmers in drier areas opted for landraces with greater drought tolerance, which further reduced trait and landrace diversity. Leaf wax coverage, leaf number, plant height growth rate, leaf temperature, and stomatal conductance are correlated with farm aridity and show plasticity in certain landraces; they therefore likely contribute to enset's drought tolerance. However, climate does not account for all observed trait variation. Based on other studies, farm size, wealth, and cultural preferences also influence which landraces farmers grow. Our study identified traits linked to enset's drought tolerance and highlights the impact of domestication and environmental filtering on trait diversity in an indigenous staple crop. Understanding these interactions is crucial for ensuring the sustainability of enset production, a key pillar of the region's food security. In addition, this study also has wider implications for other cropping systems facing climate change, as reduced genetic diversity in drier environments may result in less adaptive capacity.

#### AUTHOR CONTRIBUTIONS

Rachel R. Chase, Lucie Büchi, and James S. Borrell conceived and designed the study, with contributions from Jonne Rodenburg, Nicolas Roux, and Abebe Wendawek. Rachel R. Chase collected the data with the help of Abebe Wendawek. Rachel R. Chase curated the data and performed the analyses with the help of James S. Borrell and Lucie Büchi. Rachel R. Chase wrote the original draft of the manuscript, and all authors reviewed and edited the original draft and approved the final manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

#### DATA AVAILABILITY STATEMENT

The datasets generated during the study are available at <https://doi.org/10.5281/zenodo.12189492>. Climate data used in the analyses are available from CHELSA at <https://chelsa-climate.org>. Further data that support the findings of this study are available in the Supporting Information of this article.

#### ETHICS STATEMENT

The appropriate ethical approval has been received for this study, following the University of Greenwich Research Ethics Policy and with the approval of the Ethics Committee of the Faculty of Engineering and Science, University of Greenwich, application FES-FREC-

19-04.04.04. Prior informed consent was obtained from all individual participants included in the study. The authors affirm that research participants provided prior informed consent for publication.

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## SUPPORTING INFORMATION

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