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Genetic erosion in maize's center of origin

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Crop genetic diversity is an indispensable resource for farmers and professional breeders responding to changing climate, pests, and diseases. Anecdotal appraisals in centers of crop origin have suggested serious threats to this diversity for over half a century. However, a nationwide inventory recently found all maize races previously described for Mexico, including some formerly considered nearly extinct. A flurry of social studies seems to confirm that farmers maintain considerable diversity. Here, we compare estimates of maize diversity from case studies over the past 15 y with nationally and regionally representative matched longitudinal data from farmers across rural Mexico. Our findings reveal an increasing bias in inferences based on case study results and widespread loss of diversity. Cross-sectional, case study data suggest that farm-level richness has increased by 0.04 y⁻¹ nationwide; however, direct estimates using matched longitudinal data reveal that richness dropped -0.04 y⁻¹ between 2002 and 2007, from 1.43 to 1.22 varieties per farm. Varietal losses occurred across regions and altitudinal zones, and regardless of farm turnover within the sector. Extinction of local maize populations may not have resulted in an immediate loss of alleles, but low varietal richness and changes in maize's metapopulation dynamics may prevent farmers from accessing germplasm suitable to a rapidly changing climate. Declining yields could then lead farmers to leave the sector and result in a further loss of diversity. Similarities in research approaches across crops suggest that methodological biases could conceal a loss of diversity at other centers of crop origin.

in situ conservation | crop evolution | climate change | corn

A decade ago, crop scientists considered maize (*Zea mays* L.) diversity in danger across wide areas of Mexico, its center of origin and diversity: seven races at risk for extinction and many others under threat (1, 2). However, those appraisals, like others before them (3, 4), were anecdotal. In 2011, the Global Project on Native Maize—a 3-y effort involving 55 institutions and 138 researchers—reported encouraging findings from its first nationwide inventory: all 59 races previously described for Mexico were recorded, including those formerly considered nearly extinct (5). Scientists also found unexpectedly high diversity of races endemic to northern Mexico, several maize types in Michoacán that could represent new races, and new records for some locations (including Vandeño in Sonora and four Guatemalan races). Contrary to previous appraisals, only two races (Palomero Toluqueño and Chapalote) were listed under threat based on small population sizes. Leading experts remain cautious nevertheless (6).

Crop genetic erosion has been a constant concern since the late 1940s, when conservation efforts began in earnest, but it has never been demonstrated by longitudinal data across environments for any major crop in its center of diversity (3, 4, 7–10). Inconsistencies in the classification of infraspecific diversity have been a serious hurdle. Utilitarian rather than natural, taxonomies reflect large disciplinary biases: crop scientists favor racial groupings, whereas social scientists prefer folk taxonomies (1–6, 9–14). Phenotypic variation across races is indeed remarkable (1, 2, 5, 6, 15, 16), yet racial groups account for only 2–3% of genetic variation in maize (6). Moreover, races are not discrete entities (13–15). Farmers recognize, value, and maintain unique traits in innumerable racial variants and mixtures—known as farmer

varieties or landraces—exerting an influence on maize's genetic structure (12–14, 17). Seed exchange presumably explains why 91% of isoenzymatic variation in maize landraces occurs within populations, whereas individual teosinte (wild *Z. mays*) populations remain genetically distinct (6, 18). The low genetic diversity of some accessions also has been attributed to human factors—i.e., small field sizes (or few ears used for seed) for specialty varieties (1). In fact, most maize alleles are very rare (frequencies <0.01), and many are found in single accessions that presumably correspond with farmer fields (1). Rather than segregated into discrete races, maize diversity may be spread continuously across thousands of populations (i.e., fields) in rural Mexico (13, 14, 17, 18). Accounting for maize's metapopulation structure is difficult because of farmers' extensive control of crop population dynamics (11, 13). Although maize demography can be modeled on management practices, the data required remain critically scarce (11, 19). Numerous statistics have been reported, but only average varietal richness per farm is estimated consistently across studies. This is considered the key statistic for diversity conservation in crops (10).

We compare farm richness estimates based on cross-sectional case study data and longitudinal survey data from a representative sample of rural farms to assess the state of maize conservation in Mexico. Our findings reveal significant changes in maize diversity between 2002 and 2007 that are not evident in case study data. This represents the first (to our knowledge) formal assessment of genetic erosion in a center of crop diversity. A social perspective on maize diversity allows us to explore possible reasons for recent changes and their potential implications.

