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RESEARCH ARTICLE

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Indigenous crop diversity maintained despite the introduction of major global crops in an African centre of agrobiodiversity

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Societal Impact Statement

The global success and expansion of a small pool of major crops, including rice, wheat and maize, risks homogenising global agriculture. Focusing on the agriculturally diverse Ethiopian Highlands, this study tested whether farm diversity tends to be lower among farmers who grow more introduced crops. Surprisingly, it was found that farmers have successfully integrated introduced crops, resulting in more diverse and heterogenous farms without negatively impacting indigenous crop diversity. This is encouraging because diverse farms, comprising indigenous agricultural systems supplemented by introduced crops, may help address global challenges such as food insecurity.

Summary

- The global expansion of a handful of major crops risks eroding indigenous crop diversity and homogenising agroecosystems, with significant consequences for sustainable and resilient food systems. Here, we investigate the farm-scale impact of introduced crops on indigenous agroecosystems.
- We surveyed 1369 subsistence farms stratified across climate gradients in the Ethiopian Highlands, a hotspot of agrobiodiversity, to characterise the richness and cultivated area of the 83 edible crops they contained. We further categorise these crops as being indigenous to Ethiopia, or introduced across three different eras. We apply non-metric multidimensional scaling and mixed effects modelling to characterise agroecosystem composition across farms with different proportions of introduced crops.
- Crops from different periods do not differ significantly in frequency or abundance across farms. Among geographically matched pairs of farms, those with higher proportions of modern introduced crops had significantly higher overall crop richness. Furthermore, farms with a high proportion of modern introduced crops showed

higher heterogeneity in crop composition. An analysis of socio-economic drivers indicated that poverty is negatively associated with the cultivated area of introduced crops.

- In our Ethiopian case study, global patterns of major crop expansion are not necessarily associated with agrobiodiversity loss at the farm scale or higher homogeneity across indigenous agricultural systems. Importantly, socioeconomic factors may influence farmers' propensity to adopt novel species, suggesting targets for agricultural extension policies. Given the rapid climatic, economic and demographic changes impacting global food systems and the threats to food security these entail, robust indigenous agricultural systems enriched with diverse introduced crops may help maintain resilience.

KEYWORDS
agricultural systems, crop diversity, crop domestication, Ethiopia, food security, indigenous crops, orphan crops, sustainable agriculture

1 | INTRODUCTION

Crop diversity plays a central role in delivering stable and resilient food production (Renard & Tilman, 2019). Among the multiple benefits are evidence of nutritional security (Nicholson et al., 2021), harvest asynchrony (Egli et al., 2020) and regulating ecosystem services (Kremen & Miles, 2012; Tamburini et al., 2020). While crop diversity has been shown to have increased at the national scale during the Anthropocene, particularly via the Colombian exchange and green revolution (Khoury et al., 2016; Martin et al., 2019), the success of a small number of crops (e.g., rice, wheat and maize) has also catalysed the homogenisation of global agroecosystems (Khoury et al., 2014). This has led to concerns that the global expansion of these major crops could lead to similar patterns of homogenisation at local scales (Borrell et al., 2020; Khoury et al., 2022; Shelef et al., 2017). Displacement or disruption to indigenous agroecosystems may also be associated with the loss of agrobiodiversity and associated long-term local climate adaptation, indigenous knowledge and autochthonous resilience strategies (Chase et al., 2022; Raeboline et al., 2019; Seburanga, 2013).

Previous studies that examine agricultural homogenisation make extensive use of national crop production data from the United Nations Food and Agricultural Organisation (FAOSTAT, 2021) to infer national crop diversity trends (Khoury et al., 2014; Mariani et al., 2021; Martin et al., 2019). Through longitudinal analyses, these identify a signal of increasing international homogeneity over recent decades. However, to enable comparisons and consistency, crop data are often restricted to globally or at least regionally important species and thus may overlook locally representative crops with a significant contribution to local agrobiodiversity and food security (Ulian et al., 2020). Furthermore, it is unclear how increasing international homogeneity has impacted contemporary crop diversity at the farm scale. Understanding how crop introductions have altered the composition of indigenous agroecosystems may inform strategies for enhanced food system stability and agrobiodiversity conservation, particularly under the pressures of poverty, population growth and climate change (Borrell et al., 2020; Labeyrie et al., 2021).

Here, we investigate the impact of crop introductions spanning several millennia on the Ethiopian Highlands, a major sub-Saharan African centre of crop diversity (Harlan, 1969), where over 80% of the population is engaged in subsistence agriculture on smallholder farms averaging 0.95 ha (Central Statistics Agency, 2015). With a long history of crop domestication, Ethiopia represents a critical reservoir of agrobiodiversity and indigenous knowledge encompassing a range of major and minor crops. Additionally, Ethiopia has received numerous novel crops over several thousand years, the timing of which may influence their agricultural importance (Milla & Osborne, 2021). The presence of locally domesticated and introduced crops, together with the fact that Ethiopia was not successfully colonised and therefore lacked strong external market drivers to adopt specific agricultural commodities, make it an interesting case study for investigating farmer-driven patterns of crop diversity and homogenisation.

We initially hypothesise that a long history of in situ local adaptation would favour the retention of indigenous crop species and crop combinations over less-suited introduced crops. On the other hand, an alternative hypothesis is that globally ubiquitous crops such as rice and maize have received high investment for crop improvement (Ray et al., 2012) and thus could be favoured over traditional species due to perceived or realised improvements in production (Borrell et al., 2020). In this latter scenario, we might expect that introduced crops would be associated with lower diversity farms, having displaced local crops. As a result, farm-scale agroecosystem variation may display higher homogeneity where exposure to introduced crops is greatest. We note that without longitudinal data, we cannot establish trends or rates of change and thus aim to characterise how crop diversity varies with the composition of introduced or indigenous crops.

We use a novel dataset of comprehensive farm surveys across Southwestern Ethiopia, combined with information on the period of introduction (or indigenous status) for 83 crops, to ask three questions. First, to what extent have novel crops from successive periods of introduction become integrated within Ethiopian agricultural systems? Second, what socio-economic drivers influence the proportion of introduced crops cultivated on farms? Third, are higher proportions of introduced crops associated with lower diversity or greater homogeneity of on-farm crop composition? Finally, we consider how these contemporary local-scale findings complement previously reported trends in global agricultural homogenisation, and could inform future agrobiodiversity conservation and management.

