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Back to the Origin: *In Situ* Studies Are Needed to Understand Selection during Crop Diversification

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Crop domestication has been embraced as a model system to study the genetics of plant evolution. Yet, the role of the environment, including biotic forces such as microbial and insect communities, in contributing to crop phenotypes under domestication and diversification has been poorly explored. In particular, there has been limited progress in understanding how human selection, agricultural cultivation (soil disturbance, fertilization, and irrigation), and biotic forces act as selective pressures on crop phenotypes. For example, geographically-structured pathogenic, pestiferous, and mutualistic interactions with crop plants have likely given rise to landraces that interact differently with local microbial and insect communities. In order to understand the adaptive role of crop traits, we argue that more studies should be conducted in the geographic centers of origin to test hypotheses on how abiotic, biotic, and human selective forces have shaped the phenotypes of domesticated plants during crop domestication and subsequent diversification into landraces. In these centers of origin, locally endemic species associated with wild ancestors have likely contributed to the selection on plant phenotypes. We address a range of questions that can only be studied in the geographic center of crop origin, placing emphasis on Mesoamerican polyculture systems, and highlight the significance of *in situ* studies for increasing the sustainability of modern agricultural systems.

Keywords: crop domestication, agroecology, evolutionary ecology, biogeography, epigenetics, human culture, insects, microbes

INTRODUCTION

The domestication of crop plants has fundamentally altered the relationship between humans and their environment (Larson et al., 2014). While the genetics of crops domestication has been widely studied for some common plant species (Darwin, 1868; Evans, 1993; Smartt and Simmonds, 1995; Ladizinsky, 1998; Hancock, 2012), the role of ecological interaction within centers of origin in contributing crop phenotypic diversity has been overlooked (Chen et al., 2015; Perez-Jaramillo et al., 2016). Prior to domestication, wild ancestors of crop plants evolved in association with a broad assemblage of microbes and insects, with which they engaged in a range of pathogenic,

predatory, commensal, and mutualistic interactions (Chen et al., 2013; Huang et al., 2016; Perez-Jaramillo et al., 2016). These ecological interactions were almost certainly altered by domestication and when early domesticates were introduced to new locations with unique climates, distinct local biodiversity, and different cultural methods of farming.

The majority of domestication events occurred in specific geographic regions, often within the native range of their wild ancestors (Vavilov, 1926, 1951; Meyer et al., 2012). Despite this, most studies rarely consider whether all interacting species are endemic in the center of origin. We found that only 1.6% of 1,532 studies comparing insect responses on wild and crop plants specifically accounted for biogeographical history (Chen et al., 2015). Geographically-explicit hypotheses are needed to understand _in situ_ crop diversification for two reasons. First, human-mediated migration of crops to new regions within centers of origin influenced the genetic structuring of crop populations. Second, domesticated cultivars experienced novel selective pressures imposed by new environments and the cultural preferences of different indigenous peoples (**Figure 1**; Brush, 1995; Hugo et al., 2003).

In situ field studies documenting variation of ecological interactions are important to determine the extent to which landrace phenotypes respond to local adaptation and artificial selection. After initial crop domestication, early landraces were brought to new environments that were often different from the ecological conditions experienced by their wild progenitors (Hufford et al., 2012). In these new environments, landraces interacted with new species, different cropping system, and new abiotic conditions (**Figure 1**). Also, different groups of farmers may cultivate the same crop in different polyculture systems (Casas et al., 1996, 2007; Hugo et al., 2003), which is the simultaneous cultivation of multiple crops. As a result, landraces emerge over thousands of years due to natural selection exerted by local abiotic conditions, local insect, and microbial communities, as well as human selection on traits related to ease of cultivation, aesthetics, taste, and cultural preferences (Perales et al., 2005; Brush and Perales, 2007; Casas et al., 2007; Aguirre-Dugua et al., 2013).

Here, we discuss the factors that contribute to phenotypic variation in crops and landraces. We examine the role of human selection and niche construction activities on crop phenotypic plasticity, a major factor in local adaptation (Piperno, 2017). We conceptually address two questions that could deepen our understanding of crop evolution and local adaptation: (1) To what extent are crop plants locally adapted? and (2) What are the relative roles of human selection, human-mediated migration, the local abiotic environment, endemic biotic communities, and cultivation practices in the diversification of crops into landraces? We describe polyculture systems in Mesoamerica as a suitable model in which these questions could be pursued. Ultimately, whether plants can maintain historic beneficial interactions with associated species—or form new ones in their introduced regions—have important implications for the future sustainability of agriculture.

