

## SYNTHESIS

## Evolutionary response of landraces to climate change in centers of crop diversity

Kristin L. Mercer<sup>1</sup> and Hugo R. Perales<sup>2</sup>

<sup>1</sup> Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH, USA

<sup>2</sup> Departamento de Agroecología, El Colegio de la Frontera Sur, San Cristobal, Chiapas, Mexico and Diversity for Livelihoods Programme, Bioersity International, Rome, Italy

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### Correspondence

Kristin L. Mercer, Department of Horticulture and Crop Science, The Ohio State University, 202 Kottman Hall, 2021 Coffey Road, Columbus, OH 43210, USA.  
Tel.: 614-247-6394; fax: 614-292-7162;  
e-mail: mercer.97@osu.edu

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### Abstract

Landraces cultivated in centers of crop diversity result from past and contemporary patterns of natural and farmer-mediated evolutionary forces. Successful *in situ* conservation of crop genetic resources depends on continuity of these evolutionary processes. Climate change is projected to affect agricultural production, yet analyses of impacts on *in situ* conservation of crop genetic diversity and farmers who conserve it have been absent. How will crop landraces respond to alterations in climate? We review the roles that phenotypic plasticity, evolution, and gene flow might play in sustaining production, although we might expect erosion of genetic diversity if landrace populations or entire races lose productivity. For example, highland maize landraces in southern Mexico do not express the plasticity necessary to sustain productivity under climate change, but may evolve in response to altered conditions. The outcome for any given crop in a given region will depend on the distribution of genetic variation that affects fitness and patterns of climate change. Understanding patterns of neutral and adaptive diversity from the population to the landscape scale is essential to clarify how landraces conserved *in situ* will continue to evolve and how to minimize genetic erosion of this essential natural resource.

### Introduction

Crop genetic resources are indispensable for humanity's well-being and future food security demands their conservation (CBD 1992; Gepts 2006). The last 50 years has seen a largely successful, worldwide campaign for *ex situ* conservation of crop genetic resources; thousands of samples are now stored in germplasm banks around the world (Rao and Hodgkin 2002; Gepts 2006). Although considered untenable in the past (Frankel 1970b; Hawkes 1983; Williams 1984), *in situ* (or on-farm) conservation of crop genetic resources – particularly of landraces and wild crop relatives – is now recognized as a crucial complement to *ex situ* conservation (Bretting and Duvick 1997; Maxted et al. 1997). Although almost all intensive, large-scale agriculture is planted to commercial seed developed by the seed industry, cultivation of landraces remains common in many regions of the world, particularly in crop centers of origin or diversity. For example, at the end of the 20th century, less than one quarter of Mexico's 8 million ha of maize were planted with commercial cultivars (Aquino et al. 2001); the rest were

planted with farmer-saved seeds. Such *de facto in situ* conservation of crop genetic resources has been explained in several ways (Brush 1995; Frankel et al. 1995; Bellon 1996; Byerlee 1996). We think it is best studied through an evolutionary lens.

The genetic variation found in crop centers of diversity, the key target of *in situ* conservation, has been shaped over time by farmers, the environment, and random evolutionary processes (Brush 2004). The initial domestication of wild relatives into crops that could be grown, harvested, and cleaned for consumption represents intense farmer-mediated selection. Natural selection by dynamic environmental conditions occurred continuously, facilitating the global spread of crops from their centers of origin (Harlan 1992). This combination of human-mediated and natural selection continues as farmers select for traits of interest (Louette and Smale 2000), while the environment selects for traits that augment fitness (Cleveland and Soleri 2007). Gene flow through cross-pollination and seed exchange encourages novel variation and recombination, as well as differentiation among populations when gene flow is restricted. Mutations also introduce novel variation and

genetic drift affects neutral allele frequencies, especially in small populations. Taken together, these factors produced a dizzying array of landrace diversity in many crop centers of origin (Wellhausen et al. 1952) and continually reshape that diversity now.

By landrace, we mean '...a dynamic population(s) of a cultivated plant that has historical origin, distinct identity, and lacks formal crop improvement, as well as often being genetically diverse, locally adapted, and associated with traditional farming systems' (Camacho Villa et al. 2005). Landraces exist on a continuum with improved varieties, which can be considered the product of scientific breeding methods. We use 'landraces' to distinguish our subject from improved varieties and 'landrace population' to connote a particular seed lot used by an individual farmer. Each individual landrace population can also fall within a named category used by farmers (e.g., Late Yellow; Benz et al. 2007) or a particular scientific racial category (e.g., Tuxpeño or Zapalote Chico; Wellhausen et al. 1952). Landraces tend to possess significant phenotypic variability and some have developed tolerances to particular abiotic and biotic stresses, such as disease resistance or cold tolerance (Eagles and Lothrop 1994). Many landraces are lauded for their yield stability despite lax weed control or poor soil conditions (Cleveland et al. 1994; Hammer and Diederichsen 2009). Groups of landrace populations within some centers of origin operate as metapopulations (Dyer and Taylor 2008; van Heerwaarden et al. 2009a) since gene flow between populations is common. Gene flow can occur between landrace populations and improved varieties, a process which produces a hybrid swarm with introgression of modern alleles (Bellon et al. 2006).

As we discuss evolutionary concepts as applied to domesticated species, terminology regarding individual plant and crop population performance becomes complex. In different contexts, fitness, yield or productivity could be used. We use fitness to describe effects on survival or fecundity of individual plants, especially as it relates to evolutionary processes. When addressing issues of food production, or how a farmer conceives of his or her field, we will use productivity or yield.

