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A Minor Role for Environmental Adaptation in Local–Scale Maize Landrace Distribution: Results from a Common Garden Experiment in Oaxaca, Mexico[1]

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A Minor Role for Environmental Adaptation in Local–Scale Maize Landrace Distribution: Results from a Common Garden Experiment in Oaxaca, Mexico. Agronomists usually assume that yield is a primary selection trait for farmers practicing traditional agriculture. They hypothesize that the landraces grown in farmers' fields produce higher yields than other local landraces would, if grown in the same fields. We test this hypothesis in experimental gardens using maize landraces grown by indigenous farmers in a low– to mid–elevation region in Oaxaca, Mexico. We selected four villages, two Chatino and two Mixtec, two in low and two in middle elevations. We planted reciprocal common gardens in each village, in order to test whether or not local maize landraces were higher yielding in their respective villages—a finding that would suggest they are selected because they are better adapted to local conditions than landraces from other villages. We also tested resistance to a fungal disease (ear rot caused by *Fusarium*) that is cited by farmers in the region as a major problem for maize production. We found that maize samples planted in their villages of origin did not in general have higher yields than samples from other villages. There are significant interactions among common garden site, fertilizer use, and seed source. We found that landraces from the Chatino lowlands village perform well in most sites, with and without fertilizer. Regarding ear rot, there is some evidence that landraces are less susceptible when grown away from their villages of origin. These results suggest that social factors, such as seed networks and ethno–linguistic membership, may be more important than local environmental adaptation in determining the distribution of landraces in this region.

La adaptación ambiental juega un rol menor en la distribución de maíces a escala local: resultados de un experimento de jardines recíprocos en Oaxaca, México. En la práctica agrícola generalmente se asume que el rendimiento es una de las razones por las cuales los agricultores tradicionales seleccionan una variedad local. Esto conlleva a la hipótesis de que los cultivares que utilizan los agricultores son los que tienen los rendimientos más altos en comparación con otros cultivares de la región. Nosotros probamos esta hipótesis estudiando las variedades utilizadas por agricultores indígenas en una región con un rango altitudinal de 400 a 1300 msnm en Oaxaca, México. Seleccionamos cuatro localidades, dos chatinas y dos mixtecas,

dos a baja altitud y dos a altitud media. Establecimos jardines recíprocos en cada una para probar si los maíces de cada localidad producían más que los de otras localidades. Esto podría sugerir que esos cultivares fueron seleccionados porque están mejor adaptados a las condiciones locales. También probamos resistencia a enfermedades por hongos (pudrición causada por *Fusarium* spp) porque esta enfermedad fue mencionada por los agricultores como una de las principales en el cultivo de maíz. Los resultados mostraron que las muestras plantadas en la localidad donde fueron colectadas no siempre tienen los mayores rendimientos en comparación con muestras de otras localidades. Encontramos interacciones significativas entre el sitio de la parcela, fertilización y la localidad de origen de la muestra. Las muestras de la localidad chatina localizada a baja elevación tuvieron mejor rendimiento en la mayoría de los sitios, con y sin fertilizante. En relación a pudrición de la mazorca, hay un poco de evidencia de que los cultivares son menos susceptibles cuando se siembran lejos de su localidad de origen. Estos resultados sugieren que factores sociales, tales como redes de semillas y pertenencia a un grupo étnico, podrían ser más importantes que la adaptación local en la determinación de la distribución de variedades locales en esta región.

Key Words: Maize, crop diversity, environmental adaptation, *Fusarium* spp, Oaxaca, Mexico, common gardens.

Introduction

Maize diversity and diversification in Mexico have interested researchers for many decades (e.g., Hernández and Alanis 1970; Kato et al. 2009; Wellhausen et al. 1952). Diversity is well known at the race level in almost all geographical regions of Mexico (CONABIO 2011), and traditional management has been studied in several peasant villages across the country's climatic areas (e.g., Aguirre et al. 2000; Arias et al. 2007; Bellon and Brush 1994; Bellon et al. 1999; Louette and Smale 2000; Perales et al. 2003). Since the mid–20th century, maize agronomic research in Mexico has contributed to the development of high yielding varieties, which are now used extensively outside of Mexico. However, improved seed is used only on approximately 22% of the land in Mexico devoted to maize (Aquino et al. 2001). The persistence of local landraces in the presence of improved seed has been attributed to environmental heterogeneity, even at the local scale. Although Bellon and Taylor (1993) found that farmers try to maximize investment using improved varieties in good soils, this strategy is not used everywhere. Perales et al. (2003) noted that farmers do not adopt improved seed even though they have good soils and sufficient rainfall. They attributed this to the fact that alternative commercial cultivars for the highlands of Mexico are not competitive, compared to local landraces.

In their review of the literature on agrobiodiversity, Wood and Lenné (1997) found a general opinion that varieties used and conserved by traditional farmers are "locally adapted." Cleveland et al. (1994) agree that folk varieties are adapted by farmers to local physical, social, and cultural environments. Accordingly, the distribution of maize cultivars, varieties, and landraces in Mexico should be determined by their adaptation to different growing environments. However, few experiments have tested the adaptation hypothesis for the distribution and richness of maize landraces at a local scale. Some exceptional studies have shown local environmental adaptation. For example, in a recent study on pearl millet, adaptation to reduced rainfall is suggested by earlier flowering times in Africa's Sahel region (Vigouroux et al. 2011). In a 26–year study in France, Enjalbert et al. (2011) found evidence of local adaptation for wheat varieties. Adaptation expressed by grain weight was present in one of three sites. Disease resistance was detected in sites where disease pressure was higher (Enjalbert et al. 2011). In southern Mexico, Mercer et al. (2008) tested local adaptation of maize at different elevations, finding that landraces from the lowlands have a broader range of environmental adaptation than those from the highlands. They suggested that highland landraces have specific physiological and morphological traits adapted to their growing conditions.