GENETIC AND ENVIRONMENTAL CONTRIBUTIONS TO CROP PHENOTYPIC VARIATION

We focus on landraces as a natural experimental system to understand how natural and human selective forces have shaped the diversity of phenotypic traits of domesticated crop plants during local adaptation. In order to detect local adaptation, it is important to characterize the extent of variation and fitness of phenotypic traits in response to local selective pressures (Kawecki and Ebert, 2004). Variation in landrace phenotypes is affected by their genotype, local environmental variation, and plant phenotypic plasticity. Equation 1 describes how the components of phenotypic variation can be partitioned (Pigliucci, 2001):
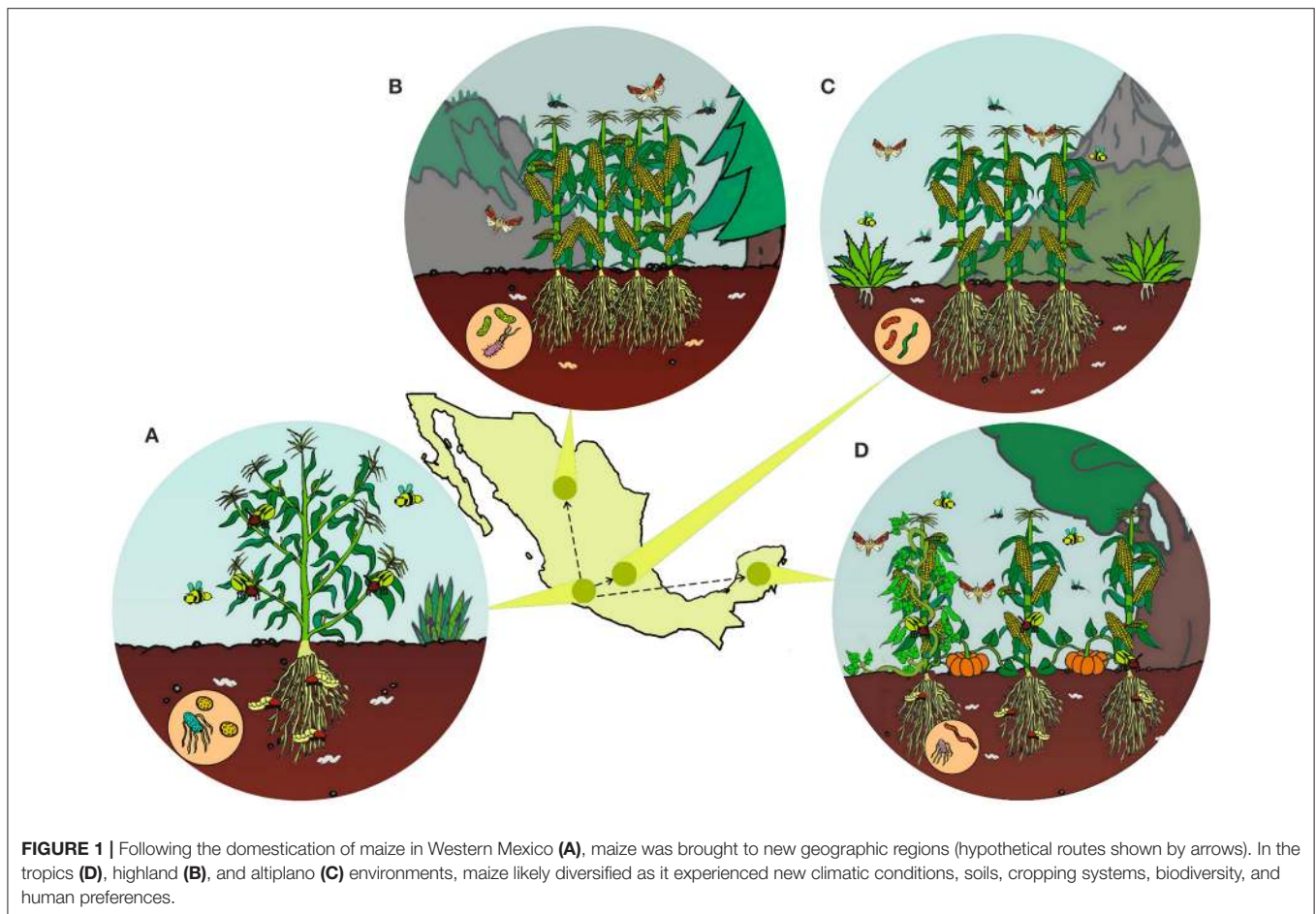
$$V_P = V_G + V_E + V_{G \times E} \qquad (1)$$