### The climate challenge

The world's climate is projected to change radically. Along with increases in CO<sub>2</sub> in the atmosphere, the world expects a 3–5°C increase in temperature, as well as altered precipitation regimes in the next half century (see IPCC 2007). For some locations, expected temperatures by the end of the century may not overlap with current temperatures (Battisti and Naylor 2009). Climate change will almost certainly have significant effects on the productiv-

ity and composition of managed ecosystems; agricultural food and fiber production may be affected profoundly. Nearly every abiotic factor that influences agricultural production will shift (Fuhrer 2003), along with responsive biotic factors, such as disease (Goudriaan and Zadocks 1995) and herbivores (Zvereva and Kozlov 2006). Yet we have little information about how these compositional and productivity shifts will affect agroecosystems where *in situ* conservation of landraces is practiced.

There is a rich literature using improved varieties in highly controlled growth chamber and field experiments that examines how changes in CO<sub>2</sub> concentration, higher temperatures, and altered moisture may affect crop production (reviewed in Hatfield et al. 2008). From these studies, certain patterns are clear: C3 crops seem to benefit more than C4 crops from increases in CO<sub>2</sub>; temperature increases are better tolerated at high latitudes than low latitudes (where crops are already stressed). Scholars have used these data, as well as historical production and weather data, to speculate on the future productivity of the world's major crops under conditions of climate change (Naylor et al. 2007; Ziska and Bunce 2007; Challinor et al. 2009). For instance, Lobell et al. (2008) were able to identify 'at risk' crops and regions where climate change could increase hunger by reducing yields of essential crops. Such analyses are invaluable for anticipating variability in food supplies in an era of climate change.

Although some have emphasized the need to breed crops for future climatic conditions (Cutforth et al. 2007; Naylor 2007; Araus et al. 2008), much of the world's farming population relies on landrace populations, not formal breeding networks (Almekinders et al. 1994). Especially in centers of crop origin and diversity (Harlan 1971; Vavilov 1987), we should reflect upon how landraces conserved *in situ* will tolerate and adapt to climatic change. Whether we consider maize in Mexico, cassava in Brazil, teff in Ethiopia, or wheat in Turkey, the responses of landraces – and the farmers who grow them – will determine much about the genetic resources available for the world's agriculture. To our knowledge, few authors have analytically examined the role that genetic diversity could play in weathering climatic change, and how the diversity of traditional varieties grown by the world's peasant and subsistence farmers will respond. Due to the great risks for genetic erosion, this is our aim.

Our central question is: How will climate change affect the productivity, diversity, and conservation of crop landraces? We will pursue this question in three parts. First, we will discuss the expected responses of crop diversity to climate change and the ways that empirical data can help us understand them. Second, we will explore which factors will determine the expected response. Third, we will

discuss the potential for genetic erosion and impacts on the *in situ* conservation of crop genetic resources.

We draw principally on examples from the well-studied system of maize in Mexico. Although not all patterns seen in maize from this region can be generalized to other crops, the wealth of knowledge gained about Mexican maize landraces provides keen insights for other crops and regions. Throughout this article, we will draw parallels to, or contrasts with, other crops or regions. Yet, effects of climate change on the diversity of different crops in different areas will necessarily vary depending on particular patterns of genetic diversity and climatic change. Thus, maize in Mexico can only serve as a general guide.

### Biological responses to climate change

How might landrace populations in centers of crop diversity respond to environmental change? As we have seen in discussions of responses of natural ecosystems to climate change (Jump and Peñuelas 2005; Parmesan 2006), there are four main possibilities. In particular, phenotypic plasticity, evolution, and gene flow are possible avenues for surviving major shifts in biotic and abiotic conditions, although each presents its own uncertainty. Of course, extinction is another possible outcome. We explore each in turn.

#### Plasticity

Plants can adjust their phenotype in response to different environmental conditions (Sultan 1995). Despite the genetic basis for phenotypic plasticity, a plastic response of this nature does not require changes in gene frequencies (i.e., evolution). In some cases, such phenotypic shifts can allow current populations to maintain their fitness as conditions change. In particular, environmental shifts result in phenotypic changes in some trait, which can in turn maintain plant fitness. Therefore, as climate changes, phenotypic plasticity may 'buffer' landrace populations and allow them to continue yielding as before due to a plastic response to the new environmental conditions (Scheiner 1993). For instance, in response to increased temperatures, a crop plant will probably respond through shifts in its morphology, phenology, or development, which may help it maintain fitness. The ability of a given plant or landrace population to maintain fitness will depend on its norm of reaction, or how the phenotype of traits which increase fitness change under different environmental conditions (Stearns 1989). Little change in productivity with changes in environmental conditions could indicate a plastic response without necessarily clarifying the traits responsible. Plasticity can also be selected for, as we explain below.

To maintain productivity with climate change through phenotypic plasticity, landraces would have to respond plastically to multiple environmental changes at once (e.g., concurrent CO<sub>2</sub> and temperature increases). Unfortunately, a particular plastic response may be beneficial in response to one environmental cue, but detrimental in response to another. For instance, plasticity of internode length in shade avoidance responses has been shown to collaterally reduce drought tolerance (Huber et al. 2004), indicating that plastic responses are not free of consequences. In a study aiming to mimic global change, Fraser et al. (2009) predicted that plastic increases in stomatal density could be adaptive in the face of concurrent moisture and temperature shifts. They expected increases in stomatal density to be beneficial with increases in temperatures, albeit detrimental under conditions of increased precipitation predicted for some regions. In an experimental setting, they found that the plastic response of stomatal density in wild populations of bluebunch wheatgrass was limited to water additions, not temperature increases. Specifically, physiological change of increased stomatal density was somewhat greater at intermediate stress levels (reduced moisture, control temperatures) than at high stress levels (reduced moisture, increased temperatures), suggesting a possible physiological or ecological constraint on expression of putatively beneficial plasticity. However, without any analysis of how the ability to alter stomatal density affected fitness, it is difficult to estimate the contribution of particular phenotypic changes to variance in fitness. Studies of landraces populations employing various conditions – across years, locations, or with experimental treatments mimicking climate change – where fitness, and traits with effects on fitness, are measured, can clarify the range of environments under which landrace populations may be able to maintain fitness, and how.

