

Review: Adaptive Introgression Expanded the Genetic Base of Crops during post-Domestication Spread

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The process of domestication is often conceptualized as geographically constrained, with crops originating from a wild progenitor within one or more defined centers followed by expansion to the modern-day extent of cultivation [1]. However, archaeological and genetic evidence are beginning to reveal that, in many cases, domestication has been temporally protracted and geographically diffuse [2, 3, 4, 5, 6]. An additional important aspect of the emerging complexity of domestication is beneficial gene flow (*i.e.*, adaptive introgression) from locally adapted wild relatives during crop expansion following initial domestication.

Adaptive introgression has three components: hybridization between two genomes, backcrossing to one of the parents, and selection on different recombinant genotypes with progressively diminished linkage drag [7, 8]. In domesticated species, adaptive introgression would consist of crop/wild hybrids backcrossing to a crop, retention and increase in frequency of adaptive wild haplotypes in the crop, and selection against undesirable wild background. To date, literature on crop-wild gene flow has focused on the risk of transgene introgression from domesticated crops into wild relatives (for a review, [9]) and on modern plant breeding efforts to introgress desired traits from wild relatives (for a review, [10]). The history of natural and potentially adaptive introgression of wild alleles into domesticated crops over evolutionary timescales has received considerably less attention. However, new tools and methods have recently been employed to detect genome-wide patterns of introgression, granting new insights into the prevalence of adaptive introgression in crop histories. Preliminary results suggest a need to expand our conception of domestication to include the broadening of the genetic base of crops that occurred during post-domestication expansion through gene flow with newly encountered wild relatives.

In this review, we will: 1) briefly describe recently developed methods for detecting adaptive introgression and provide a summary of how they can be applied to detect crop-wild introgression, 2) present case studies suggesting wild-to-crop introgression has conferred local adaptation, 3) consider how introgression bears upon fundamental questions of domestication, and 4) describe future advances in both basic and applied genetics that can be made through the study of introgression in agroecosystems.

Introgression methods and their application

In this section, I think the overall content is good, but we need to edit to make it more accessible and more explicit about how methods are implemented to detect adaptive introgression

The decreasing cost of genome-wide resequencing and availability of reduced-representation genotyping (*e.g.*, GBS and RAD-Seq), combined with new analytical methods, has facilitated comprehensive study of introgression across a number of species (**Table 1**). High-density marker data can be used with haplotype-based and other methods to assign specific genomic regions to a taxon of origin and identify introgression across taxa [11, 12, 13, 14, 15, 16]. The methods reviewed here do not include those marginally estimating introgression/migration rate as a component of demographic history (*e.g.*, Approximate Bayesian Computation (ABC) [17], diffusion approximations for demographic inference (*δaδi*) [18], isolation with migration models [19], and a series of methods utilizing the sequentially Markovian coalescent (PSMC, MSMC and SMC++) [20, 21, 22]). Rather, we focus on methods that explicitly identify introgressed genomic segments based on the extent of differentiation, on patterns of nucleotide/haplotype sharing, and phylogenetic relationships.

First, introgressed segments are expected to show low differentiation from their source population. The F_{st} and d_{XY} statistics and their derivatives including G_{min} [16] and RND_{min} [15] gauge differentiation. The former two statistics are insensitive to rare migrants and therefore lack power to detect recent introgression, while the latter two overcome this limitation. Additionally, RND_{min} accounts for variable mutation rate, which is detected based on branch length to an outgroup:

$$RND_{min} = \frac{d_{min}}{d_{out}} \quad (1)$$

where d_{min} is the minimum sequence distance between haplotypes in species X and Y and d_{out} equals $(d_{XO} + d_{YO})/2$, the average sequence distance between each species and the outgroup (O).

These statistics have recently been further developed by adding differentiation between both non-admixed (A) and admixed populations (B) and a source population (C) [23]. For example, the $U_{A,B,C(w,x,y)}$ statistic summarizes number of sites where an allele at frequency y in the source population (C) has a frequency higher than x in the admixed population (B) and lower than w in the non-admixed population (A). A similar statistic, $Q95_{A,B,C(w,y)}$, sets a hard cutoff at the 95th percentile of allele frequencies in the admixed population (B) [23]. Further modifications have allowed specification of more than one source population (see details in [23]).