This paper challenges the notion that crop diversity is explained by interactions between genes and local environments (G x E), and affirms recent proposals that social factors are perhaps equally important in shaping diversity. Following research findings in small–scale farming systems in areas of crop origins, Leclerc and d'Eeckenbrugge (2011) proposed the G x E x S model, where S stands for social differentiation. An association between culture and crop diversity is intuitively obvious, given that different cultural groups often have different

food preferences, rituals involving crops, and attachment to local expressions of cultural identity. Socially derived factors are known to contribute to the maintenance of particular landraces (Bellon 1996; Brush and Meng 1998; Hernández 1972; Zimmerer 1996).

The most common approach for exploring farmer selection and landrace distribution is based on rational choice and analysis of cost–benefit and risk. This approach links environmental variability to the persistence and differentiation of maize populations (Aguirre et al. 2000; Bellon and Taylor 1993). Nevertheless there is evidence that other social and human factors affect farmer–mediated selection; for example, biased cultural transmission (Henrich 2001) and cultural differences in maize perception and preference (Benz et al. 2007). Working in highland Chiapas (elevation >1,800 masl), Perales et al. (2005) demonstrated that the distribution of two races, Olotón and Comiteco, follows the distribution of the Tzotzil and Tzeltal ethnolinguistic groups. While each group's maize was adapted to its local environment, the maize of one group was competitive in both ethnic areas. In the present paper, we test environmental adaptation as a force shaping maize landrace distribution in a heterogeneous region where two ethno–linguistic groups inhabit two distinct environments.

If yield is a primary variable in landrace selection, we can posit that farmers use particular sets of landraces because they yield more and, by inference, are better adapted to their lands and climate compared to landraces from neighboring villages. Several factors affect the composition of landraces and cultivars managed by a particular farmer. According to Bellon (1996), farmers face several concerns, such as environmental variability, yield, and diet, and no single variety meets all of these concerns. Consequently, farmers select a set of cultivars or landraces. Numerous factors shape the selection of cultivars, and farmers try to maximize the benefits related to those factors. Despite the diversity of selection criteria, yield remains a paramount attribute for understanding the selection and distribution of landraces. We expect that because farmers continuously experiment and test varieties, the group of cultivars actually grown in a village is the best combination of varieties known to the households of that village. Under the local adaptation hypothesis, yield is a fundamental measure of this goodness of fit.

Along with yield, we consider another proxy for local adaptation—resistance to ear rot that is caused mainly by *Fusarium* spp. and other fungi that are significant problems for farmers in tropical lands (White 1999). Although estimates of harvest losses to fungi in Mexico are unavailable, *Fusarium* is understood to be one of the most important diseases of maize (CIMMYT 2004). In our study area, farmers change their field sites at least every two years; they know that maize planted in the same plot after two years will be more severely affected by ear rot. Changes of seed to avoid varieties known to suffer ear rot are routine. In the common garden experiment, we ask whether local maize cultivars show greater resistance to fungal diseases than landraces from other villages.

Methods

STUDY SITE

The study was carried out in the Sierra Sur in the state of Oaxaca, located in southern Mexico (Figure 1). The Sierra Sur region is part of the Sierra Madre del Sur, a mountain range extending along the Pacific Coast from southern Jalisco to the Isthmus of Tehuantepec in the state of Oaxaca. The region is bordered on the north by La Mixteca and the Central Valleys regions; on the south by the Coast region; on the east by the Isthmus region; and on the west by the state of Guerrero. The Sierra Sur is narrowly shaped, with a west–east orientation. Elevation ranges from 200 masl to 3,700 masl, and the climate varies from temperate to hot and dry. The most representative climate types are hot subhumid (41%), temperate subhumid (25%), and semi–hot subhumid (17%). Annual precipitation ranges from 500 to 2,500 mm per year. Mean annual temperature varies from 10°C to 26°C. Soils are very diverse because of the geologic origins of the mountain range, but four soils are the most common: Regosol (59%), Litosol (15%), Acrisol (14%), and Cambisol (10%) (INEGI 2013). Due to climate and other environmental variables, land cover is also diverse. The representative vegetation types are pine–oak forest, pine forest, induced grassland, oak forest, cloud forest, rainforest, and tropical shrubs. Rain–fed agriculture covers 13% of the area; irrigated agriculture, 1%; and pastures, 1% (INEGI 2005).