#### Selection

Changes in environmental conditions could also induce crop landraces to evolve, which may allow for maintained productivity. In other words, landrace populations could 'keep up' with climate change as the result of selection on beneficial characteristics, resulting in population level changes in allele frequencies at loci controlling these traits. For such selection to occur there must be sufficient genetic variation within the landrace population; moreover, this variation must be correlated with fitness under the new conditions. We would then expect a response to selection by shifts in the landrace population's mean phenotype. The degree of response in phenotypic traits and the relationship of these traits to fitness would dictate the corresponding response in crop fitness.

Due to a simple lack of genetic variation, there may be few opportunities for selection in landrace populations of particular species. Clonally propagated crops and those with self-pollination systems would be expected to have more variation among populations that within them. At the extreme, selection may operate by eliminating entire populations (i.e., clones), rather than causing genetic shifts within populations.

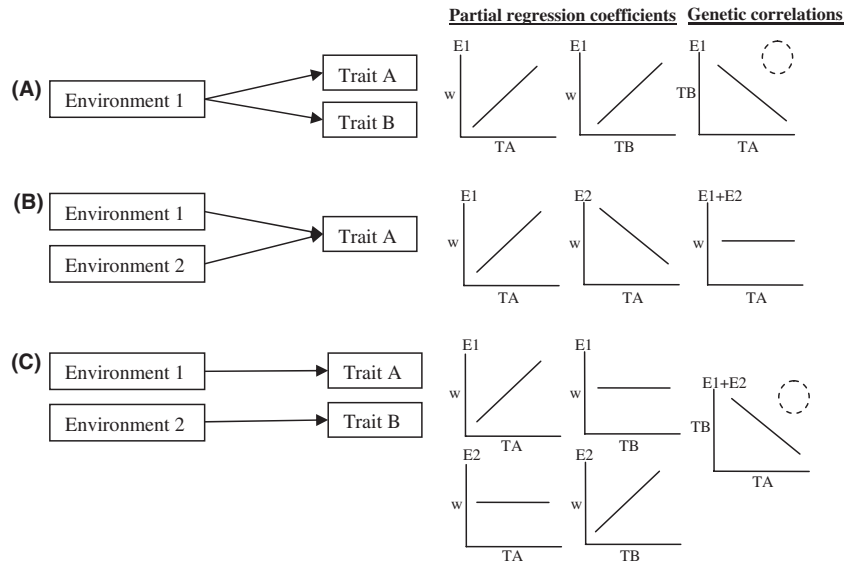
We have evidence of natural selection by environmental clines having acted on crop landraces (Eagles and Lothrop 1994), as well as evidence of selective sweeps thought to have taken place during the process of domestication (Burke et al. 2005; Buckler and Stevens 2006). Studies by plant breeders document selection on breeding populations (e.g., high and low oil corn lines from Illinois; Dudley et al. 1977; Dudley and Lambert 1992; and others). Overall, adaptive differentiation, seen as variability in heat tolerance and disease resistance (among others), attests to past selection by important determinants of fitness. For instance, maize races are found to inhabit different environmental conditions (Corral et al. 2008); molecular analyses of crop races have established groupings based on particular environmental tolerances (Doebly et al. 1985; Sanchez et al. 2000); and breeders have quantified genetically based differences among highland and lowland landraces of maize (Eagles and Lothrop 1994; Jiang et al. 1999). Recent work with candidate gene loci has begun to describe large-scale geographic patterns of putatively adaptive genetic variation. Ducrocq et al. (2008) have shown, for example, that a particular allele at a flowering time locus, *Vtg1*, in maize is more frequent in high latitude and high altitude populations globally, presumably due to the adaptive significance of early flowering under such conditions. Yet little testing has been done to assess the degree or patterns of local adaptation on the landscape. Mercer et al. (2008) found greater local adaptation of highland than lowland landraces of maize in southern Mexico (see section 'Patterns of adaptive genetic diversity' below), but we have much to learn about geographical and annual patterns of ongoing natural selection.

Although adaptive evolution has occurred in the past within and among landrace populations, continued evolution with climate change could be limited in a number of ways (Antonovics 1976), including negative genetic correlations, contradictory farmer selection, or contradictory responses involving interspecific interactions. Responses of multiple traits to selection from a single environmental factor can be constrained by negative genetic correlations among those traits (Falconer and Mackay 1996). For instance, hotter temperatures could select for faster growth rate and smaller leaves in crop landraces, but if these two traits have a negative genetic correlation, responses to selection will be retarded (Etterson and Shaw

2001). This retardation could restrain the landrace population from what might be expected to be an optimal phenotype with the highest fitness (Fig. 1A). Such 'antagonistic' correlations may be based on negative genetic linkage or pleiotropic effects (Baatz and Wagner 1997). The fact that climate change will alter multiple conditions at once complicates the picture further since the question then becomes: will populations be able to evolve optimally to multiple conditions, given their responses to selection on one trait due to changes to a single environmental factor? They may not have the appropriate structure of their genetic variation to be able to respond to multiple selection pressures at once. For instance, landrace populations may be limited in their evolution if these selection pressures select in opposite directions on the same trait (Fig. 1B). Alternatively, the traits that are being selected upon by multiple conditions could be negatively correlated (as above), constraining their response (Arnold 1992; Etterson and Shaw 2001; Fig. 1C).