Where V_p denotes the total phenotypic variation found for a population or subspecies, V_G is the total genetic variation, V_E is the total environmental variation, and V_{GxE} is the genotype × environment interaction. We limit our treatment of V_p and V_G because they have been discussed elsewhere (Olsen and Wendel, 2013; Piperno, 2017). In contrast, there has been a minimal effort to understand the contributions of V_E and V_{GxE} to crop domestication and diversification. **Table 1** provides a set of examples illustrating the range of plant adaptations to abiotic, biotic, and human selection.

Total genetic variation (V_G) is influenced by evolutionary forces including selection, genetic drift, inbreeding, and gene flow (Hartl and Clark, 2006), which likely differ between wild progenitor and crop populations. Domesticated crops have reduced effective population sizes and are under intense selection for a suite of traits favored by humans (Doebley et al., 2006; Moreno et al., 2006). Cultural factors can also structure landrace populations and dispersal patterns, as people in different ethnolinguistic groups are less likely to trade seeds (Orozco-Ramírez et al., 2016).

The contribution of the environment to phenotypic variation (V_E) strongly differs between wild progenitors and domesticated crops grown in human constructed agricultural niches. In natural systems, V_E is affected by local abiotic conditions such as climate, precipitation, soil type, and nutrient availability. Domesticated crops are found in a range of cultivation systems, where the purpose of cultivation is to lessen the unpredictability of the local environment in order to favor uniform plant growth and yield. Cultivation has been shown to strongly affect plant-associated microbial and insect communities (Berg, 2009; Berendsen et al., 2012; Chen et al., 2013). Surprisingly, the majority of the insect and microbial species associated with a given crop in its center of origin remain undescribed (Chen et al., 2015; Coleman-Derr et al., 2016). Given that plant-biotic interactions can influence plant phenotypes (Henning et al., 2016), human niche activities can indirectly influence crop phenotypes by influencing the diversity and community structure of biotic assemblages.

Genotype by environment interactions (V_{GxE}) describe phenotypic plasticity, or how genotypes responds to a range of environmental conditions. Crops respond to agricultural

FIGURE 1 | Following the domestication of maize in Western Mexico **(A)**, maize was brought to new geographic regions (hypothetical routes shown by arrows). In the tropics **(D)**, highland **(B)**, and altiplano **(C)** environments, maize likely diversified as it experienced new climatic conditions, soils, cropping systems, biodiversity, and human preferences.

conditions differently from their wild ancestors in growth (**Table 1**). Also, plasticity itself may have been constrained by domestication. Wild progenitors may have retained a greater plasticity to unpredictable environments, whereas domesticated may have lost phenotypic plasticity. Growing plants in different environments can provide important insight on the origin of important traits associated with domestication. For instance, teosinte grown under historic Pleistocene conditions (atmospheric CO_2 and temperature) displayed maize-like phenotypes such as reduced tillering, uniform seed maturation, and bract-less seeds (Piperno et al., 2015). Therefore, hypotheses that account for environmental variation and the selective environment can provide important insight on how crop species adapted to divergent environmental conditions.

Crop responses to the environment can be heritable, independent of changes in the DNA sequence, which contributes another dimension to V_{GxE}. An emerging frontier is to understand the role of transgenerational epigenetics in crop adaptation to local environmental conditions (Piperno, 2017). Epigenetics studies can reveal how the environment can shape heritable gene expression (and thus the phenotype) without changing the underlying DNA sequence (Jablonka and Raz, 2009; Laland et al., 2014). Epigenetic changes in DNA methylation can regulate gene expression patterns during stress, which

can influence the ability of crop varieties to respond to local environments (Ferreira et al., 2015). Therefore, *in situ* studies are critically needed to test the relative roles of genetics, epigenetics, and the environment in contributing to crop diversification.