This region is one of the poorest in the state of Oaxaca, ranked sixth with respect to the other seven regions within the state. Poverty and marginalization are associated with lack of access to utilities like
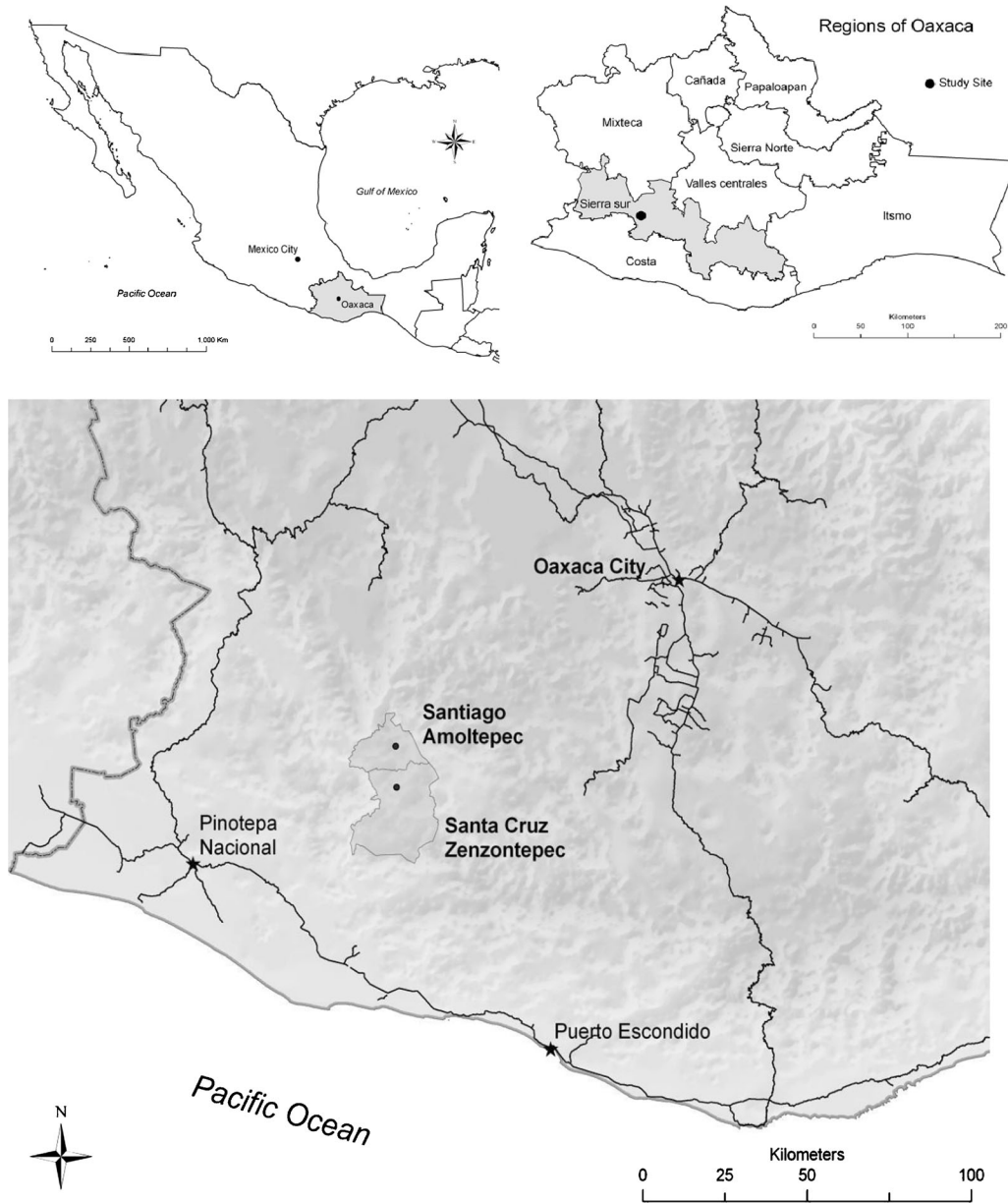
Fig. 1. Location of the study site.

potable water, paved roads, telephone, and very limited industrial development. The population's dispersal across the mountains and reliance on subsistence production also contribute to the region's poverty. Agricultural production in the Sierra Sur represents only 7% of the total production in Oaxaca. The main crops are maize, representing 72% of the agricultural area and 36% of the value

of agriculture products of the region; agave (6% of the area and 26% of the value); coffee (10% of the area and 6% of the value), and beans (5% of the area and 6% of the value) (Hernández–Ramos 2011). Maize yields in the Sierra Sur region are below the state average. In 2012, maize yields were 0.98 ton/ha in Zenzontepec and 0.91 ton/ha in Amoltepec (SIAP 2014).

Maize Collections and Reciprocal Common Gardens

To test whether landrace distribution is shaped by local adaptation for yield and fungal resistance, we collected a stratified sample of maize seeds and planted reciprocal common gardens. Four villages were selected: two Chatino, one at middle elevation (1,000–1,300 masl) identified as Ch–M and another in the lowlands (400–600 masl), Ch–L; and two Mixtec, one at middle elevation, M–M, and another in the lowlands, M–L. Villages in the same elevation range have similar climates (Table 1). The villages are located in the municipalities of Santa Cruz Zenzontepec and Santiago Amoltepec, which are Chatino and Mixtec, respectively.

Maize collections were obtained by stratified and systematic sampling in order to obtain samples that represented the diversity of maize grown in each village. After determining the number of households in each barrio (village section), the first household sampled was selected close to the main road entering the barrio, then a fixed number of households was skipped before selecting each subsequent household for inclusion. The number skipped depended on the total number of households in the barrio, and was chosen to achieve an approximate sampling fraction of 10% of the barrio.

We collected 135 maize samples across the four villages. Each maize sample consisted of 12 seed quality ears of each seed lot that the household planted in the previous year. Ecological information and the local name of each landrace were recorded. Prior to selecting a final set of five samples from each village for planting in common gardens, the samples of each village were grouped by local name and race, and organized according to variation in ear morphology. The five samples finally selected from each village (see Table 2) were understood to best represent the total variation in their respective villages, based on ear descriptors (Carballo and Benítez 2003). Our interest is in the aggregate performance of the five samples comprising the set from each village, rather than in individual seed samples.

Four reciprocal common gardens were planted; environmental and management characteristics of the plots are shown in Table 1. Because Chatino villages commonly use fertilizer while Mixtec villages do not, the experiment included fertilizer application as a treatment. Each of the common gardens had a complete random block design with three repetitions, except in location M–L, which had only two repetitions. The common gardens

Table 1. CLIMATE VARIABLES OF THE VILLAGES AND CHARACTERISTICS OF THE COMMON GARDENS PLOTS.