2 | METHODS

2.1 | Stratified farm surveys

We sampled 1369 farms across eight transects in southwestern Ethiopia between February and July 2019. Transects were oriented perpendicular to elevational gradients, systematically encompassing substantial variation in temperature, precipitation and soils (see Methods S1). Transects were 20–50 km in length, and sampling ranged from 1200–3240 m asl (Figure S1), thus covering the zones into which the Ethiopian highland agroecosystems have traditionally been partitioned: Kola (<1500 m asl), Weyna Dega (1500–2300 m asl) and Dega (>2300 m asl) (Hurni, 1998). There is little agriculture below approximately 1200 m. On each farm, we recorded the presence and cultivated area of all actively managed plant species. For some perennial crops that tend to be grown in low numbers outside of farmer fields (see, for example, Mellisse et al., 2018), the number of individuals was recorded and converted using a constant area per individual, derived from an initial measurement of >10 individuals per crop (e.g., 0.002 ha for avocado trees). While 124 crop species were recorded in total, for subsequent analyses, we retained only those that yield human edible products ($n = 83$, Table S1); the excluded species were predominantly used for timber and fodder. Each farm's total harvest area was estimated by summing the area of all cultivated crops. We also recorded the total farm area by integrating the areas of wood lots (mostly eucalyptus), pasture and other non-cultivated land. Farm diversity data is available in Dataset S1 and a summary of crop areas in Figure S2.

2.2 | Characterisation of crop introduction categories

To investigate interactions between indigenous and introduced crops, we sought to determine the period of introduction of the 83 crops in our dataset (Table 1). We note that our analysis focuses on crop species and does not account for landrace or varietal diversity (see Section 4). We surveyed the literature and assigned crops to one of four categories: (i) Indigenous, comprising crops for which there is evidence of domestication or the occurrence of wild progenitors in Ethiopia ($n = 25$). (ii) Pre-modern crops, likely introduced before c. 1500 AD, often with evidence of a secondary centre of diversity within Ethiopia ($n = 25$). (iii) Early modern, those introduced during a period of increased international introductions from 1500–1900 arising in part from the Colombian Exchange (Williams, 2017) ($n = 18$). (iv) Late modern, those introduced in the last century, predominantly associated with global trade and the green revolution ($n = 15$). All analyses were performed using R v3.6.3 (R Core Team, 2019).

2.3 | Agricultural system composition and integration of modern crops

To test the hypothesis that indigenous or introduced groups of crops may be more or less abundant, we used analysis of variance (ANOVA) to test for differences in the frequency and cultivated area across farms ($n = 1369$). To understand whether on-farm crop assemblages are partitioned into distinct agroecosystems in Ethiopia (i.e., Kola, Weyna Dega or Dega), we applied non-metric multidimensional scaling (NMDS) based on a scaled Bray–Curtis dissimilarity matrix. NMDS was implemented in the R package vegan (Oksanen et al., 2019) over two to six axes with up to 500 random starts and 2000 iterations. We treated farms as observation units and the fraction of the farm area covered with each crop as descriptors. We used multiple regression in the function *envfit* to determine the extent to which crop species covaried with the NMDS axes and performed ANOVA to understand whether certain categories of crop introductions were disproportionately important in describing variation in farm composition. We plot NMDS values with the corresponding Ethiopian agroecological zones by calculating 95% ellipses around farms in each elevational band.

TABLE 1 Time periods for crop introduction to the Ethiopian Highlands.

Introduction category		Time period of introduction	Number of species
Modern			
	Late modern	1900 AD to present	15
	Early modern	1500–1900 AD	18
Historic			
	Pre-modern	Prior to 1500 AD.	25
	Indigenous	Domestication in Ethiopia	25

To further evaluate the relative importance of both early- and late-modern introduced crops to agroecosystem composition, we investigated patterns of crop co-occurrence using network visualisation in the iGraph package (Csardi & Nepusz, 2006). We weighted node size by frequency of crop occurrence across farms and plotted undirected edges proportional to the number of farms in which the species co-occur. We then used ANOVA to compare eigenvector centrality by crop introduction category (i.e., indigenous, pre-modern, early modern or late modern), which measures the influence of a node in a network. Higher scores denote nodes that are themselves connected to many other high-scoring nodes, an indication of crop importance within the regional agricultural system.

2.4 | Socioeconomic drivers of introduced crop cultivation

For subsequent analyses, we grouped indigenous with pre-modern and early modern with late modern crop introduction categories to form 'historic' and 'modern' categories, respectively. We used mixed effects models implemented in the R package *nlme* (Pinheiro et al., 2023) to investigate the socioeconomic drivers influencing the proportion of modern crops cultivated on farms and the package *effectsize* to estimate Eta^2 effect sizes (Ben-Shachar et al., 2020). We used both species richness and cultivated area as response variables. Fixed effects comprised total harvested area (ha) and number of livestock, both serving as proxies for farmer affluence (Shumetie & Mamo, 2019). We also applied a proxy for regional accessibility, comprising travel time to the nearest town (extracted at 1 km resolution from Ethiogis 3; www.ethiogis-mapserver.org) and a poverty index. The latter index is a composite of six regional health, wellbeing and development indicators, including access to safe drinking water, months of food insecurity, child vaccination, child stunting and male and female literacy rates, all derived from the Ethiopia 2016 Demographic and Health Survey (USAID, 2021) (see Methods S1). The eight transects that we performed for recording farm data were treated as random effects, and a Gaussian covariance structure was applied to farm coordinates to account for spatial autocorrelation. Model spatial autocorrelation structures were evaluated using AIC and model fit via examination of residual plots following Zuur et al. (2009). Finally, we fitted two further models to understand the association between farm size and crop richness for historic and modern crops and then tested for a significant difference in regression coefficients.

2.5 | Testing the association between introduced crops and agroecosystem diversity and homogeneity

We applied three approaches to test the association between introduced crops and contemporary patterns of crop diversity and homogeneity in indigenous agroecosystems. First, we used a linear mixed effects model to evaluate the relationship between counts of historic versus modern introduced crops within farms while accounting for spatial autocorrelation using a Gaussian correlation structure with transect as a random effect. Second, we evaluated the correlation between the proportion of farm area allocated to modern crops and overall farm crop richness and evenness using Simpson's diversity index (Hurlbert, 1971). To do this, we applied similarly structured linear mixed effects models, including a quadratic fixed variable to accommodate a non-linear relationship in the response. We additionally report this relationship using Shannon entropy as an alternative evenness index in Methods S1.