In some ways, landraces may have an advantage over improved varieties since they tend to have relatively high levels of genetic variation (Tang and Knapp 2003; Reif et al. 2004; Yamasaki et al. 2005; Warburton et al. 2008), which could be a source of adaptive variation (Altieri and Koohafkan 2008). Whether each landrace population from any number of races within a crop species or from any given species has the necessary genetic variation is another question. Studies of breeding populations generated from landrace accessions may provide information on variation in traits that could be adaptive under a changing climate (e.g., Lafitte and Edmeades 1997). But whether the information would be relevant under conditions in farmers' fields or across a varied landscape depends on how sensitive heritabilities are to environmental conditions. In particular, stressful conditions that accompany climate change could alter additive genetic variance within landrace populations, affecting their evolutionary potential (Bennington and McGraw 1996; Hoffman and Merilä 1999; Visscher et al. 2008). Consistent selection pressure could also reduce genetic variances and change patterns of covariation among traits, so estimation of responses to selection over time may be even more difficult (Arnold 1992; Etterson and Shaw 2001).

We are aware of few studies that examine whether and how plant populations in general, or landrace populations in particular, may evolve in response to multiple environmental changes simultaneously. Most studies combine a suite of selection pressures, comparing selection in one location (with its suite of environmental factors) with another (with its own suite of factors). Or, if they do separate out different conditions and investigate differences in selection across environments (Donohue et al. 2000; Stanton et al. 2000, 2004), there is a focus on the strength



**Figure 1** Constraints on response to selection with climate change. (A) Selection on traits (TA or TB) in response to a single environmental factor (E1), depicted here as the relationship (partial correlation coefficients) between trait values and fitness ( $w$ ), can be constrained due to negative genetic correlations between TA and TB. (B) Contrary directions of selection on a single trait (TA) by multiple environmental factors (E1 and E2) can result in no net selection on that trait when both environmental factors are present (E1 + E2). (C) Selection on one trait (TA) by one environmental factor (E1) and selection on another trait (TB) by a second environmental factor (E2) could be constrained by negative genetic correlations between TA and TB when both environmental conditions are present (E1 + E2). Dashed circles represent optimal phenotypes expected to be selected for based on the partial regression coefficients.

and direction of selection in the different environments, albeit with little focus on how selection may be constrained by treatment combinations. Stanton et al. (2004) studied the selection operating in field plots where light levels and density of interspecific competitors were varied and found that patterns of selection varied. In this case, it did not appear that differential selection across controlled conditions resulted in constraints on evolution for a given trait. Another study investigated the independent and joint selection on a native plant by an invasive plant and an invasive herbivore (Lau 2006). Despite the lack of evidence for evolution of the native in response to the serial invasion by multiple species, experimental removal of the herbivore revealed underlying adaptation to the plant invasion. In other words, the native population appeared to have previously evolved to better tolerate the plant invasion, but the insect invasion, with its novel selection pressures, may have reversed or masked evolution due to direct trade-offs, indirect effects through the plant invader, or feeding preferences (Lau 2006). This provides a case where evolution in response to multiple novel conditions may constrain adaptive evolution.

Farmer-mediated selection may also contradict natural selection. Natural selection operates on traits which, at least in part, positively affect seed production and farmer-mediated selection in many crops is primarily for higher yield per plant (e.g., ears with many seeds). Thus, traits

which increase fecundity should be under similar patterns of selection by both natural and farmer-mediated selection. For instance, farmers select for larger volunteer seedlings in cassava due their greater vigor (Pujol et al. 2005); natural selection might also do the same since those larger seedlings would be better competitors, possibly able to produce more or bigger tubers. Yet, this might not always be the case for all traits. Take a hypothetical example. A characteristic like grain size may be selected for in a positive direction through natural selection due to its influence on successful seedling establishment, yet in a negative direction by farmer-mediated selection in varieties where smaller seed size is valued. Or under conditions of climate change, farmers could select for seed characteristics, such as grain size, which, if negatively correlated with the tolerance to heat during the grain filling stage, could reduce the populations' productivity in high temperatures. In this way, natural and human-mediated selection may contradict one another.

Interspecific interactions could also constrain future evolutionary responses (Antonovics 1976). As biotic conditions, such as competitor, herbivore, and pathogen communities, shift with new environmental conditions (Fuhrer 2003), there may be evolutionary responses in crop populations. Herbivore communities associated with a particular crop may shift if physiological tolerances of insect species make them more or less abundant in a

given area, or if changes in plants newly encourage or deter particular insect species (Zvereva and Kozlov 2006). Traits that improve crop fitness in the presence of new pathogens or competitors could oppose those that are required to face the new environmental conditions. For instance, due to linkages or negative correlations, selection for novel pathogen resistance might not be able to proceed along with selection for tolerance to high temperatures due to negative correlations in necessary leaf characteristics (see Fig. 1C).

Experiments which measure selection (both natural and farmer mediated) within landrace populations are sorely needed. Experiments performed across years, environments, or with relevant treatments would be especially enlightening. Contemporary selection has only rarely been measured in landrace populations, with the focus on farmer-mediated selection. Louette and Smale (2000) were able to show that selection by maize farmers in Mexico concentrated more on ear characteristics than whole plant characteristics. Assessments focused on how much farmers changed the composition of the populations, as opposed to quantifying selection pressures, *per se*. Pujol et al. (2005) showed that the larger and more heterozygous volunteers were selectively maintained in French Guianan cassava fields and quantified selection on heterozygosity. However, we still lack comparisons of the strength and direction of human-mediated and natural selection acting on landrace populations across environmental gradients.

### Gene flow

Migration or gene flow could facilitate adaptation and maintenance of productivity with climate change because gene flow can introduce novel variation into landrace populations on which selection can act (Davis et al. 2005; Jump and Peñuelas 2005). (Mutation can also introduce novel and potentially adaptive variation, which could be selected upon as climate shifts.) In contrast, gene flow could constrain adaptation if there is repeated introduction of alleles from maladapted landrace populations. If adaptive alleles exist within some distance, they could be directly (or via a bridge population) available to a population in need (Morjan and Rieseberg 2004). Pollen or seed movement can introduce alleles to a new population through interbreeding or simply allow for colonization of new areas, allowing the population to exist in environments that maximize fitness (Jump and Peñuelas 2005). Thus, gene flow may be key to the maintenance of productivity with climate change.

