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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

decade ago, crop scientists considered maize (Zea mays L.) Adversity 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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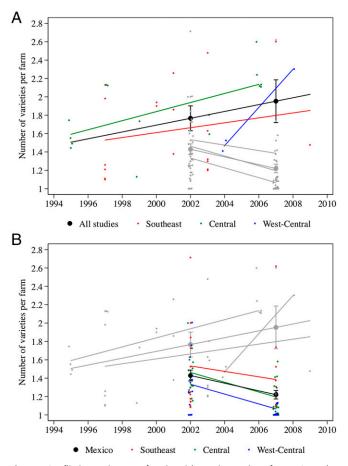


Fig. 1. Conflicting estimates of maize richness in Mexican farms. Over the last 25 y, social scientists have reported that farmers in centers of crop origin continue growing diversity. A regression on cross-sectional, case study data for Mexican maize (A) suggests that farm-level richness increased significantly between 1995 and 2009. Nationwide matched longitudinal data nevertheless show decreases of similar magnitude (*B*), revealing the extent of case study selection bias due to preference for high-diversity sites and the lack of matched panels in past studies. The solid lines represent fitted values; error bars are 95% confidence intervals.

Results

We analyzed data from 38 published case studies of maize richness in Mexican farming communities between 1995 and 2009 (Table S1). Time explains 12% of variation across observations (z = 6.47; P = 0.02). Averages range from 1.10 varieties per farm in Amatengo, Oaxaca, in 1997 to 2.60 in Atzalan, Puebla, a decade later. A regression on these data suggests that richness increased nationwide by 0.04 y⁻¹ (t = 2.20; P = 0.03) between 1995 and 2009. Regional rates of change in west-central, central and southeast Mexico were 0.21 y⁻¹ (t = 7.99; P = 0.08), 0.05 y⁻¹ (t = 2.76; P = 0.02) and 0.03 y⁻¹ (t = 0.86; P = 0.40), respectively (Fig. 1*A*). No regressions were run for northeastern or northwestern Mexico as no useful records were found for these regions (*Methods*).

For the direct longitudinal analysis, we used matched-panel data from the nationally representative Mexico National Rural Household Survey (ENHRUM). In 2002, maize was sown in 63 of the 80 ENHRUM localities. Data for these localities reveal a wider range of richness values for 2002 than all case studies combined: 1.00–2.71 varieties per farm (Fig. 1B). ENHRUM farmers sowed up to five maize varieties in 2002, yet most maintained only one; the nationwide average, 1.43 ± 0.06 , is significantly lower than the estimate from case studies, 1.77 ± 0.14 .

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Average richness was highest in the southeast highlands, 2.21, and generally decreased moving northward ($X^2 = 28.0$) and toward lower elevations ($X^2 = 34.1$; P < 0.0001) (Table 1); 95% of northern farmers and virtually all farmers in the northeast low-lands grew a single variety.

Data from the second round of the ENHRUM survey show that average maize richness per farm dropped across Mexico from 1.43 ± 0.06 in 2002 to 1.22 ± 0.05 in 2007. Large decreases occurred in west-central (-0.05 y^{-1} ; t = 3.41, P < 0.001), central (-0.05 y^{-1} ; t = 4.10, P < 0.001), and southeast Mexico (-0.03 y^{-1} ; t = 2.03; P = 0.04) (Fig. 1B). Significantly, richness in westcentral Mexico became indistinguishable from that in northern regions ($X^2 = 0.42$; P = 0.51), where decreases were not significant. In 2007, farmers continued sowing more varieties in high than mid ($X^2 = 20.28$) or low elevations ($X^2 = 23.48$; P < 0.0001), but richness decreased in most altitude-by-region environments (Table 1). Of 68 localities, 38 exhibited lower richness, whereas 18 saw no change and 12 increased in richness. Similarly, 29% of farmers sowed (up to four) fewer varieties, 66% made no changes, and 5% sowed (up to three) more.

Richness estimates for both 2002 and 2007 include the number of improved and creolized varieties in addition to landraces. Only 86% of maize seed lots recorded in either year were landraces, but significant differences are evident across regions (G = 123.5; P < 0.001): 6% and 8% of seed lots in the southeast and central regions, respectively, but 36% and 30% in west-central and northern Mexico were improved varieties, mostly hybrids. The changes in farm richness described above prevail nevertheless when the analysis is restricted to landraces (Table S2).