Third, to assess the association between the frequency of modern introduced crops and overall crop richness, we collated our dataset of 1369 farms into clusters of 10 farms based on geographic proximity. As farms were sampled sequentially along an elevational gradient within each transect, elevational and geographic proximity corresponded with similar climatic and edaphic conditions, as well as regional agricultural practices. This approach aims to control for the effects of these variables. From each cluster, we then selected the farm with the highest and lowest proportion of modern crops (considering early and late introductions jointly), which generated 137 pairs of farms. We applied our previous NMDS model to visualise changes in agroecosystem homogeneity between these two groups. In other words, this approach tests for a difference between the two extremes of a distribution of farmer adoption of modern crops and should maximise the chance of detecting changes in crop diversity, should they exist. Following an approach similar to Khoury et al. (2014) (but note that we do not present longitudinal data), we fitted ellipses to each set of farms and compared the volume of multivariate space encompassed by each group, enabling characterisation of beta and gamma diversity. We tested for differences in the composition and dispersion of these groups using the analysis of similarities (Oksanen et al., 2019), which compares multivariate rank order of dissimilarity values. Finally, to capture alpha diversity, we also performed a t-test comparing historic crop richness between the two groups.

3 | RESULTS

3.1 | Agricultural system composition and integration of new crops

Ethiopia has been characterised by the arrival of novel crop species over several millennia (Figure 1). Despite this, of the 83 crops recorded in our study area, the largest proportion were of indigenous ($n = 25$, 30.1%) or pre-modern ($n = 25$, 30.1%) origin, consistent with Ethiopia's role as both a major centre of crop domestication and an ancient secondary centre for crops such as wheat (Table S1). We found no significant difference in the frequency of on-farm occurrence ($F_{3,79} = 0.54$, $p = .65$) or cultivated area ($F_{3,79} = 0.77$, $p = .51$) among the four categories of crop origin (Figure 1a,b). Fruit crops, followed by roots and vegetables, represent

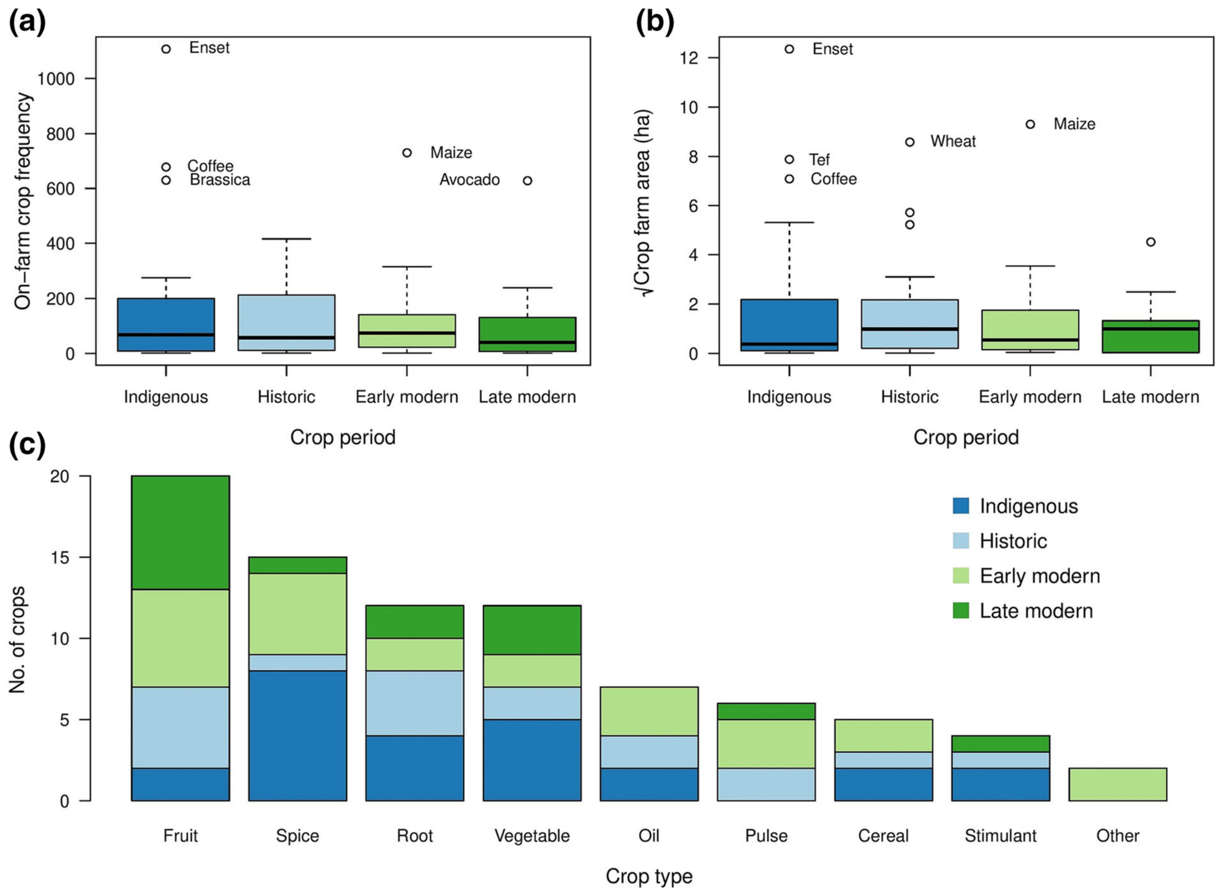

FIGURE 1 Crop frequency, area and period of introduction across 1369 surveyed farms in the Ethiopian highlands. (a) Boxplot of observation frequency for indigenous and introduced crops, grouped by period of introduction. (b) Boxplot of total cultivated farm area for crops by period of introduction. (c) Stacked bar chart of crop types occurring in the study area; category 'other' comprises olive (*Olea europaea*) and sugarcane (*Saccharum officinarum*).

the most frequently (successfully) introduced crop types of the modern era (Figure 1c).