Significance

Unlike germplasm banks, on-farm conservation allows crops to evolve continuously in response to changing conditions. Agricultural adaptation to climate change, emerging pests, and diseases thus depends on conserving crop genetic diversity in situ. However, increasing awareness of these issues has not translated into effective conservation policies. We find that previous assessments of on-farm maize diversity in Mexico are flawed and conceal widespread genetic erosion that could thwart current food security strategies for climate adaptation. Unable to mitigate declining yields by recourse to diversity, farmers might abandon agriculture, leading to a vicious cycle of yield and diversity losses. A reassessment of the conservation status in other centers of crop diversity is similarly urgent but could take a decade given data requirements.

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of maize diversity. Important differences among these groups were found. Farmers abandoning maize grew significantly fewer varieties in 2002 than continuing farmers (1.21 vs. 1.49; $X^2 = 23.95$; $P < 0.001$). Although the latter group grew fewer varieties over time (1.49 vs. 1.27; $X^2 = 25.00$; $P < 0.001$), it still held greater richness in 2007 than those adopting maize that year (1.27 vs. 1.06, respectively; $X^2 = 32.31$; $P < 0.001$). New adopters also grew significantly fewer varieties than those abandoning maize after 2002 ($X^2 = 8.87$; $P < 0.01$).

Discussion

Various disciplinary and methodological approaches have nurtured an enduring debate on farmers' role in crop evolution (1, 5, 9–21). The social sciences have contributed much to our understanding of crop diversity, often contradicting alternative perspectives on issues as urgent as in situ conservation (2–16). A flurry of social studies conducted over the last 25 y seems to indicate—in opposition to agronomists' early forecasts—that farmers in centers of crop origin continue to grow considerable diversity (9, 10). Unsurprisingly, given wide disparities in methods, social studies do not present a unified perspective on this question, as exemplified by the literature on maize (8, 11, 20, 21). Similarly, some within the social sciences emphasize the human influence in the distribution of maize diversity, whereas others consider it secondary to the environment's dominant role (14–16, 19–21). Our analysis helps explain these contradictions as a result of the constrained perspective—both static and local—that cross-sectional case study data have imposed on this debate.

Adaptive radiation is perhaps the most obvious expression today of the evolution of maize, and the environment's role in it has been inferred generally from observations associating diversity with geographic location (19, 20). Studies have found that morphological, physiological, and molecular diversity in maize often correlates with altitude and/or latitude, and various scholars have construed causality in these associations (19, 20). On first impression, our results seem to support this hypothesis. ENHRUM data reveal a distinct geographic pattern in maize diversity: in both 2002 and 2007, average richness per farm generally was lower moving northward and toward lower elevations (Table 1). A pattern of such scope and scale has not been documented before, and a possible environmental role is conceivable, but there is no direct evidence to support this suggestion.

On the other hand, significant changes in diversity were observed between dates that are not easily explained by changes in the environment. Although the possible effect of climate change cannot be discounted (21–24), changes in varietal richness per farm must be explained first and foremost as a result of farmers' decisions. There is no reason to expect these decisions to reflect environmental variation along a geographic gradient. In fact, farm richness is probably not the result of a single decision. More likely, the number of varieties maintained on farm reflects multiple considerations, e.g., simultaneous but separate demands for food staples, culinary specialties, or production technologies. Various factors, including agronomic (e.g., yield, resistance to biotic and abiotic pressure), consumption (taste, texture, grain color), and market factors, help “explain” differences in crop diversity across farms (12, 19, 25). Farm households are said to demand diversity, and they maintain it by culling true-to-type seed assiduously, or alternatively, allowing pollen exchange across fields to create new, hybrid types (13). However, on-farm varietal richness ultimately results from the replacement and exchange of individual seed types, and these practices do not exhibit a consistent altitudinal pattern (19).