Second, local ancestry deconvolution (also known as chromosome painting) assigns genomic regions to various source populations based on patterns of allele/haplotype sharing [24]. One form of chromosome painting utilizes hidden Markov models to evaluate ancestry across admixed genomes through comparison to reference, non-admixed individuals (*e.g.*, HAPMIX [12]). Another clusters admixed populations with reference samples using a sliding-window approach (*e.g.*, PCAdmix [25] and LAMP [26]). And finally, introgression can be detected through chromosome painting by using a Bayesian model [27] in which deviations from Hardy-Weinberg equilibrium are minimized through creation of genetic groups (*e.g.*, fineSTRUCTURE [13]).

Li, are you familiar with the analytical tools MIGRATE-N and BAYESASS? Rieseberg compares these two to STRUCTURE at some length in the discussion of this paper: <https://biology.unm.edu/Whitney/Whitney> Should we include these two methods, even in passing, in this portion of the paper? Garrett, I donot know these two methods. I am reading the paper you mentioned here.

Third, the ABBA-BABA statistic (also known as the D-statistic) and its derivatives are widely applied to introgression detection. These statistics make inferences regarding introgression based on genomic patterns of derived variants that are shared between populations or species. Patterns of allele sharing are interpreted in a phylogenetic context and the method is best suited to detection of introgression at the genome level. Elaborations of the D-statistic capable of localizing introgression to specific genomic regions include \hat{f}_d [11] and the five-taxon D-statistic [14]. The former is quite similar to the D-statistic but uses allele frequencies from each population/species, and the latter

detects introgression based on the localized phylogenetic pattern and is capable of determining introgression directionality.

Application of these approaches across a number of plant and animal species suggests introgression can play an adaptive role. For example, introgression from ancient hominins (*e.g.*, Neanderthals and Denisovans) to humans has been detected at loci controlling skin pigmentation, defense against pathogens, and toleration of high altitude (reviewed in [28]); introgression of wing coloration loci has conferred Müllerian mimicry (a type of mimicry in which two unpalatable species resemble one another, compounding the efficacy of their repellent signal) across butterfly species [29]; introgression has spread insecticide resistance across mosquito species [30], and introgression across *Mimulus* (*i.e.*, monkeyflower) species has resulted in adaptation to pollinator preference and contributed to speciation [31].

Crop adaptation through introgression

Genome-wide data from extensive samples of crops and their wild relatives, in combination with the new methods described above, have recently allowed detailed analysis of wild-to-crop introgression in some of the world’s most important crops (**Table 2**). Below we present a summary of findings from maize, barley, and rice, three promising systems in which introgression from wild relatives may have played an adaptive role.

1. Maize:

The relationship between maize (*Zea mays* ssp. *mays*) and the teosinte *Zea mays* ssp. *mexicana* (hereafter, *mexicana*) offers a prime case study of adaptive wild-to-crop introgression. Maize was domesticated from *Zea mays* ssp. *parviglumis* (hereafter, *parviglumis*) approximately 9,000 years ago in the lowlands of the Balsas River Valley in Mexico [32]. From this domestication center, maize spread into the highlands of the Mexican Central Plateau, where it came into sympatry with *mexicana*. Introgression from *mexicana* to maize in the Central Plateau has been reported based on both morphological [33] and molecular [34, 35] data. However, [36] first localized *mexicana* introgression to chromosomal regions and provided evidence that it was likely adaptive. The authors identified nine genomic regions in several maize populations which consistently showed evidence of *mexicana* introgression based on chromosome painting methods including HAPMIX and the linkage model of STRUCTURE (Figure 1). These introgressed segments overlapped QTL that had previously been found to control anthocyanin content and leaf macrohairs [37], traits known to be adaptive at high elevation. In a growth chamber experiment, the authors demonstrated that maize populations with *mexicana* introgression showed greater plant height (a proxy for fitness) under highland environmental conditions than populations that lacked introgression. Height differences were not detected under lowland conditions.