Farms contain up to 29 edible species (mean = 8.08, SD = 3.49), and harvest area varies from 0.004–3.07 ha (mean = 0.48 ha, SD = 0.41 ha). We found no evidence of distinct crop assemblages (i.e., clusters of points) in a fitted four-dimensional NMDS (stress = 0.12; Figure 2). Similarly, crop assemblages in the Ethiopian Dega (<2300 m asl) and Weyna Dega (1500–2300 m asl) zones strongly overlapped, suggesting little differentiation. Crops that covaried most strongly in a multiple regression with the four NMDS axes (i.e., contribute to variation in between-farm crop composition) encompass both historic and modern introduced species, including wheat ($R^2 = 0.44$), maize ($R^2 = 0.37$), tef ($R^2 = 0.35$) and enset ($R^2 = 0.25$). Overall, we found no significant difference in correlation across species with different periods of introduction ($F_{3,79} = 0.9$, $p = .45$), which suggests that no category of crops disproportionately contributed to variation or structure in farm composition across the study area. Similarly, network analysis identified no evidence of clustering in on-farm crop assemblages, which would indicate frequent associations between particular crop species (Figure 3). The most commonly recorded and interconnected crops included indigenous (enset, coffee) and modern (avocado, maize) representatives. We found no significant difference in eigenvector centrality across historic and modern crops from different periods ($F_{3,79} = 0.45$, $p = .72$), suggesting that variation in the connectedness of nodes (i.e., crops) is not associated with the length of time since introduction.

3.2 | Factors influencing the proportion of modern introduced crops

Mixed effects models identified no significant variables that influenced the proportion of crop diversity comprised of modern crops found on farms (Table 2). However, the proportion of cultivated area allocated to modern crop introductions was strongly negatively associated with poverty ($p < .01$, $Eta^2 = 0.03$, 95% CI 0.01–0.05). In addition, increasing travel time and total cultivated area were also associated with a lower proportion of modern introduced crop cultivated area, whereas head of livestock (a proxy for farmer wealth) was associated with a greater proportion of modern introduced crop area, though effect sizes for these variables overlapped with zero.

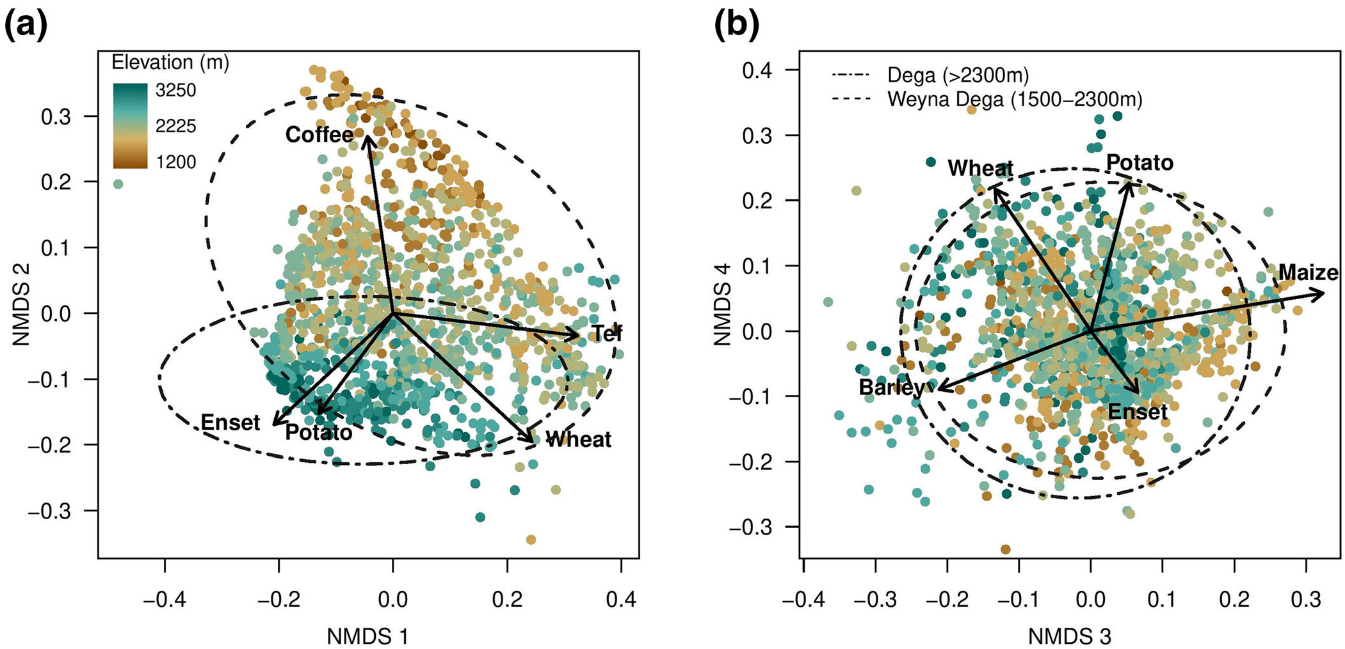

FIGURE 2 Non-metric multi-dimensional scaling analysis (NMDS) of farm crop composition in the Ethiopian highlands. Each point is one of 1369 farms, with plots showing (a) the first and second axes and (b) the third and fourth axes. Ellipses encompass the environmental space occupied by farms in two predominant Ethiopian agroecological zones, Weyna Dega (1500–2300 m asl) and Dega (>2300 m asl), at 95% confidence. Arrows indicate the direction and magnitude of correlation for key species on the ordination.