In addition to the demand for diversity on farm, varietal richness reflects the diversity of supply available across farms and localities. Supply often is measured using alternative criteria (i.e., race) and follows entirely different patterns from varietal diversity at the farm level; e.g., in Chiapas, Mexico, maize richness per farm is highest at high elevations despite fewer races being

available there than in the state's lowlands (20). Varietal richness itself is typically lower at the farm than community level, but community-to-farm richness ratios for maize, as for most crops, vary widely (10), which raises questions regarding the appropriateness of alternative measures of diversity. For major crops in general, varietal richness is a good indicator of evenness at the farm level (10); but richness estimates necessarily depend on scale, and community richness presumably captures important variation across farms. The disadvantages of richness estimates beyond the farm nevertheless preclude meaningful comparisons (10, 12). Measures of community-wide richness depend on ill-defined community sizes and boundaries, as well as on sampling intensities. They also require transforming continuous variation across farms into discrete, often-subjective categories (12, 26). None of these limitations applies to richness at the farm level. Although year-to-year fluctuation in farm-level richness seems common, there is no record of systematic changes in crop diversity over time or space (9, 10, 26).

Recent Changes in On-Farm Diversity. Analysis of Mexican case studies supports social scientists' casual assessments of the state of maize conservation (9, 10, 21). Cross-sectional regressions reported here suggest a significant increase in richness nationwide over time, from 1.51 varieties/farm in 1995 to 2.03 in 2009 (Fig. 1A). (The lower limit on farm diversity is 1.0.) Similar increases across regions would suggest that the process driving this pattern is widespread; but these estimates are clearly inferential, because neither farms nor localities were resampled. Given that scientists favor high-diversity sites for research, case study data are bound to suffer from site selection bias and not be representative. A shared methodological bias could then be the common driver of findings across regions.

Reliably gauging the extent of genetic erosion (or lack thereof) requires longitudinal data across diverse environments, but such data have been elusive until now (9, 10, 19). ENHRUM's nationally representative sample is a trusty source of data on maize management (19). Analyses based on the survey's first round revealed that maize management is highly location specific; case study findings often fall outside the norm in their respective areas (11, 19). Analysis of ENHRUM's longitudinal dataset reveals the increasing site selection bias implicit in case studies. Direct estimates of maize richness show a nationwide decrease from 1.43 varieties per farm in 2002 to 1.22 in 2007 (Fig. 1B). Similar patterns across regions suggest that the process underlying these changes could be prevalent across Mexico. In fact, the insignificance of decreases in the north could signal that the lower limit on farm diversity nearly has been reached there. Outside the north, losses were widespread (Table 1). Richness decreased in most altitude-by-region environments, albeit not in every locality, and it increased on 5% of farms. Significantly, richness in west-central Mexico became statistically indistinguishable from estimates in northern Mexico, suggesting a southbound trend.

Unfortunately, the recent, optimistic expectations generated by the Global Project on Native Maize appear to be misguided. Our results lend credence instead to several generations of scientists worried about genetic erosion in centers of crop diversity. Until recently, most experts unanimously discounted in situ conservation as impracticable. Not surprisingly, the Global Project has no formal benchmark against which to assess relative changes in on-farm diversity. Its protocols were developed >40 y ago by crop scientists sampling populations for collection (4), not ecological analysis. Hence, the project cannot assess genetic erosion with any confidence (*Methods*).

Drivers of Change. Our focus has been largely on describing changes in maize diversity. Nonetheless, discussions about the drivers of change are urgent in light of their practical implications. Survey data can be used to test current hypotheses on this subject.

that control these factors remain as diverse as the genetic resources they help maintain. Otherwise, the patterns observed in Mexico may be widespread. This is the new economics of crop diversity.

Methods

Analysis Based on Published Case Study Data. In principle, measures of crop varietal richness at the farm level can take any nonnegative integer value. However, in the case of maize, as with most nonclonal crops, values rarely exceed “five” (10). Observed richness distributions across farms often exhibit an excess of “zero” values compared with a Poisson distribution, where zeros represent farms where maize is not grown. This excess means that maize richness at the farm level is the result of at least two decisions on the part of farmers: (i) whether to grow maize and (ii) which varieties to sow. Studies of crop diversity rarely report the complete richness distribution in a locality. With few exceptions, researchers focus on farms growing the crop of interest at the time of the survey and report average-richness estimates that exclude zero values.

We compiled 51 published records of average maize richness on Mexican farms (Table S1); 13 of these records were discarded due to one or more of the following reasons: (i) the richness datum represents the number of varieties grown on a farm over more than one growing cycle; (ii) various inconsistent data are reported in the same study; (iii) the datum has been reported before, or (iv) it falls well outside the time frame of most other studies. Unfortunately, the large database collected by the Global Project on Native Maize and published by the Comisión Nacional de Biodiversidad does not include number of varieties maintained by individual farmers but only the number of biological samples collected. Sample collection can underestimate or overestimate actual richness sown on farm during a particular cycle; e.g., the 2002 ENHRUM recorded 861 seed lots sown by sample farmers during that year while collecting only 419 samples.