Gene flow between, within, or among geographic regions can occur naturally or with human influence in centers of crop diversity. Pollen-mediated gene flow, arising

through hybridization, occurs at different distances depending on the crop's mode of pollination (wind, insect), the pollen's ability to disperse, and the degree of cross-pollination normally found in the crop. For instance, maize – a wind pollinated, primarily outcrossing, monoecious crop, with heavy pollen – hybridizes primarily within 10–20 m of the pollen donor, although longer distance hybridization is possible (Ma et al. 2004). However, flowering time must also overlap for gene flow by pollen to be successful. Genetic variation in this trait (Pressoir and Berthaud 2004b) or timing of planting can influence this overlap and farmers have been known to manipulate synchrony to increase or decrease hybridization (Bellon and Brush 1994). Expected changes in crop phenology, including flowering time, with altered environmental conditions (Craufurd and Wheeler 2009) could affect gene flow patterns (Franks and Weis 2009). If some landrace populations responded more strongly than others (e.g., cold-adapted types), synchrony of flowering among landrace populations could be affected, increasing or decreasing hybridization accordingly.

Of the evolutionary forces acting on crop landraces, we probably know the most about gene flow. Due to interest in how farmers manage their diversity, it has been studied from both anthropological and molecular perspectives (Louette and Smale 2000; Barnaud et al. 2007). Farmer seed networks have been well-explored; even more, neutral genetic structure, best elucidated using molecular markers, such as isozymes or SSRs, can be analyzed for patterns of gene flow. In this way, marker data indicate opportunities for movement of neutral alleles across a landscape and the structure of neutral genetic diversity. Maize is especially well studied. Some authors have assessed large-scale, long-term, historical gene flow since domestication (Matsuoka et al. 2002; Vigouroux et al. 2008). At a continental scale, Vigouroux et al. (2008) found that geographic distance best correlated with genetic distance resulting in patterns of isolation by distance. Genetic distance was lower, but rose most quickly with geographic distance within 50 km, while continued to increase more slowly at greater distances (to at least 6000 km). This pattern could be linked to seed sharing attenuating with distance and should be further investigated. A regional study focusing on the highlands of Guatemala determined that gene flow was not only distance dependent, but also environmentally dependent: less gene flow occurred among landrace maize populations at high elevations than at low elevations (Van Etten et al. 2008). On an even smaller scale, Pressoir and Berthaud (2004a) worked with 31 populations from six neighboring villages and found little among-population differentiation ( $F_{ST} = 0.011$ ), no isolation by distance, and small among-village differentiation ( $F_{ST} = 0.003$ ). There are few cases

where this kind of intensive assessment of neutral alleles is paired with analyses of patterns of adaptive diversity, such as candidate genes (but see Pressoir and Berthaud 2004a,b).

Farmers' seed networks control seed-mediated gene flow, which dominates longer distance dispersal. For maize in Mexico and Guatemala, most seed is exchanged within a community, with infrequent exchange of seed between people at greater distances (Perales, unpublished data; Van Etten et al. 2008). Because most seed-mediated gene flow requires human agency, we would not expect it to reach necessarily a new optimum as climate shifts without intentional changes. Such 'assisted migration' (McLachlan et al. 2007) or 'assisted colonization' (Hunter 2008) may be adjusted toward adaptive ends in cropping systems of centers of crop origin by facilitating a more evolutionarily responsive distribution of crop diversity on the landscape. However, it would require a strategy informed by understanding of how to best face changing conditions.

### Extinction

Whether or not there are constraints on evolution in response to the abiotic and biotic alterations that accompany climate change, adaptation may not keep up enough to maintain fitness (Davis et al. 2005; Jump and Peñuelas 2005). Phenotypic plasticity and gene flow may not produce environmentally suited phenotypes or the necessary genetic variation. In this scenario, falling yields in landrace populations would cause great concern for farmers' households and their livelihoods. In their attempt to maintain yields, farmers would undoubtedly consider switching seed sources and discarding their unproductive landrace populations. Thus, reductions in crop productivity could result in the loss of certain landrace populations, entire races, or whole species. A complete treatment of how the response of farmers to climate change could affect the diversity encompassed by landrace populations is outside the scope of this article. However, we will discuss it briefly here since genetic erosion could devastate future sustainability of cropping in centers of origin by reducing the diversity available for future farmer-mediated crop evolution, as well as reducing diversity available for future breeding efforts.

Extinction in crops is strongly shaped by farmers' perception of utility. The decision to retire seed from a particular landrace populations or discard a species altogether would likely be determined by economic and social factors, in addition to productivity *per se* (Perales et al. 1998). The likely loss of landrace populations with climate change, and resulting genetic erosion, can be likened to the expectation that modernization of agriculture

would inevitably replace landraces with modern cultivars (Frankel 1970a). The social, economic, and agronomic conditions in many, but not all, locations have retarded this process (Perales et al. 2003b). For farmers to discard their landrace populations as climate shifts would require awareness of alternative landrace populations, commercial cultivars, or other crop species whose cultivation would bring greater certainty of success. Farmers would probably rely on their current seed networks for sources of new seed (Brush and Perales 2007; Sperling et al. 2008), unless novel conditions induced a change in those human systems. Data on frequency of crop switching could be informative (Dyer and Taylor 2008): it may be possible to learn through interviews whether farmers have recently begun to discard their current landrace populations and seed new ones in response to increased yield variability, and to ascertain the kinds of conditions that generally induce them to do so. This could also clarify how quickly such a change could occur.