Populations of *mexicana* cannot be found outside of the highlands of Mexico, yet maize has colonized and adapted to high elevation in a number of other regions. A recent study [4] employed the ABBA-BABA and \hat{f}_d statistics to evaluate whether maize with *mexicana* introgression was transferred to other highland regions or whether highland adaptation was obtained *de novo* outside of Mexico. Overall, analyses revealed that *mexicana* introgressions were transferred to nearby high elevation regions in Guatemala and the southwestern United States, but more distant high elevation regions (*e.g.*, the Andes) showed no *mexicana* ancestry. Since *mexicana* haplotypes appear to have played an important role historically in adaptation of maize to challenging high-elevation conditions, modern breeding programs may further

benefit from drawing on *mexicana* germplasm, particularly in regions like the Andes where *mexicana* alleles are not known to have spread.

2. Barley:

Barley (*Hordeum vulgare* subsp. *vulgare*) was domesticated at least twice roughly 8,000 to 10,000 BP: once from the wild subsp. *spontaneum* in the Fertile Crescent and once from subsp. *spontaneum* var. *agriocrithon* in Tibet [38, 39, 40, 41, 42?]. Presently, the distribution of subsp. *spontaneum* stretches from the eastern Mediterranean through the Middle-East to west-central Asia spanning clines in temperature, precipitation, soil type, and altitude [43]. Barley-*spontaneum* hybrids are fertile and found spontaneously when these taxa co-occur. Introgression between wild and domesticated barley is frequent [42], at times occurring over distances greater than a kilometer [44].

Poets and co-authors [45] recently investigated the range-wide contribution of wild barley to landraces, assessing both genome-wide and geographical patterns. This study identified several lines of evidence consistent with wild introgression aiding the dispersal and adaptation of domesticated barley. Genomic regions of shared ancestry were detected linking particular landraces to several distinct wild relative populations, suggesting landraces may have received wild introgression on a continual basis during post-domestication expansion. However, barley landraces showed an excess of ancestry from nearby wild relatives, indicating a prevalence of local and potentially adaptive gene flow. Low linkage disequilibrium and small blocks of identity by state indicated even these locally introgressed regions are old, perhaps dating back to the early expansion of barley following domestication. While these results are suggestive, wild barley haplotypes have yet to be definitely linked to specific local adaptations in landraces.

3. Asian Rice:

The story of Asian rice (*Oryza sativa*) domestication is still debated, with hybridization between wild and domesticated rice contributing to the complexity of this crop's history. Certain genetic and archaeobotanical evidence point toward independent domestications of the two prominent varietal groups *japonica* and *indica* from the wild species *Oryza rufipogon* (*rufipogon* hereafter) in the Yangtze Basin of China and the Indian Ganges plain, respectively [46]. Other studies support a single domestication occurring 8,200-13,500 BP in the Yangtze Basin, with later divergence of *indica* and *japonica* [47]. Huang and colleagues [48] developed a genetic map of rice variation, which they used to measure genetic distance between wild and domesticated rices at and around domestication loci for various geographical locations, finding that *japonica* was likely domesticated in the Pearl River area of Guangxi province, China (just south of the Yangtze Basin), and that *indica* was likely the result of hybridization between *japonica* and local *rufipogon* populations in Southern and South-eastern Asia.

Vaughan and colleagues [49] posit a hypothesis combining elements of both theories. According to this hypothesis, the non-shattering allele arose in a single cultivated rice population and then introgressed into many diverse cultivated populations (some *japonica*-like, some *indica*-like) in the region. This would have facilitated the subsequent spread of other domestication alleles among those populations. As these domesticated populations then spread into new environments, they would have received introgressions from locally-adapted wild relatives, retaining alleles that improved fitness (in agreement with [50]). Contemporary populations of wild and domesticated rice show evidence of this history of local adaptation. The wild relatives *rufipogon* and *nivara* both maintain high genotypic and phenotypic diversity and exhibit locally-adaptive traits (*rufipogon* is adapted to forested wetland environments, whereas *ni-*

Table 1: List and brief description of recently developed methods and examples of empirical studies employing these methods.