Maize was not grown consistently across farms. Only 77% of rural farmers growing maize in 2002 sowed it again in 2007, but total numbers remained unchanged as others adopted maize: 23% of maize farmers in 2007 did not grow the crop in 2002. We defined three groups according to this information: farmers abandoning maize after 2002, those adopting maize by 2007, and continuing maize farmers; and we compared their management AGRICULTURAL SCIENCES

Table 1. On-farm maize richness (farm-level averages) across Mexico, 2002–2007

Region	Altitude	Varieties/farm		X ² for difference
		2002	2007	of means
Mexico		1.43	1.22	29.34 (P < 0.001)
	High	1.66	1.40	9.64 (P < 0.01)
	Mid	1.28	1.12	6.21 (P = 0.01)
	Low	1.32	1.12	22.68 (P < 0.001)
Southeast		1.53	1.39	4.15 (P = 0.04)
	High	2.21	2.07	0.40 (P = 0.53)
	Mid	1.26	1.33	0.22 (P = 0.64)
	Low	1.38	1.16	14.91 (P < 0.001)
Center		1.46	1.20	16.75 (P < 0.001)
	High	1.56	1.30	6.95 (P < 0.01)
	Mid	1.45	1.06	7.47 (P < 0.01)
	Low	1.28	1.08	5.90 (P = 0.02)
West-central		1.33	1.07	12.00 (P < 0.001)
	High	1.38	1.05	11.14 (P = 0.001)
	Mid	1.30	1.12	1.90 (P = 0.17)
	Low	1.27	1.00	1.09 (P = 0.30)
Northwest		1.05	1.03	0.05 (P = 0.82)
Northeast		1.08	1.04	0.42 (P = 0.52)

Average number of varieties per farm includes improved, creolized, and farmer varieties. In 2002, richness was highest in Mexico's southeast highlands, renowned bulwarks of maize diversity. In general, farm-level richness was lower moving northward and toward lower elevations. By 2007, farmers continued sowing more varieties in high than mid or low elevations, but richness decreased in most areas. 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 crosssectional 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 illdefined 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. 1*A*). (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 altitudeby-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. However, apportioning responsibility between humans and the environment could be misleading, as it ignores the strong interdependence of social and environmental processes. In centers of diversity, for instance, crop adaptation to climate change necessarily is mediated by farmer perceptions and responses to local events (21, 22). Farmers also respond readily to events on much shorter timescales, particularly economic signals, with important repercussions on a crop's distribution. Prices presumably explain why rain-fed maize in Mexico contracted by 880,000 ha between 2002 and 2006 but then rebounded after prices surged (27). A focus on farming practices—e.g., seed selection and exchange before sowing—should allow us to foresee changes in crop dynamics well before their consequences become apparent in the fields (11, 21, 28). Analysis of these practices should also shed light on the causes of recent diversity loss.

Cross-sectional studies for various crops have identified numerous social and economic factors that may lead to diversity loss in general (9, 25). That the impact of farmers' abandoning a crop has not been discerned reflects the scarcity of longitudinal studies. Farm turnover in the maize sector has been substantial. The sector's restructuring after 2002 could reflect commercial growers' abandoning maize in response to domestic and international price decreases at that time. In contrast, subsistence farmers were expected to continue growing maize diversity for home consumption (29). According to this logic, farmers adopting maize by 2007 would consist of commercial producers enticed by the price surge in that year (27). This would be significant, because an increasing market orientation is presumed to be a major cause of diversity loss (9, 25). Observed differences in maize management across farms support this possibility.

Farmers adopting maize in 2007 sowed significantly fewer varieties than those growing maize in 2002. Thus, new maize farms decreased average farm richness in Mexico, but farm turnover was not critical. Farmers who abandoned maize after 2002 also grew fewer varieties than other farmers. Conceivably, opportunistic, price-sensitive growers could sow fewer varieties than loyal maize farmers without endangering diversity. However, loyal maize farmers also held fewer varieties over time in every region where richness declined, suggesting an enduring loss of diversity.

Ascertaining the causes of diversity loss is crucial for effective in situ conservation, and other possible explanations for observed losses should be examined, including climate change. Climate departure could arrive in Mexico by 2031 (24), and ENHRUM localities are expected to experience increasingly adverse conditions (22). Nevertheless, a single, overriding explanation for decreases in farm richness is unlikely given the complexity and local specificity of crop management and dynamics (11, 19). Identifying conditions leading to the current situation will require characterizing farms and localities exhibiting losses. In-depth studies will be needed then to sort out local dynamics linking diversity across farms, including seed exchange, which is considered a measure of the state of in situ conservation (9).