Village	Village Climatic Characteristics					Common Garden Site Characteristics			
	Elevation (m)	Rainfall[1]	Mean annual temp.	Min temp.[2]	Max temp.[3]	Elevation (m)	Soil Characteristics	Slope	Management
M–M	1,261	1,032	21.1	9.0	32.0	1,220	Loam texture, middle rocky. About 10 to 30 cm deep.	30%	One year fallow. Maize was last crop
M–L	574	865	24.7	13.4	34.9	580	Silt loam texture. No rocks. About 5 to 15 cm deep.	34%	Two years fallow. Maize was last crop
Ch–M	1,318	1,072	20.9	8.9	31.6	1,230	Sand texture. Rocky. From 0 to 10 cm deep.	40%	Two years fallow. Maize was last crop, but pasture was planted after maize crop.
Ch–L	460	807	25.3	14.2	35.4	680	Clay texture. No rocks. More than 1 m deep.	5%	One year fallow. Maize was last crop

Mixtec middle elevation: M–M; Mixtec lowlands: M–L; Chatino middle elevation: Ch–M; Chatino lowlands: Ch–L.
[1] Rainfall of the wettest quarter of the year.
[2] Minimum temperature of the coldest month.
[3] Maximum temperature of the hottest month (Hijmans et al. 2005).

Table 2. Maize samples used in the reciprocal common gardens.

Village		Landrace Name	Elevation range (m)	Primary Race	Secondary Race
Mixtec middle elevation	M001	Maíz del cerro	1,100–1,600	Tepecintle	Tuxpeño
Mixtec middle elevation	M003	Blanco	1,100–1,600	Tuxpeño	
Mixtec middle elevation	M005	Corto	1,100–1,600	Conejo	
Mixtec middle elevation	M016	Maíz del cerro	1,100–1,600	Olotillo	Tuxpeño
Mixtec middle elevation	M043	Largo	1,100–1,600	Olotillo	Tepecintle
Mixtec lowlands	M018	Largo	400–800	Olotillo	Tuxpeño
Mixtec lowlands	M022	Olotillo	400–800	Olotillo	Tuxpeño
Mixtec lowlands	M029	Blanco	400–800	Tepecintle	Tuxpeño
Mixtec lowlands	M032	Largo	400–800	Tepecintle	
Mixtec lowlands	M040	Olotillo	400–800	Olotillo	Tepecintle
Chatino middle elevation	M075	Amarillo	1,000–1,500	Olotillo	Tepecintle
Chatino middle elevation	M086	Cuarenteño	1,000–1,500	Conejo	
Chatino middle elevation	M087	Olotillo maíz Delgado	1,000–1,500	Olotillo	Tuxpeño
Chatino middle elevation	M090	Olotillo corto	1,000–1,500	Tuxpeño	
Chatino middle elevation	M094	Olotillo	1,000–1,500	Olotillo	
Chatino lowlands	M104	Olotillo largo	400–800	Olotillo	Tuxpeño
Chatino lowlands	M109	Delgado	400–800	Olotillo	
Chatino lowlands	M121	Corto	400–800	Elotes Occidentales	Tuxpeño
Chatino lowlands	M131	Olote Delgado	400–800	Olotillo	
Chatino lowlands	M137	Maíz de sapo	400–800	Tuxpeño	

with three repetitions had 120 experimental units, 60 treated with fertilizer and 60 without fertilizer (60 = 5 samples × 4 villages × 3 blocks); the garden with two repetitions had 40 treated and 40 untreated units. Each experimental unit had four furrows, each 5 meters long and 0.8 meters wide. Three seeds of each sample were sowed by hand at each planting position; the distance between positions was 50 cm. About 30 days after germination, plants were thinned to two per position. The final planting density was 50,000 plants/ha. Fertilization consisted of 88 kg/ha of N, 26.5 kg/ha of P, and 26.5 kg/ha of K in two applications. The first application was in the first two weeks after emergence, applying all P and K, and 30% of the N. The second application before silking contained the remaining N (70%).

THE MODELS

We fitted separate models for yield and ear rot resistance. The independent variables are the same for each model: source (M–M, Ch–M, Ch–L, M–L), defined by the village of seed origin; site (M–M, Ch–M, Ch–L, M–L), defined as the location of the common garden; treatment (no fertilizer, fertilizer); and block (random effect). The dependent variable for the yield model is Log(yield) (Log[Grams per Plant]). We applied the log transformation to stabilize the variance and produce an approximately Gaussian distribution. The dependent variable for the ear rot model is the Log–odds of ear rot, where the odds are defined as the ratio of rotted ears to healthy ears.

All statistical analyses were performed in the R statistical language, version 2.15.2 (R Core Team 2012). We fitted a linear mixed model for Log(yield) using the function *lme* from the package *nlme* (Pinheiro et al. 2013). Sample variances of Log(yield) were different for experimental units with and without fertilizer, so the model incorporates distinct error variances for these two conditions. We fitted a generalized linear (binomial) mixed model for Log(odds of ear rot) using the function *glmer* from the package *lme4* (Bates et al. 2013).

The model for yield has the form:

$$\text{Log(yield)} = \text{General Mean} + \text{Source} + \text{Site} + \text{Treatment}$$
$$+ (\text{Source by Treatment interaction})$$
$$+ (\text{Site by Treatment interaction})$$
$$+ (\text{Source by Site interaction})$$
$$+ \text{Random Block} + \text{Error}.$$

The model for ear rot has the same right–hand side, though the final Error term is omitted.

Coefficient estimates and standard errors for both models are in the Appendix (Electronic Supplementary Material, ESM).

Characterization of the source by site interaction (SxS) is very important for questions about local adaptation. A positive and statistically supported SxS effect may indicate that yield is improved when landraces are grown in their villages of origin (depending on the particular levels involved in the interaction). The opposite holds for ear rot, where a *negative* source by site interaction may indicate that fungal infection is lower when landraces are planted in their villages of origin. The hypotheses we tested are: 1) landraces planted in their villages of origin will have higher yields and better ear rot resistance, compared to landraces from other villages; and 2) local adaptation is therefore one of the main factors determining local landrace distribution.