MESOAMERICA AS A FIELD LABORATORY FOR *IN SITU* STUDIES

Centers of domestication offer field locations to understand how local environments and human cultural influences contributed to crop domestication and diversification into landraces. The legendary Russian botanist Nikolai Vavilov delineated eight geographic regions as "centers of domestication" where multiple crop species were domesticated (Vavilov, 1926, 1951). One such center is Mesoamerica, which is the region of origin for maize, beans, squash, peppers, avocado, vanilla, and thousands of non-commercialized plant species (Casas et al., 2007). Crop domestication in Mesoamerica has received far less attention than in other centers of origin (Casas et al., 2007). Mesoamerica is particularly well-suited for field studies on crop domestication and diversification for several reasons: (1) It hosts a dazzling array of landrace varieties that are often cultivated sympatrically with their wild ancestors, (2) It has an archeological record confirming

TABLE 1 | Phenotypic variation (V_P) in wild progenitors and landraces can be attributed to genetic variation (V_G), environmental variation (V_E), and variation attributed to genotype by environment interactions (V_{GxE}).

	Phenotypic variation	Genetic variation	Environmental variation	Genotype × environmental variation
Abiotic	Wild emmer, bean, and lupine populations show adaptations to drought (Peleg et al., 2005; Cortés et al., 2013; Berger et al., 2017).	Drought-resistant wild emmer populations differ in gene expression in stress, transport, and metabolism genes (Huang et al., 2016).	Precipitation is a major factor explaining the wider geographic range of the domesticated Mesoamerican fruit tree, *Spondias purpurea* (Anacardiaceae), compared to its wild progenitor (Miller and Knouft, 2006).	Teosinte growth and a high affinity nitrate transport gene were more highly inducible under low nitrogen availability (Gaudin et al., 2011).
	The common bean, *Phaseolus vulgaris*, shows higher phosphorous efficiency than wild *P. vulgaris* populations (Araújo et al., 1997).	Geographic distribution of genetic diversity in historical barley landraces shows local adaptation to latitude (Aslan et al., 2015).	Temperature plays a major role in structuring the distribution of four early landraces of maize (Hufford et al., 2012).	Teosinte grown under Pleistocene-like climatic conditions produced maize-like phenotypes (Piperno et al., 2015).
Biotic	Wild emmer wheat (*Triticum turgidum* spp. *dicoccoides*) and chili show geographic variation in disease resistance (Tewksbury et al., 2008; Huang et al., 2016).	Wild watermelon roots are resistant to root-knot nematode damage while cultivated species are susceptible (Thies et al., 2016).	Irrigation increases susceptibility to fungal pathogens and increases the risk of fungal pathogen emergence (Stukenbrock and McDonald, 2008).	Wheat genotypes differ in their plasticity in terms of yield and suppression of aphid population growth (Tétard-Jones and Leifert, 2011).
	The microbiome of domesticated barley differs from wild barley (Bulgarelli et al., 2015).	The 6H chromosome of barley, *Hordeum vulgare*, is coevolving with the net form *Pyrenophora teres f. teres* but not the spot form of barley net blotch (Rau et al., 2015).	Cultivated chickpea is extremely susceptible to Ascochyta blight in the Near East in the fall, which selected for spring sowing of chickpea (Abbo et al., 2007).	Domesticated sunflowers respond to nitrogen inputs by developing larger flower heads, which leads to higher sunflower moth, *Homeosoma electellum*, herbivory but lower parasitism (Chen and Welter, 2005).
Human selection	Breadfruit, *Artocarpus altilis* in Oceania are seedless and dependent upon humans for dispersal (Xing et al., 2012). Domesticated lupines, *Lupinus* spp., set seed earlier, produce larger seeds than wild lupines (Berger et al., 2017). In Cassava, *Manihot esculenta*, levels of toxic cyanogenic glucosides are dependent upon local preferences and knowledge on processing (McKey et al., 2010).	A SNP mutation in the promoter region of a P450 gene, CYP78A increases fruit size and reduces branching in tomato plants (Chakrabarti et al., 2013). Several species of domesticated cucurbits show signs of convergent evolution in the interruption of the cucurbitacin biosynthesis pathway (Zhou et al., 2016).	Insect communities are less diverse and show a shift in community composition in cultivated rice agroecosystems compared to wild rice (Chen et al., 2013). Agave grown in cultivated soils have lower diversity of soil prokaryotes in the rhizosphere than those in native soils (Coleman-Derr et al., 2016).	Domesticated chickpea, *Cicer arietinum*, have been selected to be insensitive to veralization compared to their wild ancestor, *Cicer reticulatum* (Pinhasi van-Oss et al., 2016). Maize shows lower tiller plasticity and lower nitrogen use efficiency compared to teosinte. Under low nitrogen, maize plants have lower leaf size (Gaudin et al., 2011). The common bean, *Phaseolus vulgaris*, shows higher phosphorous efficiency than wild *P. vulgaris* populations (Araújo et al., 1997).