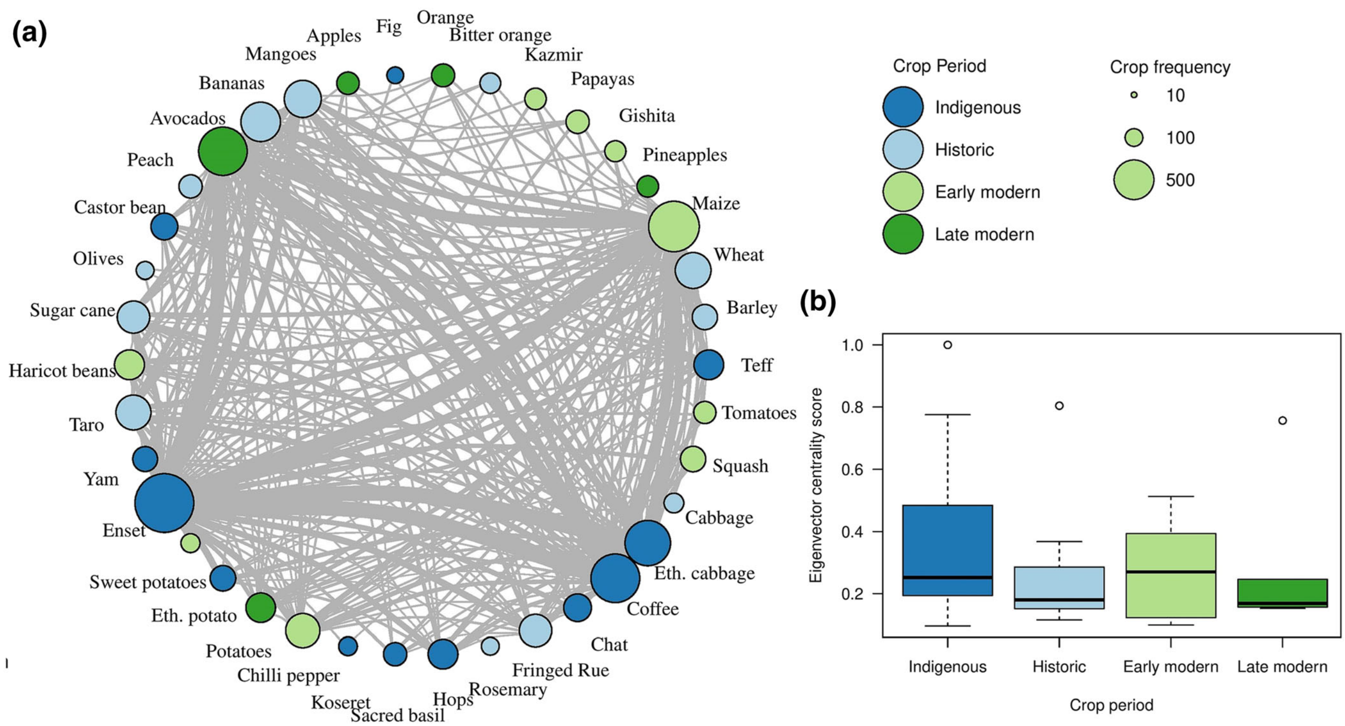

FIGURE 3 Agroecosystem network composition and eigenvector centrality analysis for Ethiopian Highland farms. (a) Network analysis, where node size denotes the number of farms with crop presence and edge width between nodes corresponds to the frequency of co-occurrence. Crops occurring on less than 5% of farms are omitted for plotting purposes. (b) Boxplot of eigenvector centrality across indigenous and introduced crops (grouped by crop period of introduction).

TABLE 2 Influence of socio-economic variables on the proportion of modern introduced crop richness (count) and area cultivated (ha) in Ethiopian Highland farms, estimated via mixed effects modelling. Bold text indicates variables for which effect size confidence intervals do not overlap with zero.

	Proportion of modern introduced crops			
	Richness (count)		Area (ha)	
Variable	t-value	*p*-value	t-value	*p*-value
Total cultivated area	−0.97	.33	−2.75	.01
Travel time to main town	−1.84	.07	−3.27	<.01
Total livestock	−0.13	.9	3.03	<.01
Poverty composite variable	−1.36	.17	**−6.24**	**<.01**

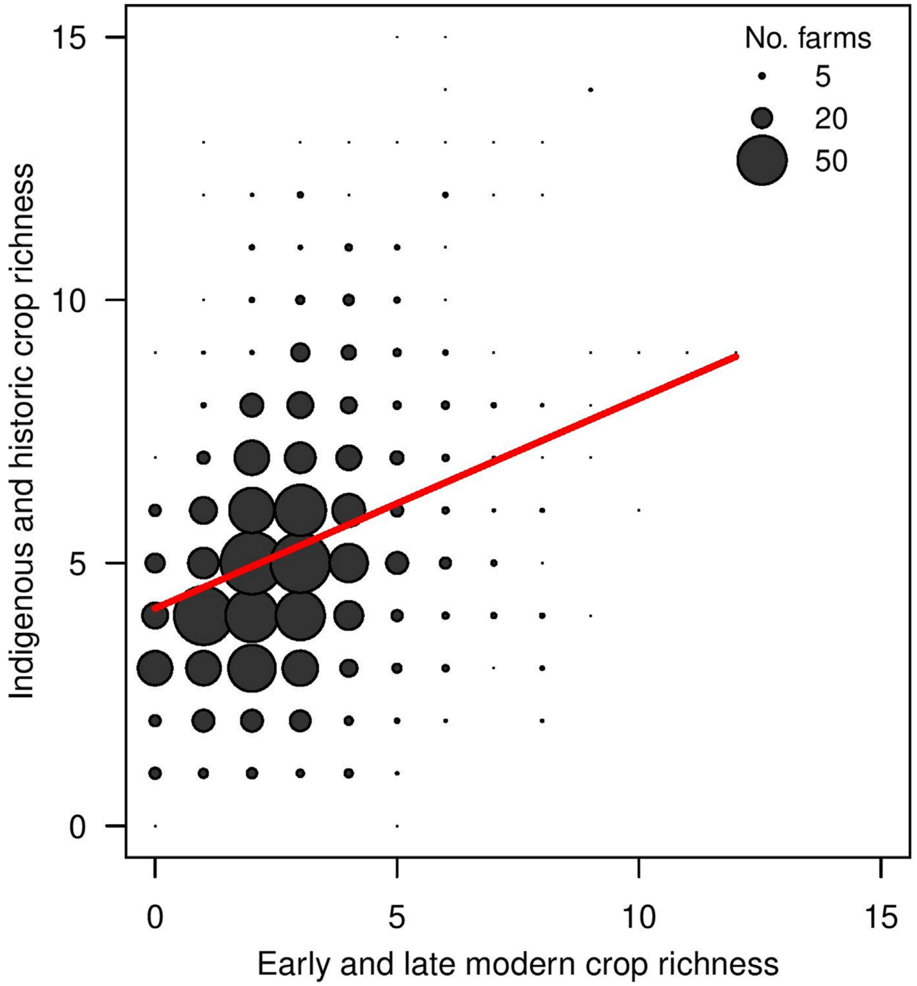

FIGURE 4 Relationship between early and late modern crop richness versus indigenous and historic crop richness across 1369 farms in the Ethiopian Highlands. The red line indicates the fit of a linear mixed effect model, and points are scaled by the number of farms.