methods	data type	reference
chromosome painting		
Hapmix	phased haplotype; reference panel	Price et al. 2009
RASPberry	phased haplotype	Wegmann et al. 2011
MultiMix	phased/unphased genotype; reference panel	Churchhouse and Marchini 2013
PCAdmix	phased haplotype	Brisbin et al. 2012
LAMP	phased haplotypes; reference panel	Sankararaman et al. 2008
phylogenetic relationship		
ABBA-BABA/D-statistics	biallelic SNP	Durand et al. 2011
fd statistic	biallelic SNP	Martin et al. 2015
five taxon D statistics	biallelic SNP	Pease and Hahn 2015
divergence		
Gmin	biallelic SNP	Geneva et al. 2015
RNDmin	phased haplotype	Rosenzweig et al. 2016
(see .tex file for comment)	biallelic SNP	Racimo et al. 2016

vara is adapted to dryer conditions and has life cycle adaptations to survive grazing pressure), suggesting that either offered (and offers) adaptive genetic potential. Likewise, domesticated rice varieties display patterns of local adaptation (for examples, two of the domesticated rice deepwater varieties (*rayada* and *ashwina*) are said to be selected for the environment along the Ganges river, the *japonicas* are split into temperate and tropical subgroups, and the *indicas* are best suited for lowland environments.

To date, research into adaptive introgression in the domestication of rice has been insufficient to detect clearly-supported examples (though [51] emphasizes the necessity of this research). There are perhaps some practical reasons why research has not yet been devoted to this inquiry. As with many other domesticated crops, gene flow between wild and domesticated rices is highly asymmetric (estimates of wild rice admixture in domesticated rice are less than 5 percent [52]). This asymmetry is due in part to the closed floret architecture of the domesticated rice, which hinders outcrossing. Crop-wild ybridization is frequent enough that nuisance weedy hybrids commonly arise amongst cultivated populations and must be managed with difficulty [49]. During early domestication, introgression may have been more prevalent than at present because barriers to crop-to-wild introgression may have been less severe and because the inbreeding reproductive system of rice would not have been as firmly established [49]. Furthermore, the contemporary distribution of wild rice does not capture the range and diversity of wild rice during early domestication and range expansion of rice.

Re-evaluating domestication

A framework in which crops are domesticated from a single wild population or even a single species is an oversimplification when introgression during the geographic expansion of crops is extensive.

Crop	Compatible Wild Relatives	Hybrids and/or Hybridization	Evidence of Crop Introgression	Evidence of Adaptiveness	Source
Maize (<i>Zea mays</i> subsp. <i>mays</i>)	<i>Z. m.</i> subsp. <i>mexicana</i> , <i>Z. m.</i> subsp. <i>parviglumis</i>	X	X	X	[53]
Asian Rice (<i>Oryza sativa</i>)	<i>O. rufipogon</i>	X	X	X	[48]
Barley (<i>Hordeum vulgare</i>)	<i>H. v.</i> subsp. <i>spontaneum</i>	X	X	X	[45]
Sunflower (<i>Helianthus annuus</i>)	<i>H. argophyllus</i> , <i>H. bolanderi</i> , <i>H. debilis</i> , <i>H. petiolaris</i>	X			[54]
Cassava (<i>Manihot esculenta</i>)	<i>M. glaziovii</i>	X	X	X	[55]
Potato (<i>Solanum tuberosum</i>)	many	X	X	X	[56?]
Tomato (<i>Solanum lycopersicum</i>)	<i>S. pimpinellifolium</i>	X	X	X	[57]
Olive (<i>Olea europaea</i> ssp. <i>europaea</i> var. <i>sativa</i>)	<i>O. e.</i> ssp. <i>europaea</i> var. <i>sylvestris</i>	X	X		[58]
Soybeans (<i>Glycine max</i>)	<i>G. soja</i>	X	X		[59]
Common Bean (<i>Phaseolus vulgaris</i>)	<i>P. v.</i> var. <i>aborigineus</i> , <i>P. v.</i> var. <i>mexicanus</i> [[not in this source]]	X	X		[60]
Grapes (<i>Vitis vinifera</i> subsp. <i>vinifera</i>)	<i>V. v.</i> subsp. <i>sylvestris</i>	X	X		[61]
Sorghum (<i>Sorghum bicolor</i> subsp. <i>bicolor</i>)	<i>S. b.</i> subsp. <i>arundinaceum</i> , <i>S. b.</i> subsp. <i>drummondii</i>	X	X		[62]
Wheat (<i>Triticum monococcum</i> , <i>T. dicoccum</i> , <i>T. aestivum</i>)	<i>T. m. boeoticum</i> , <i>T. diocoides</i> , <i>T. urartu</i> , <i>Aegilops speltoides</i> , <i>A. tauschii</i>	X	X		[63]
Apple (<i>Malus domestica</i>)	<i>M. sylvestris</i> , <i>M. orientalis</i> , <i>M. baccata</i> , <i>M. sieversii</i>	X	X		[64]