Results

YIELD

Figure 2 shows model estimates of yield (known as "adjusted means"). The most salient result is that landraces planted in their local environments—for which *Village of Seed Origin* and *Common Garden Location* are the same—do not have higher yields than landraces planted in non–local environments. This result holds whether or not fertilizer is applied and is supported by two facts. First, a sequential analysis of variance (ANOVA) shows that the SxS effect is not significant, after incorporating the other effects (p–value= 0.1694; Table 3). Second, the Akaike Information Criterion (AIC) does not support inclusion of the SxS effect: the AIC for the full model of Table 3 is 585.4, whereas the AIC excluding SxS is 558.6. The difference in AIC is large enough that the full model is said to have little to no relative support (Burnham and Anderson 2002, p.70). If landrace distribution derives from local adaptation, we would reasonably expect seeds to have higher yields in their own common gardens. Our results, however, contradict this expectation and do not support the hypothesis of local adaptation for yield.

Figure 2 also leads to the conclusion that landraces in the region are not specially adapted to their altitudes. Landraces from the middle elevation villages (M–M and Ch–M) and from lowlands (Ch–L and M–L) generally yield no better in their own

elevation than the other. On the contrary, middle elevation landraces (from M–M and Ch–M) tend to be more productive in the lowland village Ch–L than in their villages of origin.

Treatment Effect on Yield

Fertilizer has a positive, statistically supported effect for all sources and sites (Figure 2 and Table 4). Adding this treatment effect to a model containing source and site effects improves the model (P < 0.0001; see Table 3). However, the size of the treatment effect depends on both source and site (note the variation in distances between filled and open circles, across rows and columns of Figure 2). As an example of site by treatment interaction, in site M–L the yield increment due to fertilizer application is lower than in any other site; and for source M–M it is negligible (Table 4).

The effect of treatment for source Ch–M is an important one. In Table 4, we can see that fertilizer use produces the highest percent increment in yield for Ch–M across all sites (rows). As noted previously, farmers in Ch–M and Ch–L commonly use fertilizer, whereas farmers in M–L and M–M almost never use fertilizer. We might conjecture that landraces from Ch–M have been selected because they respond to fertilizer. However, fertilizer increases the yield of M–L seeds relatively more than Ch–L seeds (Table 4); the response to fertilizer is therefore not consistent across sources where fertilizer is, or is not, used.

Source Effect on Yield

The effect of source on yield is important. However, because the source by treatment interaction is present, the total source effect is not simple and additive. Seeds from Ch–L perform relatively well across sites without fertilizer (Figure 2), but with fertilizer in low elevation gardens (sites M–L and Ch–L), seeds from Ch–M perform better. Seeds from Ch–M have a significant positive treatment interaction (Figure 2 and Appendix ESM, Table 1) and have high yields in low elevation gardens with fertilizer; the same seeds have poor yields without fertilizer.

Ch–M is located above 1,200 masl and M–L and Ch–L are at 500 masl. Nevertheless, we observe that maize from Ch–L yields relatively well across environments. Samples from Ch–L are more characteristic of *Tuxpeño*, a race with more rows and larger

Village of seed origin
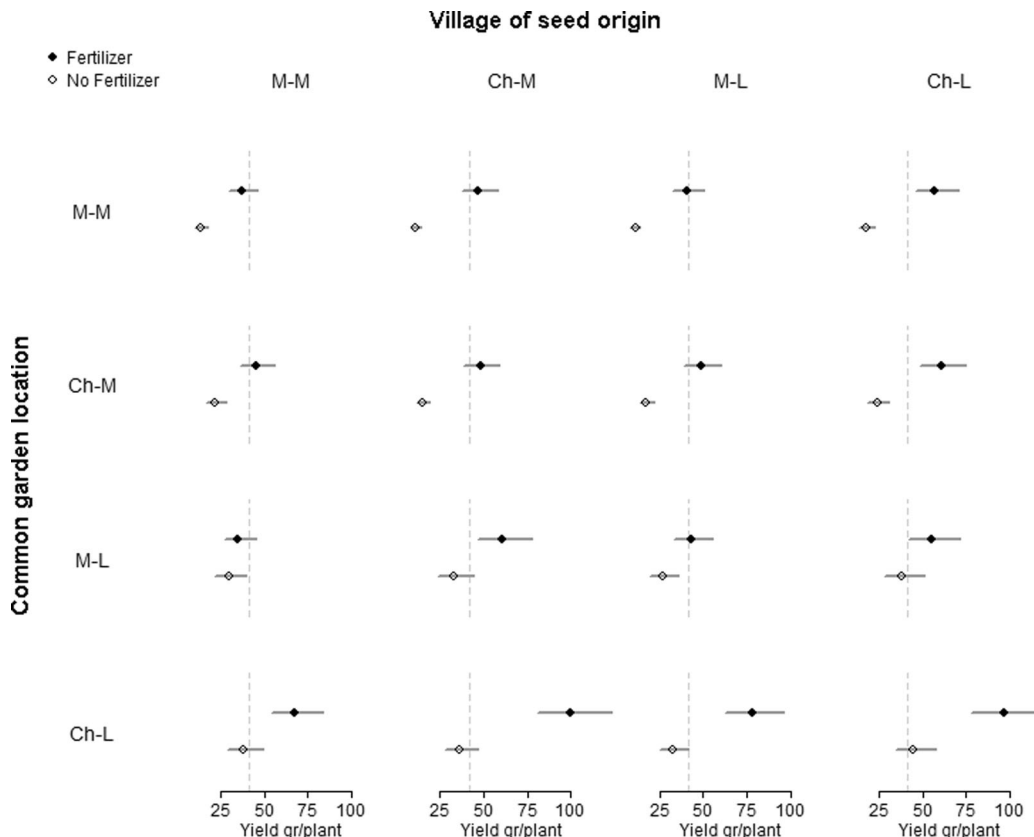
Fig. 2.   Model estimates and approximate 95% confidence intervals for the four common gardens, showing effects of source of seeds, treatment and site on yield (gr/plant).

ears than others in the region. *Tuxpeño* is extensively used by breeders because of its high yielding ability and wide adaptation to the lowlands. One might ask why seeds from Ch–L have not replaced other landraces over time; we return to this question in Discussion.