### Factors determining responses to climate change

We can expect considerable variability in how these four outcomes combine for a given crop in a given region. For instance, in one crop, evolution within landrace populations might be the most common result; with another, extinction may be most likely outcome. This raises the question, which factors will shape a particular response? The patterns of response across centers of crop diversity will depend largely on two main factors: (i) the distribution of genetic variation that affects plant productivity and survival and (ii) actual patterns of climate change and, thus, selection. We recognize that farmer responses will also strongly determine the outcomes, but must be reserved for further discussion elsewhere. Box 1 highlights the research questions and interventions that would best address these issues.

### Patterns of adaptive genetic diversity

The same factors structure diversity across crop types and regions. However, it is the specific character of each crop – both biological and social – that determines the distribution of its genetic variation across the landscape. The particulars of the mating system (i.e., whether it is selfing or outcrossing and whether the crop is propagated by seed or clones) will affect whether the variation is distributed among populations or within populations (Hamrick and Godt 1996). The diversity within populations of outcrossing, seed propagated crops would tend to be the highest, likely allowing for more evolutionary capacity. Selfing or clonally propagated crops would have less variation within the population and more among popula-

**Box 1.** Research questions on genetic structure and implications of various climate change patterns to understand how landraces in crop centers of diversity may respond to climate change. Applicable to all crops in all centers of diversity.

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#### Genetic structure

- Is available genetic variation appropriate for evolutionary response to climate change, especially for selfing or clonal crops?
- At what rate will evolution proceed given heritability of traits and strength of selection?
- Might there be constraints on evolution to multiple environmental changes given the genetic correlations among traits?
- Is there capacity for evolution of plasticity?
- Might populations be plastic in response to climate change, especially for selfing or clonal crops?
- Will different types within a species, or landraces from different regions, respond differently?
- Will adaptive or novel variation be available to populations for evolution based on patterns of gene flow and mutation rates?
- Would gene flow from improved varieties improve or reduce the evolutionary potential or plastic response of landrace populations?

#### Climate change patterns

- What aspects of climate change will impose directional, disruptive, or fluctuating selection?
  - Could selection be strong enough to reduce genetic variation within or among populations?
  - Could it reduce effective population size or cause major mortality, which should reduce genetic variation?
  - Would yearly variability in selection reduce genetic variation or lead to greater plasticity?
- 

tions. For crops with genetically depauperate landrace populations, selection may act to eliminate or maintain them based on their existing levels of adaptation to novel conditions, rather than selecting within the population for a more optimal phenotype. Centers of diversity, which typically encompass a range of environmental conditions, may currently have, or evolve to have, locally adapted landrace populations or phenotypically plastic ones depending on the levels of gene flow between populations, the degree of environmental heterogeneity, and the costs of plasticity (Sultan and Spencer 2002). Areas that have recently experienced strong bouts of selection or where landrace populations tend to repeatedly go through periods of low population size (e.g., due to farmer seed management or field size), could have reduced levels of genetic variation within populations (i.e., genetic bottlenecks). This is common, for example, in maize varieties planted only in minor quantities in small plots which have small effective population sizes (Perales et al. 2003b).

The way patterns of gene flow affect structure of diversity will also influence how well populations will be able to respond to selection. Patterns of farmer seed networks – such as the sharing of seed primarily within a small region – could reduce variation among populations

within a region, but increase differentiation among regions, thereby increasing variation in regional responses to climate change. Growing improved varieties and landrace populations interspersed in the same region (and resulting hybridization between these types) could offer landraces unique genetic diversity (Bellon and Risopoulou 2001; Bellon et al. 2006; van Heerwaarden et al. 2009b). Improved varieties are often bred for stability of phenotype (i.e., low genotype by environment interaction;  $G \times E$ ), so alleles from improved varieties could provide stability to landraces in the face of some components of environmental change. However, introgression of improved crop genetics into landraces could alternatively result in populations with fewer total alleles encoding for traits with effects on fitness. Thereby, the evolutionary capacity of these landrace populations could be stunted.

Although studies employing neutral molecular markers can give us a sense of the patterns and amounts of diversity found in and among landrace populations, only few studies have investigated relevant phenotypic variation using markers (Doebley et al. 1985; Pressoir and Berthaud 2004b). Patterns of genetic diversity found with neutral molecular markers and those created by adaptive processes rarely correlate (McKay and Latta 2002; Holderegger et al. 2006). Thus, to determine how landraces in centers of crop diversity will respond to future environmental change, we must examine two aspects of the structure of genetic diversity in these regions. First, we need to understand how diverse genetic materials respond to environmental variation. Second, we need to investigate the structure of the traits affecting fitness. One would think that for maize, which has been well studied by breeders, we would have a wealth of information on both counts. Although studies of variation among breeding populations derived from landraces (e.g., Lafitte and Edmeades 1997) can be rich in possible mechanisms for adaptation, these data do not provide appropriate information from which to make predictions about evolution. Due to the focus on population level data rather than individual trait data (e.g., date of 50% flowering or yield) and the disassociation between experimental locations and the place of origin of the studied landrace population, it is difficult to assess the degree to which important phenotypic variation is associated with fitness within a population. However, certain kinds of studies may allow us to discern these two aspects of the structure of genetic variation.

To clarify how climate change might affect the productivity of maize landraces, we study the distribution of adaptive genetic diversity across the landscape using reciprocal transplant experiments. In particular, we have investigated the degree of local adaptation of maize landraces from Chiapas, Mexico to elevation (Mercer et al.