The addition of ongoing gene flow to our understanding of crop demography could bear importantly on fundamental questions of crop domestication:

What is the progenitor of a crop?

Depending on the extent of post-domestication gene flow with new wild relatives, identification of a crop’s progenitor can be complicated or completely confounded. The level of divergence of a crop from newly encountered populations and species will decrease due to introgression, a signal that could be mistaken for origin rather than gene flow. For example, when determining a single origin of maize from *parviglumis*, Matsuoka and colleagues [32] identified a paradox: while *parviglumis* is found exclusively in the lowlands of southwest Mexico, maize with allele frequencies most similar to *parviglumis* was found in the highlands of the Mexican Central Plateau. Several years later, van Heerwaarden *et al.* [34] resolved the paradox by determining that widespread introgression in the highlands from *mexicana*, which is closely related to *parviglumis*, has caused maize from this region to appear ancestral. Similarly, extensive post-domestication adaptive introgression from potato wild relatives long obscured this crop’s origin. Recent work has shown that, following the original domestication event of *Solanum tuberosum* in the central Andes, potato received introgression from as many as four additional species during colonization of the highest elevations of the Andes and the lowlands of the Chilean coast [65, 66]. Beyond confounding detection of progenitor taxa, extensive introgression may necessitate a reevaluation of crop origins. In cases like maize and potato it is important to recognize the substantial contributions of introgressing taxa to the genetic base of modern crops. Broad recognition of the role these wild relatives have played in crop adaptation could further their use in breeding and elevate their conservation status.

When was a crop domesticated?

Estimates of the timing of initial domestication are often based on levels of sequence divergence between a crop and populations of its presumed progenitor (*e.g.*, [32, 47]). In highly introgressed domesticates, these estimates will be based on comparison of either crop or introgressant haplotypes

to those of the progenitor. In such cases, divergence is a mixture of time since domestication and time since split of the progenitor and the introgressing species. This phenomenon, in combination with divergence of samples from true ancestral populations, ongoing evolution of crop progenitors, and problems with assuming evolution under a molecular clock [67], may explain discrepancies between domestication dates based on genetic and archaeological data. More accurate estimates of the timing of domestication may be obtained from genetic data by excluding loci that show signatures of introgression.

How was genome-wide diversity impacted by a domestication bottleneck?

Measurement of the strength of the initial domestication bottleneck may also be impacted by adaptive introgression during the spread of crops. Crop wild relatives have distinct demographies when compared to domesticates and may therefore have contrasting effective population sizes (N_e). The influence of wild relative introgression on estimates of the domestication bottleneck will depend on a number of factors including the magnitude of gene flow, the N_e of the introgressing taxon, and the strength of selection on haplotypes following introgression. For example, substantial introgression at neutral loci from a wild taxon with a historically higher N_e will lead to underestimates of the overall strength of the domestication bottleneck.

What candidate genes were targeted by selection during domestication?

Loci targeted by selection during domestication can be identified through so-called “bottom-up” approaches based on population genetic signatures [68]. Ideally, candidate loci will be identified by first constructing a demographic model representing the history of the domesticate. In this approach, diversity data from neutral loci are fit to potential models of a crop’s demography and then statistical tests of selection are used to identify candidate domestication genes under the most likely model. Due to the difficulty of this approach and the uncertainty associated with any given demography, many studies identify domestication loci using a strict outlier approach in which loci showing the greatest reduction in nucleotide diversity or the highest allele frequency differentiation in the domesticate relative to the wild progenitor are identified as candidates. Introgression during crop expansion may influence candidate gene detection using both demographic-modeling and strict-outlier approaches. For example, *mexicana* introgression into maize described above accounts for approximately 20% of the genome of maize in the highlands of Mexico [34]. Takuno and co-authors [69] have shown that a demographic model incorporating this introgression is a significantly better fit to empirical data than a model lacking introgression. Failure to account for introgression in maize would therefore compromise domestication candidate detection, particularly if a study contained maize samples from the Mexican highlands. Likewise, introgression that increased nucleotide diversity in the domesticate or decreased differentiation at domestication loci would confound a strict outlier approach. However, previous work, also in maize, has shown that known domestication loci are particularly resistant to introgression [53], likely due to ongoing selection favoring the domesticated phenotype.