Site Effect on Yield

In Figure 2 we can see the effect of site by comparing yield estimates in different rows. Overall, landraces yield differently depending on site. However, due to the site by treatment interaction (Table 3), the site effect is not simple and additive. Yields in Ch–L were the highest for all sources, and yields in M–M were the lowest for most sources (Figure 2). The garden in Ch–L was located on flat land, with deep soil, while the other three gardens were located on steep plots with shallow soils. All sets of landraces appear to have a positive response to the good soil in Ch–L, even

when the plot is located at low elevation, with a higher mean annual temperature than higher elevations. In both lowland sites (M–L and Ch–L), estimated yields for all sources are higher without fertilizer than in the higher elevation sites.

RESISTANCE TO FUNGI

We calculated the percentage of grain lost to *Fusarium* and other fungi by source, site, and treatment, averaging over seed samples and blocks. Losses range from 3.3% to 36.6%—the lowest corresponding to seed from M–M planted in site Ch–M and treated with fertilizer, and the highest for seed from Ch–M planted at site M–M and untreated.

Model estimates of the odds of rotten ears are shown in Figure 3. In contrast to the yield model, a source by site interaction for fungal resistance is supported. A sequential ANOVA shows that the SxS effect is significant, after incorporating the other

Table 3. ANOVA FOR YIELD MODEL. SEQUENTIAL F–TESTS FOR THE ADDITION OF TERMS IN THE ORDER LISTED.

	Numerator d. f.	Denominator d. f.	F–value	p–value
Source	3	398	14.9	<.0001
Site	3	14	26.7	<.0001
Treatment	1	14	164.4	<.0001
Source x Treatment	3	398	4.9	0.0022
Site x Treatment	3	14	5.2	0.0126
Source x Site	9	398	1.4	0.1694

effects (p–value = 0.0056; Table 5). And the model that includes the SxS interaction has an improved AIC (566.0) compared to the model without the interaction (AIC = 571.3). The direction of the SxS effect varies across sources and sites, thus it is difficult to make general claims about the resistance of landraces to local versus non–local fungi. However, as described below, interpretable patterns can be seen in Figure 3.

Treatment Effect on Fungal Resistance

In most cases, fertilizer use reduced the occurrence of rotten ears. In Figure 3, filled circles are usually to the left of their unfilled partners, indicating relatively lower odds of rotten ears with fertilizer than without. Colonization of the grain by fungi usually is enhanced by insect and bird damage and by stalk lodging (White 1999). One explanation for the association between fertilizer and the reduction of fungal attack is that fertilizer produces stronger plants with better ear cover (husk) and less lodging. The protective effect of fertilizer is less pronounced for sources M–M and M–L. For the combination of source M–M and site M–M, the protective effect is reversed: seeds from M–M planted at M–M were less resistant to fungi with fertilizer than without. Table 6 summarizes the reduction in odds of rotten ears when fertilizer is applied.

Table 4. EFFECT OF FERTILIZER ON YIELD FOR EACH SOURCE AND SITE. DIFFERENCE BETWEEN ESTIMATED YIELD WITH AND WITHOUT FERTILIZER, AS A PERCENTAGE OF THE YIELD WITHOUT FERTILIZER.

	Village of origin of seed (source)			
Site	M–M	Ch–M	Ch–L	M–L
M–M	169%	318%	229%	267%
Ch–M	105%	219%	151%	180%
Ch–L	78%	176%	117%	142%
M–L	19%	85%	45%	62%

Source Effect on Fungal Resistance

The source effect on fungal resistance is not simple and additive; it is complicated by the presence of source by treatment, as well as source by site, interactions. Broadly speaking, seeds from sources Ch–M and Ch–L were relatively susceptible to ear rot, especially when fertilizer was not applied (Figure 3). Fertilizer use is common in Ch–M and Ch–L and landraces from these sources appear to suffer disproportionately from ear rot when grown without fertilizer. Seeds from source M–M seem to be relatively resistant to rot in all sites. In Figure 3, row–by–row comparisons indicate that ear rot was prevalent in the M–M common garden; therefore, the overall resistance of M–M seeds suggests that landraces from M–M are adapted to high *Fusarium* levels.

Site Effect on Fungal Resistance

Site is a significant predictor of ear rot infection, both as a main effect and in interactions with treatment and source. Negative impacts of ear rot for all landraces are evident at site M–M (Figure 3). The odds of ear rot were relatively low at sites Ch–M and Ch–L, especially when fertilizer was applied.