We used the remaining 38 useful records, falling between 1995 and 2009, to estimate implicit rates of change in average richness at the farm level. Inferences on annual rates of change, β , were generated by an ordinary least-squares regression (using Stata software, version 12.1) on the following equation:

$$y_i = a + \beta x_i, \quad [1]$$

where y_i is average maize richness at the farm level in locality i , x_i is the year of the survey yielding that particular observation, and a is a constant.

Rates reported in the text and regression lines in Fig. 1A represent separate analyses at the national level and for regions for which data are available. Time periods differ across regions depending on the availability of data. The national-level regression includes predicted average maize richness in 2002 and 2007 with 95% confidence intervals.

Analysis Based on Primary Data. The source of all primary data used here is ENHRUM, a collaborative effort of El Colegio de México and the University of California, Davis (<http://precesam.colmex.mx/ENHRUM.html>). The survey gathered detailed information on the activities and assets of the Mexican rural population, including data on every maize seed lot (i.e., every distinct seed type) managed by households in 2002 and 2007, the dates of the survey's first two rounds. Varietal richness is thus based on each farmer's criteria. Although subjective, these criteria have clear implications for crop management and population dynamics, and hence, also for phenotypic and genetic diversity (11, 12, 14, 17–21, 26, 28).

ENHRUM uses a stratified, three-stage, cluster sampling frame designed in collaboration with the Mexican census bureau [Instituto Nacional de Estadística, Geografía e Informática (INEGI)]. A sample of states, localities, and households (i.e., primary, secondary, and elementary sample units, respectively) was selected through simple random sampling at every stage in each of the five regions in which INEGI divides the country. The sample is representative with 95% confidence of the rural population nationwide and in each region. Because management practices are farmer decisions and management data are derived from a census of seed lots owned by surveyed households (i.e., not from a sample of seed lots), there are no sample design effects to consider besides those pertaining to the sampling of households. The degree of confidence for specific areas within regions, such as altitude-by-region environments, may be lower than 95%, but test statistics reported in the text remain valid.

In contrast to case study data, which consist of local averages, the ENHRUM data provide information on 1,725 individual households. This allowed the fitting of a specific distribution of frequencies to the data. To preserve consistency with the literature, we considered only farmers sowing maize in each year of the survey in estimates for that particular year. We used the ENHRUM sample and a left-truncated Poisson regression to estimate average maize richness at the farm level nationwide, and differences across regions, elevations, and time periods.

In contrast to the equidispersion that characterizes the Poisson distribution, the expected value and variance of the left-truncated Poisson distribution are given by the following:

$$E[y_i | y_i > 0] = \frac{\mu_i}{1 - e^{-\mu_i}}, \quad [2]$$

$$V[y_i | y_i > 0] = \frac{\mu_i}{1 - e^{-\mu_i}} \left[1 - \frac{\mu_i e^{-\mu_i}}{1 - e^{-\mu_i}} \right], \quad [3]$$

where y_i is the number of varieties sown by household i . The econometric model is obtained by defining $\mu_i = e^{x_i \beta}$, where x_i is a $k \times 1$ vector of regressors (i.e., year, region, altitudinal zones) and β is a $k \times 1$ parameter vector (31). Maximum likelihood estimation of this model was done using Stata software (version 12.1). Average values and test statistics reported in Table 1 are the result of estimating a series of truncated Poisson regressions with regional, elevation, and time period variables as needed. SEs were obtained using robust estimates of the variance-covariance matrix. Richness estimates and tests also were performed separately for continuing farmers, new adopters, and farmers abandoning maize and reported in the text.

Statistics in Table 1 represent the results of several regressions testing for temporal and geographic differences across regions and altitude-by-region environments. Regression lines depicted in Fig. 1B were generated based on estimated parameters for each region using ordinary least-squares regressions and farm-level data. To allow comparisons with case study results, the points shown in Fig. 1B are community-level averages. Confidence intervals for 2002 and 2007 at the national level were estimated taking into account the correct distribution of the data, i.e., using the truncated Poisson regression.

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