Wild progenitors and domesticated crops display adaptive responses to abiotic, biotic, and human selection. Environmental variation (V_E) can be naturally occurring or arise from human niche construction activities. Wild progenitors and domesticated crops show different responses to the habitat conditions within which they evolved (V_{GxE}).

a long history of interactions between humans and many species of crop plants, and (3) Indigenous peoples continue oral and cultural traditions associated with the cultivation of these plants (Gepts, 2004; Staller et al., 2006; Piperno et al., 2007).

We focus on Mexico, the largest country within Mesoamerica, where much of the phenotypic and genotypic variation underlying local adaptation to environments has not been characterized. Many suspected centers of domestication and regions with wild relatives remain poorly explored for most crop plants. These underexplored regions that are historically relevant for the study of crop diversification include: the Balsas River Valley (Piperno et al., 2007), the Gulf Coast (Kraft et al., 2014), and the Tehuacan Valley for species other than maize (Vallejo et al., 2016). Needless to say, there are considerable opportunities to examine the selective forces that produced the extant array of landraces for native Mesoamerican crop plant species.

In Mesoamerica, traditional agroecosystems have been maintained cohesively for hundreds to thousands of years by indigenous peoples. Different cropping systems dominate in different climatic regions (**Figure 1**). In the Yucatan Peninsula, home gardens are highly diverse polyculture systems, and include crops such as avocado, annona, and papaya (Moreno-Calles et al., 2016). The inland and coastal regions are dominated by agroforestry systems paired with ornamental and woody species (Moreno-Calles et al., 2016). The oldest Mesoamerican polyculture systems continue to be maintained in Tlaxcala (Gonzalez-Jacome, 2016). In cold and dry highland environments, prehispanic terraces for water management still exist in Oaxaca and the Tehuacan Valley (Donkin, 1979). In

arid environments, drought-tolerant plants including cactus are cultivated in polyculture with chili pepper and other crops (Moreno-Calles et al., 2012, 2016). Slash and burn agriculture is the most widespread form of cultivation in the tropical deciduous and temperate forests, where crops are rotated after the plant cover is burned every few years. Slash and burn systems can be quite diverse, with at least 57 tree species from 33 plant families and many more herbaceous species (Moreno-Calles et al., 2016).

One of the most dominant cropping system in slash and burn agriculture is the *milpa* (**Figure 1D**), which is, at its most basic, the joint cultivation of maize, beans, squash (Zizumbo-Villarreal and Colunga-GarcíaMarín, 2010). Maize serves as a trellis for beans that fix nitrogen, while squash suppresses weeds. Although, the wild progenitors of maize, beans, and squash are native to separate regions in Mexico (Smith, 1997; Gepts, 2004; Piperno et al., 2007), these core *milpa* crops have been cultivated together for thousands of years. It is highly possible that associated microbes and insects have adapted to the *milpa*. Perhaps it should not be a surprise that the most devastating contemporary native insect pests of maize can all be collected from squash flowers (Metcalf and Lampman, 1989), and that several closely related species of leaf beetles in the genus *Diabrotica* damage maize, beans, and squash (Clark et al., 2001; Vidal et al., 2005; Eben and Espinosa de Los Monteros, 2013). There are many other unexplored questions on crops and biotic interactions in *milpa* systems such as: (1) To what extent have microbiomes, pathogens, mycorrhizae, herbivores, natural enemies, and pollinators adapted to polyculture and landrace traits? (2) Does intercropping select landraces to develop complementary use for light, nutrients, and water? and (3) How has the *milpa* shaped landrace phenotypes?

The present Mesoamerican landscape is also a gradient of ecological contexts where one could study whether genes underlie phenotypes that are adaptive to local abiotic and biotic conditions. Reciprocal common garden studies with maize have found that highland landraces show higher fitness and seed quality in highland conditions, while lowland landraces have higher fitness in mid-altitude locations (Mercer et al., 2008). Traits such as pigmentation, stem hair, plant height, and flowering time have been shown to be adaptive to altitude, but completely different genes underlie local adaptation to highland conditions in Mesoamerica and South America (Mercer et al., 2008). Field sampling of Mexican teosinte populations helped to clarify that maize adaptation to the Mexican highlands resulted due to introgression from wild teosinte (Hufford et al., 2013). Understanding the genomic basis of local adaptation in crops relies on multiple *in situ* localities, where the ecological history can be reconstructed by testing for genomic regions under divergence (Pyhäjärvi et al., 2013), and the responses of candidate genes can be observed in local environments (Doust et al., 2014; Piperno, 2017). Traditional Mesoamerican agroecosystems are living biological and ethnographic systems that are suitable for studying how human-created niches in agroecosystems interact with local biotic and abiotic environments to shape landrace phenotypes. These *in situ* systems provide an important reference for examining how crop plants adapted as they have diversified within centers of origin.