Source by Site Effect on Fungal Resistance

Figure 3 hints at one facet of the source by site effect: seeds may be less susceptible to ear rot when grown away from their villages of origin. Seeds from Ch–M grown in the M–L common garden provide an example. The M–L garden was negatively impacted by ear rot, though not as severely as the M–M garden; yet seeds from Ch–M—not generally the most resistant—performed best among all sources in M–L. Seeds from M–L grown in the M–L common garden illustrate the inverse effect: M–L seeds performed well in other sites, but
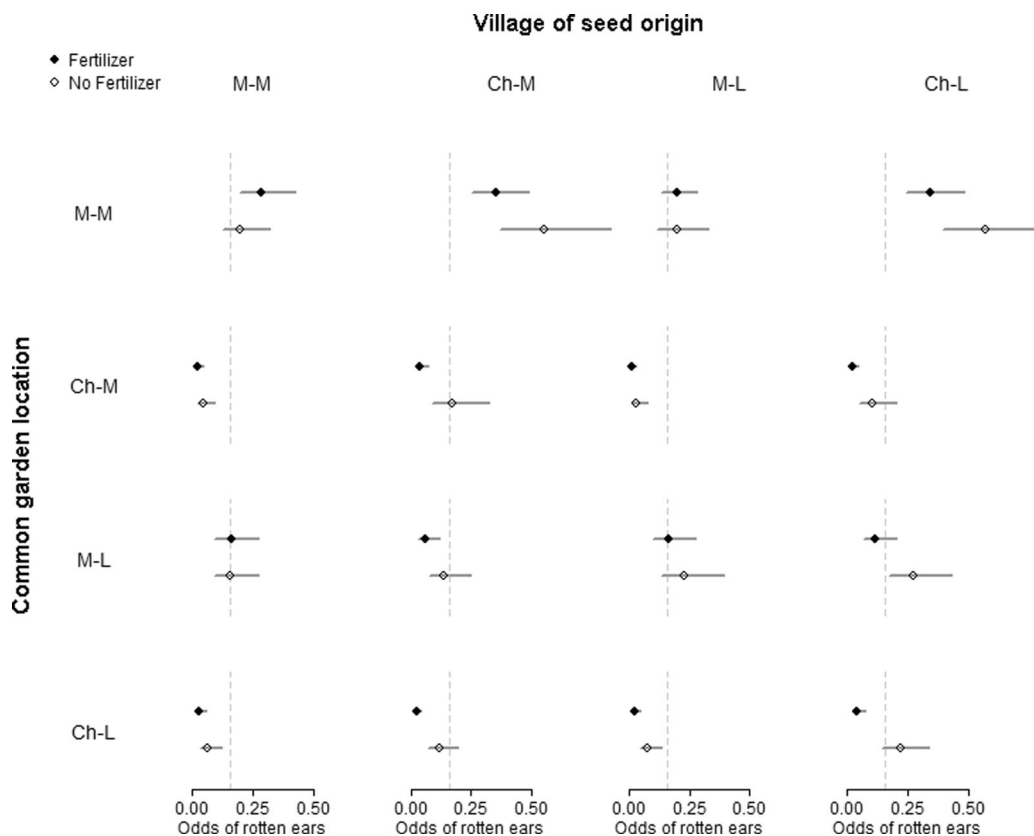
Village of seed origin

Fig. 3. Model estimates and approximate 95% confidence intervals for the four common gardens, showing effects of source of seeds, treatment and site on odds of rotten ears.

they were particularly impacted by ear rot in the M–L common garden.

We cannot say that maize cultivars are generally less susceptible to fungal diseases in their local environments. The results point somewhat in the opposite direction: landraces may be *more* susceptible in their own environments.

Discussion

Our experiments do not support the claim that yield is highest when local seeds are planted in local fields. We therefore suggest that local adaptation for yield is not the main force shaping landrace distribution in these villages.

Table 5. ANOVA FOR EAR ROT MODEL. SEQUENTIAL LIKELIHOOD RATIO TESTS FOR THE ADDITION OF TERMS IN THE ORDER LISTED.

	Chi–square	D F	p–value
Source	23.0	3	<.0001
Site	29.0	3	<.0001
Treatment	17.8	1	<.0001
Source x Treatment	9.2	3	0.0270
Site x Treatment	17.2	3	0.0006
Source x Site	23.3	9	0.0056

Table 6. ESTIMATED EFFECT OF FERTILIZER USE ON ODDS OF ROTTEN EARS, FOR EACH SITE AND SOURCE OF SEED. DIFFERENCE BETWEEN ESTIMATED ODDS WITH AND WITHOUT FERTILIZER, AS A PERCENTAGE OF THE ODDS WITHOUT FERTILIZER.

Site	Village of origin of seeds (source)			
	M–M	Ch–M	Ch–L	M–L
M–M	44%	–36%	–40%	–1%
Ch–M	–53%	–79%	–80%	–68%
Ch–L	–56%	–81%	–82%	–70%
M–L	3%	–55%	–57%	–29%

Because of different fertilizer use between Chatino and Mixtec villages, it is possible that maize selection reflects fertilizer response; however we found that samples from all sources responded positively to fertilizer, although the magnitude of the response varied by source. Looking at the differences in yield with and without fertilizer, samples from Ch–M and M–L had larger increases with fertilizer, although Ch–M farmers use fertilizer regularly while M–L farmers never do. While we do not observe obvious selection bias towards fertilizer response, it is possible that our findings depend partly on the particular soils of our experimental sites and their previous management. Climate does not appear to be involved in the fertilizer response, because Ch–M is located at 1,200 masl and M–L at 500 masl. Fertilizer use increased the differences in yield across all sources.

Resistance to fungal disease appears to be related to soils and management of the field. Farmers in this region know that a field should only be cropped for two years to avoid ear rot, especially in villages where fertilizer is not used. In villages where fertilizer use is regular, fungal infection is more severe in unfertilized fields. However, local seeds do not generally show increased resistance to ear rot. Because of interactions among sites, sources, and fertilizer use, it is difficult to reach a definitive conclusion about the factors that directly affect ear rot.