Genetic Diversity and Climate Adaptation. Genetic erosion is an intuitively appealing but poorly defined concept, applied indistinctly to loss of alleles, gene combinations, genomes, or varieties (4, 9). The extent and significance of recent changes in maize genetics are themselves unclear. It is said that maize's low evenness at the farm and locality levels indicates deliberate conservation of minor (i.e., rare) varieties for future use (10), but this seed will likely be the first discarded as farm richness decreases (26). Minor varieties possess distinctly low genetic diversity, and they may constitute a subset of more widespread populations (1, 12). In contrast, major (or dominant) varieties may contain most locally adaptive alleles (12). Hence, no significant loss of alleles may occur as minor varieties become locally extinct. However, changes in the structure and dynamics

of maize metapopulations could still result in genetic diversity declining overall.

Minor varieties include specialty maize and numerous seed types introduced recently from other localities (14). Introduced seed often is tested and discarded after a single cycle but is exchanged profusely among neighbors when saved (11). Sourced largely within a 10-km radius, it is a vector for the spread of innovations and the source of unintended gene flow that, through introgression, may replenish gene pools exhausted by selection, genetic drift, and ordinary seed management (11, 14, 21, 28). If introduced seed dwindles as richness and the demand for minor varieties decrease, populations could become isolated, stymieing the process believed to maintain crop genetic diversity—i.e., seed exchange (9). Significantly, seed exchange was substantially lower between 2002 and 2007 than during the previous 5-y period (G = 7.0; P = 0.03).

Given these changes, it is likely that Mexican farmers will find considerably impoverished supply sources when they search again for innovations should their seed become increasingly maladapted to changing climate, pests, and diseases (21–23). Lack of suitable alternatives could prevent mitigation of expected yield decreases (22), reducing the benefits of growing maize vis-à-vis more readily available livelihood options, including migration. This would likely lead to greater farm turnover and loss of diversity within the sector just as the relevance of in situ conservation increases. Unlike germplasm banks, in situ conservation allows crops to evolve in response to changing pests and diseases, such as those occurring with climate change (9, 23). Significantly, maize genetic diversity is the centerpiece of national and international strategies to safeguard food security as the climate changes (30).

Implications for Other Centers of Crop Diversity. For over half a century, discussions on crop genetic erosion remained largely anecdotal, and the presence of modern varieties in a farming system was taken as prima facie evidence of diversity loss (2, 3, 9). Remarkably, the landmark Food and Agriculture Organization report of 1967 is "distinguished by a lack of data and/or analysis of specific case studies of genetic erosion" (9). This situation changed dramatically over the last quarter century with the publication of numerous case studies in centers of crop diversity around the world (7, 9, 10). Sundry disciplinary and methodological approaches have enriched our understanding of crop management and diversity in these areas, generating a valuable trove of first-hand information. However, with few exceptions (10), efforts have been uncoordinated, and the diversity of approaches used defies systematization.

Maize's center of origin and diversity in Mexico is arguably the most thoroughly researched case. However, despite the large number of published studies, a recent survey found that our knowledge of this system is seriously fragmented (19). Surprisingly few systematic records of maize management are available, and data are rarely commensurable. Generalizations have been founded on limited evidence and conceptual models of maize dynamics put together as loosely knitted patchworks of dissimilar observations from populations in strikingly different conditions (19). Our results reveal that, furthermore, these models have been associated with increasingly biased assessments of maize diversity.

Genetic diversity clearly depends on a crop's reproductive biology. Maize is an outcrossing species, not representative of selfing or clonal crops, which limits the applicability of our findings. However, unsubstantiated generalizations and site selection bias are potentially worrisome for other centers of crop diversity, because social research methods and concomitant inferences have been shared (9, 10, 25). The current state of knowledge maintains that the same factors (i.e., agronomic, consumption, and market conditions) determine on-farm diversity across crops and agroecosystems (25). We can only hope that the processes 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:

$$y_i = a + \beta x_i, \tag{1}$$

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).

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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 altitudeby-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:

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

$$V[y_i|y_i>0] = \frac{\mu_i}{1 - e^{-\mu_i}} \left[1 - \frac{\mu_i e^{-\mu_i}}{1 - e^{-\mu_i}}\right],$$
[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 kx1 vector of regressors (i.e., year, region, altitudinal zones) and β is a kx1 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. 1*B* 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. 1*B* 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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