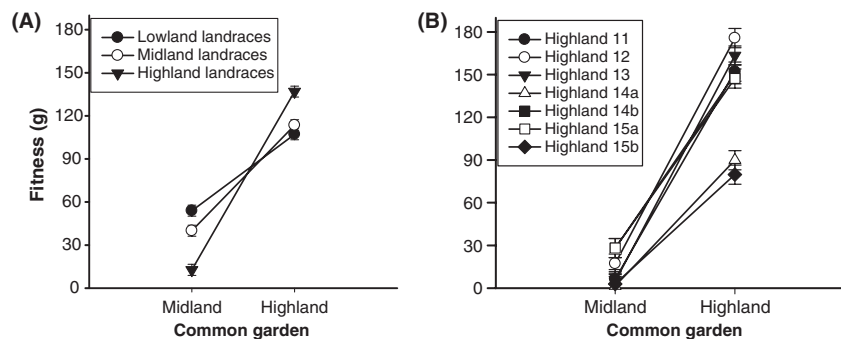
2008), a factor which parallels environmental gradients and seems to be the main determinant for maize landraces distribution (Brush and Perales 2007). The major races of maize grown in Chiapas are distributed along an altitudinal gradient from 0 to 2600 m. We collected landrace populations at high-, mid-, and low elevations and planted them into common gardens at high- and mid-elevations. After taking data on fitness (i.e., individual survival and seed production), we have found that plants from highland landraces produce poorly in the midland environment (Fig. 2A). This is of concern since the midland environment may resemble the future climate for the highlands. However, we do see some variability across highland populations for how badly they do in the midlands (Fig. 2B). Some do somewhat better than others, but none perform well.

Our research with maize landraces in Chiapas indicates that climate change may well cause difficulties for farmers who grow and depend on distinct, locally adapted landrace varieties. This local adaptation, although currently a great benefit to farmers and an essential part of crop evolution, could place limits on the future evolutionary potential and/or plastic response of landrace populations confronted with climate change. From this research, it does not appear that highland varieties express the plasticity necessary to sustain productivity under these conditions. If they did, we would not have seen such productivity deficits in the midlands. Thus, highland landraces appear to be the most threatened in this system.

Significantly, other crops may not have the same patterns of local adaptation and plasticity as maize. In other crops, highland populations may be plastic and, therefore, less threatened. Without field studies of this nature, the response of these landraces to climate change cannot be predicted. We presently cannot assess the evolutionary potential of maize landrace populations or estimate how quickly they might adapt under various strengths of selec-

tion. To investigate this further, we need studies in which the various sources of phenotypic variation can be partitioned to discern the relationship between additive genetic variation of particular traits of interest and fitness (Lande and Arnold 1983; Etterson 2004a) and document genetic variances and covariances under a range of conditions (Etterson 2004b).

We highlight two studies that can serve as models for the elucidation of genetic variation and its relation to evolutionary potential under climate change. First, Pressoir and Berthaud (2004b) planted 31 Bolita maize landrace populations collected from a small region in Oaxaca into a common garden. Phenotypic assessments of maternal families allowed for the estimation of heritabilities and **G** matrices, which summarize the genetic variance and covariances. They determined that the **G** matrices varied across populations, indicating both past selection and also differences among populations for their potential for future evolution (Pressoir and Berthaud 2004b). Studies such as this could be greatly improved by being performed in a range of environments that mimic future climate change. A pair of studies on the evolutionary potential of a native, wild legume in the Great Plains with climate change should serve as a model here (Etterson 2004a,b). She performed reciprocal transplant experiments of three populations along a drought gradient and measured how genetic variation for traits involved in drought resistance related to fitness. This allowed for estimates of selection and expected response to selection under relevant conditions. In future work in crop centers of origin, it will be important to measure traits that we would expect to play important roles in responses to farmer-mediated or natural selection with climate change. It will be essential to study how landraces respond to selection pressures under farmers' conditions (Louette et al. 1997; Pujol et al. 2005). In sum, we still lack research that takes a sufficiently ecological and evolution-



**Figure 2** Overall productivity or fitness [=survival of plant  $\times$  seed production (g)] of maize landraces from (A) lowland, midland, and highland environments grown at two common garden locations in Chiapas, Mexico, 2005. (B) Productivity of seven highland populations in the same two common gardens. Adapted from Mercer et al. (2008).

ary perspective by placing genetic variation within its appropriate environmental and management context to assess responses of that diversity to multiple sets of environmental conditions. This lacuna puts us at a great disadvantage for understanding the responses of these bastions of crop diversity to climatic shifts.

### Regional patterns of climate change and effects of selection

Even with understanding of the structure of genetic diversity within and among landrace populations within a center of diversity, it is difficult to know what responses to expect until actual patterns of climate change play out. Changes in climatic factors that will probably vary regionally include mean and extreme values of environmental variables, along with local temporal patterns of variability. Thus, the certainty of predictions for climate change at small spatial scales remains elusive. This presents problems because many centers of crop diversity are distributed across environmental and/or altitudinal gradients. Landscape heterogeneity can result in variation in expected changes with climate change. This reinforces the need to understand how the genetic variation across the landscape may differentially respond to various environmental conditions.

Selection pressures generated by climate change will probably take a range of forms. Persistent change in an environmental variable, such as gradual increases in temperature, can result in directional selection. In this case, particular values of morphological, phenological, and/or physiological traits that augment fitness as temperatures rise will be selected for. However, since climate change is promised to introduce new extremes in temperature (Battisti and Naylor 2009), these new extremes could present extreme selection events resulting in rapid evolution (Franks et al. 2007). These strong bouts of selection could likely have two impacts. First, they could radically reshape the structure of diversity within populations, i.e., reducing diversity within populations by reducing effective population size. Second, they could cause large mortality events, thereby resulting in extinction of populations that are unable to tolerate the conditions. This would have the effect of altering patterns of diversity among populations, likely reducing it if all populations evolve in similar directions. Gene flow's ability to move potentially adaptive alleles from populations inhabiting more extreme environments could reduce the severity of both impacts.