IMPLICATIONS OF *IN SITU* STUDIES FOR SUSTAINABLE AGRICULTURE

Sustainable agriculture aims to reduce reliance on pesticides and fertilizers by utilizing biodiversity to provide ecological services that provision nutrients, protect crops, and enhance yields (Altieri, 1999). For the world's most important crops, the majority of production occurs outside their centers of origin (Khoury et al., 2016). Oftentimes, crops are grown in marginal environments, where they experience low nutrient availability, excess or limited water availability, temperature extremes, or pest outbreaks (**Table 1**). Under climate change, these pressures are predicted to intensify (Hatfield et al., 2010). Perhaps because centers of origin tend to be the geographic source for the major diseases (Leppik, 1970) and insect pests of crops (Chen, 2016), they are also the source for genes for resistance (Harlan, 1976; Hijmans et al., 2003; Zhang et al., 2017), insect natural enemies (van den Bosch, 1971; van Driesche et al., 2008), and microbes (Philippot et al., 2013; Perez-Jaramillo et al., 2016) that help plants to resist pests and tolerate abiotic stress.

In situ studies can also provide insight on whether human selection for crop yield is fundamentally at odds with traits that mediate beneficial plant-biotic interactions. First, crop domestication appears to have promoted pests more frequently than beneficial species, especially for economically-important traits such as fruit size and seed size (Chen et al., 2015). However, we do not know if direct trade-offs between yield and pest resistance exist, and whether this relationship may vary with different landraces and environments within centers of origin. The diversity and community structure of microbes and insects associated with wild ancestors and landraces have been inadequately described (Chen et al., 2013; Perez-Jaramillo et al., 2016), and geographic variation in patterns of biodiversity within centers of origin remain unexplored.

Second, plant genotypes vary in their ability to form positive relationships with beneficial species (**Table 1**; Smith and Goodman, 1999; Chen and Welter, 2005; Tamiru et al., 2011). Determining the relative roles of plant genetic diversity, microbial associates, and plant gene × environment interactions in conferring resistance to biotic and abiotic stresses (Philippot et al., 2013) would help elucidate whether breeding, microbial inoculation strategies, or natural enemy introductions would better support crop production in the diverse environments where crops are grown. Finally, *in situ* studies provide insight on the ecological function of crop genes and metabolites within their natural environment, which are oftentimes only explored in environments far from centers of origin. For examples, teosinte and some maize varieties emit the sesquiterpene (*E*)-β-caryophyllene, which attracts entomopathogenic nematodes (Rasmann et al., 2005) and parasitoids (Kollner et al., 2008) in Europe. However, the role of this compound in landraces is not known, especially in Mesoamerica, where a diverse assemblage of species may be adapted to respond to plant signals. *In situ* studies can help resolve whether landrace varieties produce the compound, natural enemies are attracted to it, and whether breeding for (*E*)-β-caryophyllene would increase natural enemy

attraction and enhance yield in the diverse worldwide locations where maize is now grown.

CONCLUSIONS

In situ ecological studies are an essential, but almost completely unexplored line of inquiry for evolutionary ecologists to understand the selective forces that contribute to local adaptation of landrace varieties. As one of the major centers of crop origin, Mesoamerica is an ideal location for *in situ* studies, because wild progenitors can be found growing sympatrically with domesticated landrace varieties cultivated in traditional polyculture systems. For many crops and cultivation systems, the unique combination of local abiotic, biotic, and cultural selective forces that shaped variation in crop phenotypes during domestication and diversification continue to coexist. We advocate that geographically-explicit studies will yield new insight into how selection from humans and the local environment contribute to landrace diversification and local adaptation. Such knowledge is immediately applicable toward understanding the capacity of crop plants to respond to the biotic

and abiotic conditions over the vast geographic ranges where they are now grown, and to identify sources of germplasm that might have adaptive traits for crops in their introduced ranges.

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