3.3 | Modern crop introductions are associated with greater heterogeneity in indigenous agroecosystems

Across farms, we find a significant positive relationship between historic and modern crop richness ($t_{1360} = 12.77$, $p < .001$) (Figure 4). Consistent with this, we find significant concave relationships between the proportion of modern introduced crops and both overall crop richness (X, $t_{1358} = 6.88$, $p < .001$; X^2, $t_{1358} = -12.06$, $p < .001$) and Simpson's evenness index (X, $t_{1358} = 10.54$, $p < .001$; X^2, $t_{1358} = -21.68$, $p < .001$) (Figures 5 and S3). We note that a similar relationship is also observed for the proportion of historic crops. Analysis of farm size shows no significant difference in the rate at which historic and modern crop richness increase with farm size ($t = -0.64$, $p = .52$) (Figure 6).

Across our dataset as a whole, we used geographic proximity to match and compare a subset of farms containing a high proportion of modern introduced crops (mean proportion modern = 0.48) with a

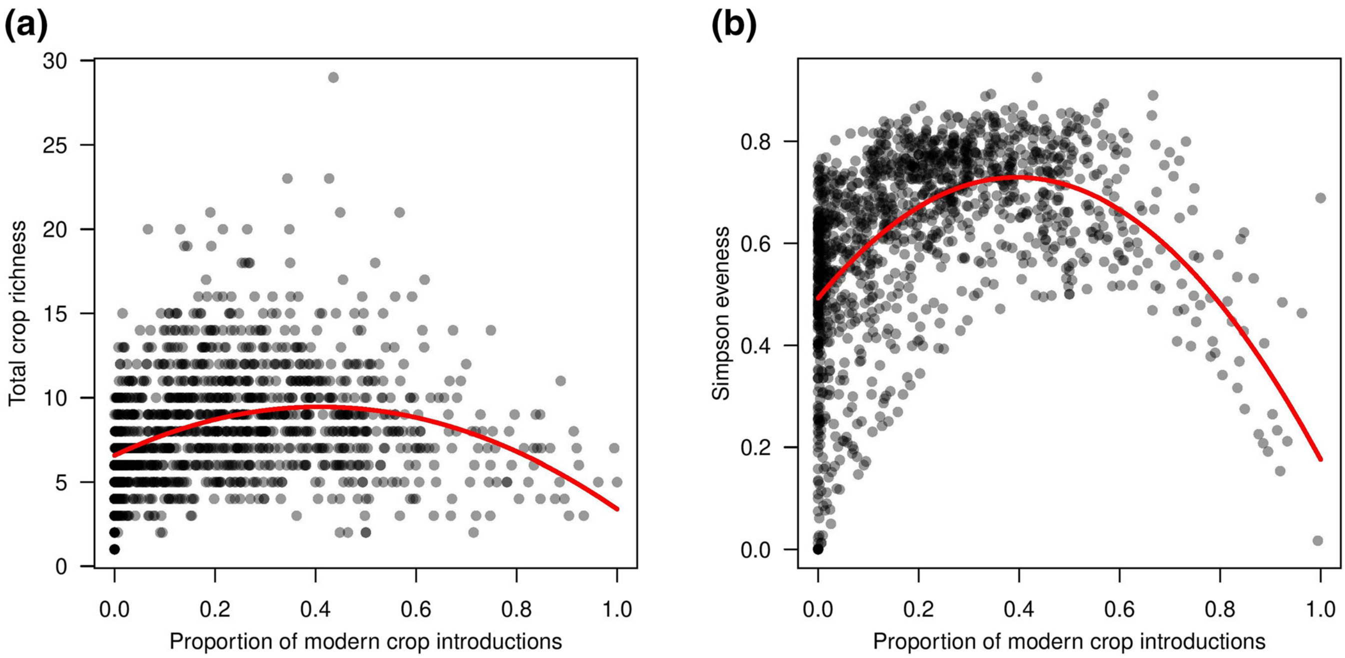

FIGURE 5 Association between the proportion of farm area under modern crops and overall crop richness and evenness across Ethiopian Highland farms. Plots show associations for (a) overall crop richness on farms and (b) Simpson's evenness index. Trend lines, shown in red, were fitted using linear mixed effects models.