With predictions of increasing variability in weather, either inter- or intra-annually, selection may not proceed unidirectionally. There are a number of possible outcomes of this, including selection for plasticity and increases in vulnerability. Because phenotypic plasticity itself can evolve

in some traits, often independently from the trait mean (Schenier 1993; Pigliucci 2005), we might expect that populations could become more plastic if future conditions become more variable and plasticity increases fitness (De Jong 1995). Theoretical conditions for evolution of plasticity are becoming well-understood (Moran 1992; Sultan and Spencer 2002), but the conditions allowing for selection toward greater plasticity have only been documented empirically for a couple of traits (van Kleunen and Fischer 2005). Nevertheless, across a center of diversity, many of which may experience metapopulation dynamics (van Heerwaarden et al. 2009a), the degree to which populations evolve to be locally adapted as opposed to evolve phenotypic plasticity will depend on levels of gene flow, the local costs of plasticity, the accuracy by which the plasticity can appropriately target environmental variation, and patterns of environmental heterogeneity (Sultan and Spencer 2002). Thus, in multiple landrace populations linked by gene flow for which moisture levels are spatially or temporally heterogeneous, selection could act for plasticity of tolerance of moisture deficits and surpluses mediated through adjustment of leaf structure, for example. In contrast, with reduced gene flow or less environmental heterogeneity, selection might favor a particular canalized phenotype (Sultan and Spencer 2002; van Kleunen and Fischer 2005). Particular patterns of environmental variation within and among populations play an important role in this outcome. As with adaptation more broadly, there can be costs of and limits to adaptive phenotypic plasticity as well, including genetic costs and developmental range limits (DeWitt et al. 1998).

Another result of environmental variability could be an increase in population vulnerability. With interannual variability in environmental conditions, distinct phenotypes may allow a plant to express high fitness in alternate years. Thus, fluctuating selection could alternately select against divergent trait values. Such strong selection in multiple directions in quick succession could prove detrimental to a population's genetic diversity since it would reduce diversity within a population (Barton and Turelli 1989), especially as effective population size plummets. If this process proceeds far enough, the population could be at a great disadvantage in terms of future evolutionary capacity or ecological vulnerability. As we know, genetically depauperate plant populations can lack the diversity required to stave off novel stresses, such as new pathogens.

### Discussion

Climate change will inevitably alter landraces conserved *in situ*. A balance may be struck between adaptive evolution, which will simply continue on (if not more quickly),

and the possibility for population extinction, which will result in genetic erosion. This was originally understood by Bennett in 1968, as discussed in Frankel (1970b):

...the difficulty is to find the border line between 'adaptive change' and 'genetic erosion'. Bennett (1968:63) sees 'no advantage in the 'steady state' [since] the purpose of conservation is not to capture the present moment of evolutionary time, in which there is no special virtue, but to conserve material so that it will continue to evolve'. Such changes are desirable as long as 'genetic erosion does not take place'. But how is one to know?

Yet, although undoubtedly difficult to predict, we should work on understanding the conditions and limits under which landraces conserved *in situ* will continue to evolve and genetic erosion is minimized. For resources so important and prevalent, it is surprising how little we know of the recent evolution of our crop landraces conserved *in situ* or can predict about their responses to impending climate change. Given that the loss of particular landrace populations can be seen as part of a 'blinking on and off' of local populations within a metapopulation structure, we ultimately need to understand how the diversity and productivity of an entire region will handle climate change. However, as discussed before, future studies could provide guidance by producing the kinds of data sorely needed.

For maize in Mexico, given our current knowledge, we might expect several general responses to climate change. The highlands of the country (>1800 m) are basically dominated by landraces (Perales et al. 2003a; Brush and Perales 2007) and we can expect that these landraces could have difficulty responding well to warmer conditions (Mercer et al. 2008). Thus, it is in the highlands that we might see the greatest genetic erosion as farmers discard populations, unless populations can evolve quickly. However, there are about 20 races of maize in the highlands of Mexico (Wellhausen et al. 1952; Sanchez et al. 2000) and we do not know if all these races would have similar problems responding to warmer conditions, or if some could be more plastic or responsive to selection. Some highland races may see introgression of newly adaptive genes from midland landrace populations, which could stave off the loss of some highland races. Moving landrace populations that are grown at lower latitudes to higher latitudes could help. However, if the combination of environmental factors is novel (see Williams and Jackson 2007), suites of characteristics not found together at present may be required. In the warmer environments of the lower elevations of Mexico where landraces have been generally displaced by commercial varieties (Bellon and Brush 1994; Ortega 2003; Brush and Perales 2007), climate change may be the final straw for their extinction

unless their apparent plasticity signals that they could be more resilient.

Empirical data can help guide a reevaluation of the conservation strategies for the *in situ* and *ex situ* conservation of crop genetic resources. For instance, given the greater local adaptation of highland Chiapan maize landraces (Mercer et al. 2008), if the environmental conditions under which highland types flourish change, their *in situ* and *ex situ* conservation will be a great challenge. *Ex situ* conservation could regain primary importance despite the fact that it is an already over-taxed system. Yet climate change promises to complicate the decisions of which locations are most appropriate for grow-outs.

Although the fate of individual populations will ultimately determine the levels and distribution of genetic diversity in centers of crop origin as climate changes, we must also monitor patterns at a regional scale. The metapopulation dynamics in these systems requires taking a landscape perspective that can investigate processes happening at the level of the individual landrace population up to the regional flow of adaptive alleles. The responses of farmers to climate change, spurred by changes in crop productivity or other economic or social stimuli, will play a significant role.

Thus, a problem of this scope, which involves complex interactions between natural and social systems, requires an integrated and interdisciplinary approach. Quantitative and molecular geneticists, sociologists and anthropologists, modelers and practitioners must discuss and study these issues together. Only by investigating crop diversity in centers of origin from this multitude of perspectives and at this regional scale will we be able to fully elucidate their future dynamics. If not, our genetic heritage hangs in the balance.

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