There is no evidence that samples from mid–elevations yield better at those elevations, or that samples from lowlands yield better in the lowlands. For example, seeds from Ch–L and M–L (lowlands) showed no differences in yield in mid–elevation gardens (M–M and Ch–M) when fertilizer was used. All sources yielded better in Ch–L compared to other sites, since that garden had very good soil. When planted in Ch–L, seeds from Ch–M performed similarly to seeds from Ch–L. The relatively small difference in elevation between our sites (700 meters on average) may be insufficient to reveal environmental adaptation of landraces. Studies in Chiapas suggest that the threshold of adaptation for lowlands and highlands landraces is around 1,400 masl (Mercer et al. 2008). The farmers in our study believe that seeds from lowland areas should not be planted in highland fields (and vice versa), because maize does not yield well when moved between elevations. Farmer surveys revealed that there is, in fact, seed movement from lowlands to middle elevation lands, but no movement in the opposite direction was recorded. It is possible that particular landraces are more affected by the change in elevation, although landraces from the lowlands can typically be planted at mid–elevation with good results (and vice versa). In this experiment, a source effect suggesting adaptation to elevation was not clearly evident, in agreement with other experiments performed at similar elevation ranges (Mercer et al. 2008).

We know that variation in soil quality is a constant, occurring both within and between fields, and that this variation contributes to landrace diversity (Bellon and Taylor 1993). Even though only one field in each village was planted, the complete random blocks design of the experiment appropriately accounted for several components of variance in yield and ear rot. In particular, source by site interactions can be estimated without bias using this design. Moreover, these experiments included sets of five landraces representative of maize variation within villages. Our aim was not to evaluate individual landraces or cultivars but rather the average performance of landraces from different sources. If local adaptation exists, the average yield of local landraces should be better than that of non–local landraces. In support of the village as the unit of analysis for maize diversity studies, Dyer and Taylor (2008) developed a population model based on seed exchange, and found that individual farmers' unplanned actions produced village–level diversity.

In the common garden experiments, we compared different maize races with different yield potentials. For example, *Conejo* is an early–maturing race that produces less than *Olotillo* or *Tuxpeño*, while *Olotillo* is a late–maturing race commonly planted in all four villages. To address the potential impact of race, we fitted the yield model again, using only *Olotillo* observations. Although yield estimates (adjusted means) were larger for the *Olotillo* dataset than the full dataset, the source by site interaction was again non–significant (p–value = 0.2832). All other effects and interactions were supported, with p–values similar to those for the full dataset.

Working in Chiapas, Bellon and Taylor (1993) found that farmers maintain traditional varieties to cope with soil variability. In our study region, improved varieties are not used, and farmers in each village recognize that certain landraces or cultivars are best for each plot in the village. Nevertheless, our common garden experiment suggests that some cultivars are potentially more productive in all four locations. These cultivars may perhaps not be grown across the whole region because they are not available in all villages, owing to seed networks or

cultivar preferences that define the landraces used in each village. This finding does not contradict the results of Bellon and Taylor (1993) because we evaluate groups of cultivars from each village, and measure their average adaptation in each common garden. We do not rule out the possibility that particular cultivars are well adapted, and are the best option for a particular soil and environment in a particular village.

According to Perales et al. (2003), working in the central Mexican highlands, farmers maintain traditional varieties because they combine good agronomic performance with desirable end–use properties, compared to improved varieties. Here, we find that in three villages, non–local traditional varieties might have higher yields than local varieties. However, replacement by these better types has not occurred in the recent past. Similarly, in highland Chiapas, Perales et al. (2005) found that in some cases, landraces from Tzeltal villages outperformed Tzotzil maize in Tzotzil villages. Based on these findings, they argued that ethno–linguistic variation contributes to maize diversity. In our work, we found that landraces from Ch–L, a Chatino village located in the lowlands, performed relatively well in all villages. One could ask why landraces from Ch–L have not replaced other landraces in the area over time. It is particularly important to explain why farmers in M–M, a Mixtec village located at middle elevation, still grow local landraces if more productive landraces are available. To answer these questions, it is necessary to look at seed networks, including the social factors that shape them, and to review the cultural and social factors involved in maize selection, management, perception, and preference. Our results appear to support Leclerc and d'Eeckenbrugge's (2011) G x E x S model for crop diversity dynamics.

In each village, farmers consciously select large, healthy ears as seed sources for the next generation, in agreement with other studies (Louette and Smale 2000). Maize yields have been modified significantly during domestication (Gepts 2004), but this empirical selection has its limits. After a rapid increase during domestication, yield has remained stable over millennia (Troyer 2000). Although ear length is positively correlated with yield (Evans 1993), present–day selection strategies focused only on larger ears do not guarantee higher yields. There is some evidence that farmers are aware of these constraints; van Etten and de Bruin (2007) reported that Guatemalan farmers believe maize varieties cannot be transformed by selection. Seed exchange among villages might be perceived as a way to obtain higher yielding seed, if limits to selection are common knowledge.

In our study, among the reasons to keep or discard a maize variety, farmers always mentioned yield. Yet farmers in some villages do not plant the highest–yielding varieties in the region, implying that other conscious criteria (like morphology or color) as well as unconscious criteria (latent preferences) contribute to the choice of cultivars. Our results, pointing unexpectedly away from selection for yield and disease resistance, suggest that unconscious criteria may contribute in important ways to crop diversity.

Farmer decision–making has important implications for landrace adaptation to climate change. Perhaps the most relevant finding from our experiment is that, although yield is nominally important for farmers, it may be only one of several conscious or unconscious criteria for cultivar choice. Consequently, traits other than yield should be considered in the evaluation of climate change effects on crop diversity (e.g., Mercer et al. 2008). A wider view of the traits relevant to farmers may help explain how they evaluate trade–offs during periods of environmental change, such as the "tolerable" reduction in yield from a familiar landrace, versus the uncertainties and socio–cultural barriers associated with switching to an unfamiliar, but perhaps better–adapted, landrace.

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