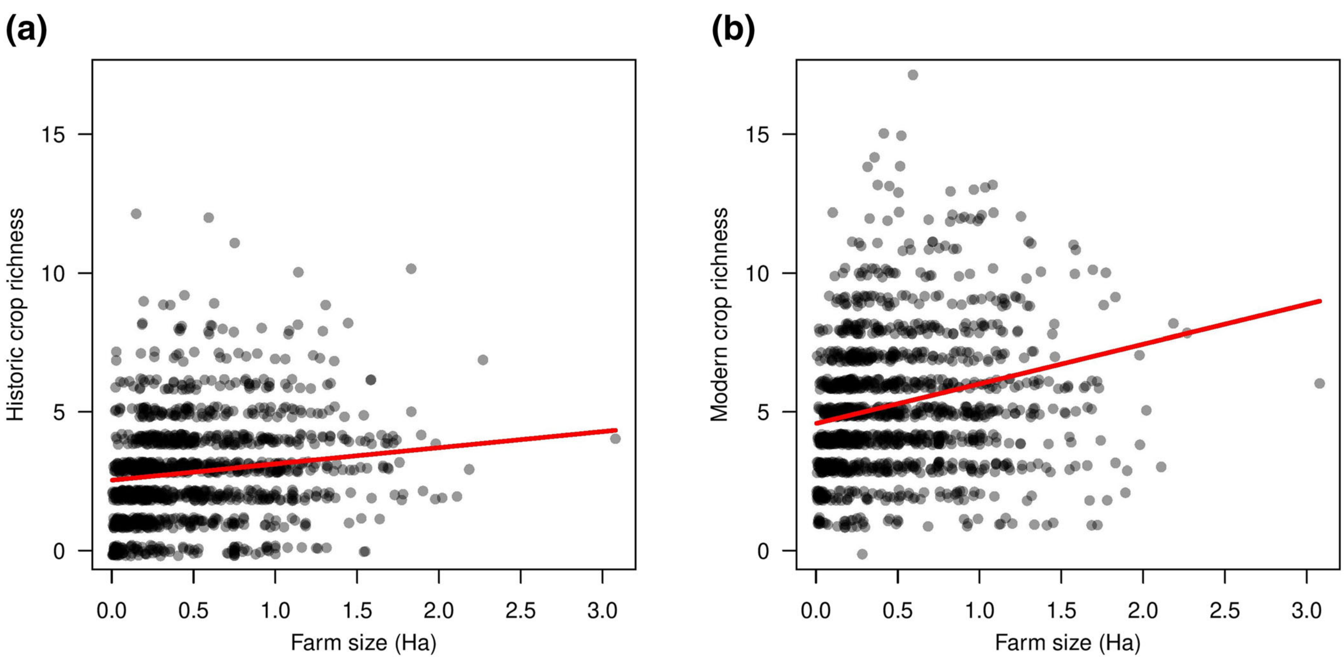

FIGURE 6 Association between farm size and (a) historic and (b) modern crop richness across Ethiopian Highland farms. The red line indicates model fit.

subset of farms containing a low proportion of modern crops (mean proportion modern = 0.04) (Figure 7). Despite maximising the possible difference in the proportion of modern crops across these two subsets, this only significantly explained a very small amount of variation (ANOSIM R = 0.08, $p = .001$). Further examination suggests that this difference may be driven by higher variance in overall crop composition, with the 'high proportion' group occupying a 12% larger volume in multivariate space, indicating greater diversity in crop species and relative crop area composition across the agricultural system. This suggests that farms with more modern introduced crops have greater

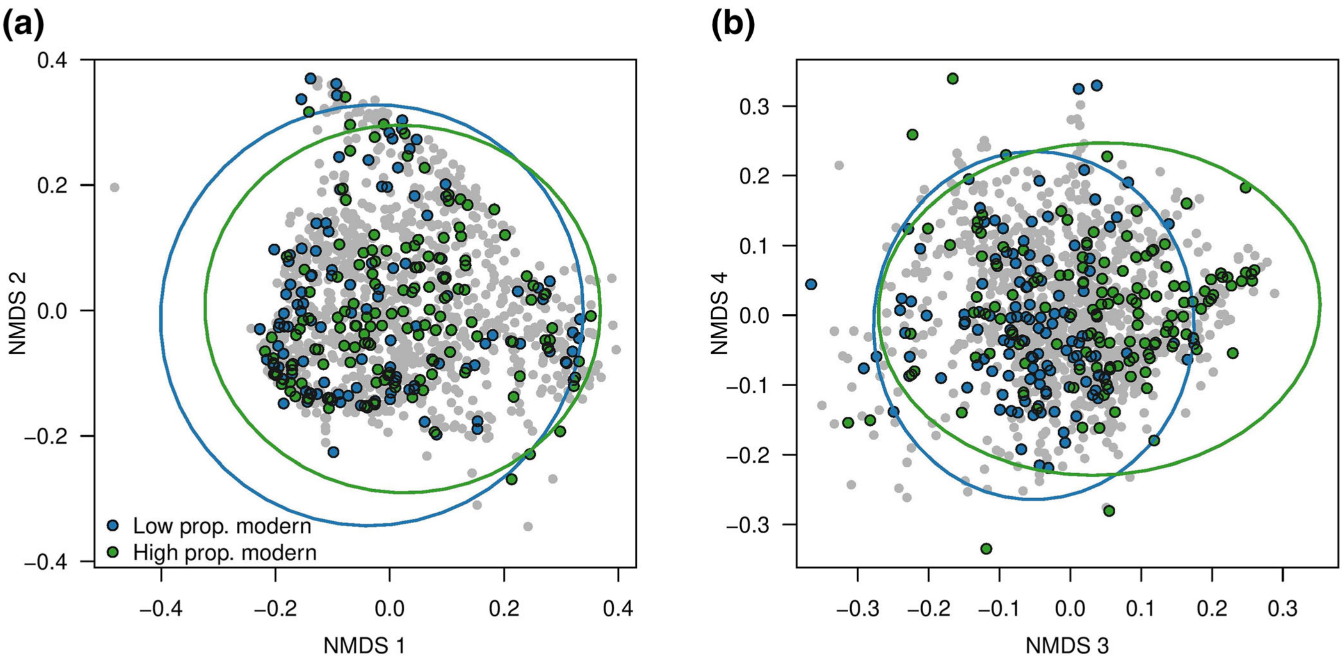

FIGURE 7 Impact of crop introductions on agroecosystem diversity in the Ethiopian Highlands. Non-metric multidimensional scaling (NMDS) of all farms with coloured points indicating two groups of climatically matched farms ($n = 137$ each) comprising low and high proportions of modern crop introductions. Ellipses capture 95% of the multivariate space for each group.

heterogeneity. Comparison of historic crop richness between these two farm subsets identified no significant difference ($t_{266} = -1.86$, $p = .063$), suggesting that higher numbers of introduced crops do not significantly impact the number of historic crops, while overall crop richness was significantly higher in the subset of farms with a high proportion of modern crop introductions ($t_{270} = 3.60$, $p < .001$).

4 | DISCUSSION

The global loss of indigenous crop diversity as a result of modern introduced crop expansion is a major food security concern and could undermine the sustainability of food systems (Antonelli, 2023; Renard & Tilman, 2019). Here, we provide evidence that greater proportions of modern introduced crops are not associated with reduced crop species richness or homogeneity in agroecosystems in Ethiopia. These findings are supported by several lines of evidence. Foremost, we observe a positive relationship between modern and historic crop richness on farms (Figure 4), and as the proportion of farm area allocated to modern crops increases, both richness and evenness also increase, except at very high values that are rare in our dataset (Figure 5). We suggest that the observation of highest diversity at intermediate values (i.e., a hump-shaped relationship) is notable and may have parallels with the intermediate disturbance hypothesis derived from community ecology (Catford et al., 2012). Second, using a matched pairs approach, whereby farms have similar geography and climate but a 10-fold difference in the proportion of modern introduced crops, we report a 12% expansion of multivariate space that characterises agricultural system diversity in farms with more modern introduced crops (Figure 7). Taken together, these provide evidence that crop introductions are contributing additional agrobiodiversity to Ethiopian agroecosystems without having a deleterious effect on indigenous and historic species richness.

A second key finding is that modern introduced crops appear to be rapidly integrated into indigenous agricultural systems. For example, NMDS across surveyed farms found little evidence of clustering of crop compositions (Figure 2), contrary to previous reports that southwestern Ethiopian agroecosystems are differentiated (Abebe et al., 2010). Within this system, we found that historic and modern crops form a highly integrated network (Figure 3a). For example, both enset (an indigenous starch staple cultivated only in south-western Ethiopia) and avocado (a late modern introduced fruit) occur frequently with a wide variety of other crops. We found no significant difference in connectedness between groups of historic or modern crops, regardless of the timing of introduction (Figure 3b). This is surprising because we might expect more recent introductions to be less well integrated (Ali & Erenstein, 2017; Uduji & Okolo-Obasi, 2018), suggesting that subsistence farmers may integrate new crops in a relatively short period.

In assessing the drivers of the proportion of modern introduced crops found on surveyed farms, we find little evidence that socio-economic variables influence modern crop richness but stronger evidence that they influence cultivated area. For example, we identified a strong negative association between the area under modern crop cultivation and poverty. We also detected negative associations with total cultivated area and accessibility (Table 2), though effect size estimates are small. Conversely, the head of livestock—a proxy for wealth—was positively associated with a larger proportion of modern introduced crops on surveyed farms. This suggests that access to modern introduced crops may be associated with (or potentially drive) economic development and, importantly, could be targeted by appropriately designed rural development policies (Welteji, 2018). While it is difficult to interpret cause and effect from these data, it is notable that there was no significant association between poverty and crop richness; rather, the association is with the proportion of cultivated area. Therefore, modern crop cultivation may be more extensive among farmers with sufficient wealth and space to meet their subsistence needs. Similarly, modern crops may require more inputs, limiting their abundance in more remote and less affluent areas.

While the expansion of major crops has resulted in relatively high species richness nationally, this has been associated with increasing similarity of species composition internationally (Khoury et al., 2014; Martin et al., 2019). Our farm-scale findings for Ethiopia complement and contrast these analyses to provide a clearer assessment of ongoing shifts in farm-scale agroecosystem composition. We find that farms cultivating more modern introduced crops have a higher number of crop species overall (Figure 4), higher evenness across species (Figure 5) and result in agricultural systems with more variation in crop composition (Figure 7). This provides an interesting comparison with Aramburu Merlos and Hijmans (2020), who found that major crops (often modern introductions) tend to be associated with less diverse farms in the USA. We suggest that the understandable omission of numerous relatively underutilised or locally important species, particularly from smallholder subsistence farms, underestimates farm-scale agrobiodiversity in global agrobiodiversity datasets such as FAOSTAT (2021). For example, 36% of species in this study are not included in the global analysis of Martin et al. (2019), including major regional staples such as enset (*Ensete ventricosum*) (Borrell et al., 2019). Similarly, while we lack time-series data at the local scale and do not assume that national agricultural systems have reached equilibrium, we also do not see trends in crop importance associated with the period of introduction. In other words, the length of time a species has been in Ethiopia does not appear to be associated with its relative importance (Figures 1 and 3). These findings support a growing body of work showing that modern agricultural transformations have not invariably led to large-scale agrobiodiversity loss (Khoury et al., 2022; Renard et al., 2016).

We note several caveats and limitations in our study. Foremost is the widely reported evidence of the loss of traditional landraces in favour of improved and often introduced genotypes (Thormann & Engels, 2015) and the associated loss of numerous generations of locally adaptive evolution (Kassahun et al., 2021). Our analysis does not capture changes at the intraspecific level, and thus we have not quantified landrace replacement, though it is likely occurring. Second, we note that dating and characterising the period of introduction for many crops is challenging, particularly where region-specific archaeobotanical or historical evidence is lacking. Nevertheless, we have attempted to draw justifiable inferences based on records of crop expansion, genetic studies and known cultural contact (e.g., the Colombian Exchange), and our results are robust to modest adjustments in the categorisation of crop introduction periods (see Table S1). Our study captures a contemporary time period, so while we detect no loss of historic crop diversity, we cannot rule out the possibility of a protracted decline in the future towards equilibrium (conceptually similar to 'extinction debt', see Kuussaari et al., 2009) or an unrecognised decline in the past. Finally, we note that as a globally important centre of crop diversity and domestication with a regionally unique climate, Ethiopia may not be widely representative of trends in other countries or regions. Indeed, the stability of indigenous agroecosystems in our study may be partly due to the comparatively minimal extent of colonial era agri-polices, partly shielding Ethiopia from the effects of mid-20th century green-revolution influenced interventions (Till, 2021) and subsequent commercial crop specialisation (Merlos & Hijmans, 2022).

In the future, emerging climate and demographic pressures may require the relatively rapid shift and rearrangement of current crop distributions (Koch et al., 2022; Sloat et al., 2020), as well as the adoption of new and better-adapted species and agroecosystems (Borrell et al., 2020; Pironon et al., 2019). In Ethiopia, the long-term maintenance of crop diversity over multiple periods of origin, combined with the rapid integration of novel species, suggests that these agroecosystems may be relatively adaptable and resilient. Future research should aim to further bridge the gap between local, national and international agrobiodiversity trends.

AUTHOR CONTRIBUTIONS

Chris Rampersad and James S. Borrell designed the study, with substantial input from all authors. Chris Rampersad, Tesfu Geto, Tarekegn Samuel, Meseret Abebe, Wendawek M. Abebe and Jonathan Stocks collected data. Chris Rampersad and James S. Borrell analysed the data with help from Marybel Soto Gomez, Samuel Pironon and Lucie Büchi. James S. Borrell, Jeremy Haggar, Richard J. A. Buggs, Sebsebe Demissew, Wendawek M. Abebe and Paul Wilkin secured funding. James S. Borrell and Wendawek M. Abebe provided supervision. Chris Rampersad and James S. Borrell wrote the manuscript. All authors contributed to the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Databases of crop origin and anonymised farm composition are provided in Table S1 and Dataset S1.

ETHICS STATEMENT

All participant farmers gave prior informed consent to participate in this study, with the principals and aims explained in the predominant local language or Amharic. The resolution of identifiable information, such as coordinates, has been aggregated.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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