Future studies in crop-wild introgression

Basic:

Research has so far shown that adaptive crop-wild introgression has played a significant role in the domestication and dispersal of many agronomically-important crops. However, the dynamics

of this process are not yet fully understood, especially in the context of individual case examples, and many questions remain.

What is the genomic architecture of this introgression, and does the architecture suggest that it has been adaptive? At what geographic scale is introgression adaptive? To what extent does this depend on the slope of environmental gradients such as temperature, precipitation, and elevation across these ranges? We can look at conservation of genomic architecture across landscapes and between populations, and make predictions about introgressions and their relations to local adaptation. If the genomic architecture of an introgressed region is conserved across a broad ecogeographical region, this suggests that the introgression imparts adaptation to general environmental or climatic variables. On the other hand, if the genomic architecture is conserved within populations but not between nearby populations in the region, this suggests that the introgressed regions offer adaptations to more local selective pressures. If the genomic architecture of an introgressed region is not conserved within a population, there is little evidence that the introgression is adaptive.

After hybridization events that lead to introgression, how long might the detectable genomic signals of introgression persist? Introgressed regions are easier to detect when there has been limited recombination to break them apart. Therefore, introgressions are easiest to detect when they are either recent (few generations means few recombination events) or involve structural variation (which diminishes recombination rate). Because recombination progressively breaks apart LD in introgressed regions, measurements of LD can be used to date introgression events (as in [45]).

At what taxonomic scale does introgression occur? When do species become so diverged that introgression is either maladaptive or impossible (due to Dobzhansky-Muller incompatibilities or other mechanisms)? Theory indicates that the most significant limiting factor to gene flow between progenitor and domesticated is divergence time. Over time, diverged populations drift and become increasingly incompatible. Small effective population size, and correspondingly high genetic load, of the introgressive population also limits gene flow. Although perhaps less applicable in crop systems, this effect is seen in other well-documented cases of introgression (for example, Neanderthal introgression into humans, [?]). *I tracked down the sources that indicate that introgression is suppressed around genes. The case example was Neanderthal alleles into humans, the paper titled "The genetic history of Ice Age Europe" [?], cited by the Graham Coop paper. However, I'm unclear if this is a general rule, or simply a consequence of Neanderthal being high in deleterious genetic load. Wouldn't crop systems, with wild relatives harboring putatively adaptive alleles with low load, show a different pattern? I could also talk about cross-incompatibility factors in maize/teosinte hybridization vs. highly compatible asian rice and its relatives. I probably wouldn't need a new source for the rice, but I might need to cite a paper about *tcb1*, *ga1*, and *ga2*.*

Applied:

Our identification and understanding of introgression in agroecosystems would be augmented by the development of wild relative genomic resources, such as annotated genomic sequence assemblies and functional genomic data sets [?]. Additional study of introgression in agroecosystems could lead to advances in both basic and applied genetics, and specifically the continued improvement of modern crops. Loci underlying the domesticated phenotype can be more clearly identified by removing the confounding population genetic signal of introgression. These loci are potentially beneficial targets for crop improvement. Furthermore, adaptive introgression that is demonstrably tied to a specific environment may include beneficial alleles that can be utilized in crop breeding.

I could here include a handfull of examples of crops that farmers have bred adaptive alleles into.

Conclusions

The study of crop domestication has been revolutionized by the advent and application of genomic tools. The genomes of crops and their wild relatives tell a story of give-and-take that extends well beyond the initial stages of domestication. Likewise, population genetic theory reinforces the proclivity of wild relatives to provide advantageous, locally-adapted alleles to crops as they disperse beyond their domestication centers into new geographies with new ecological pressures and niches.

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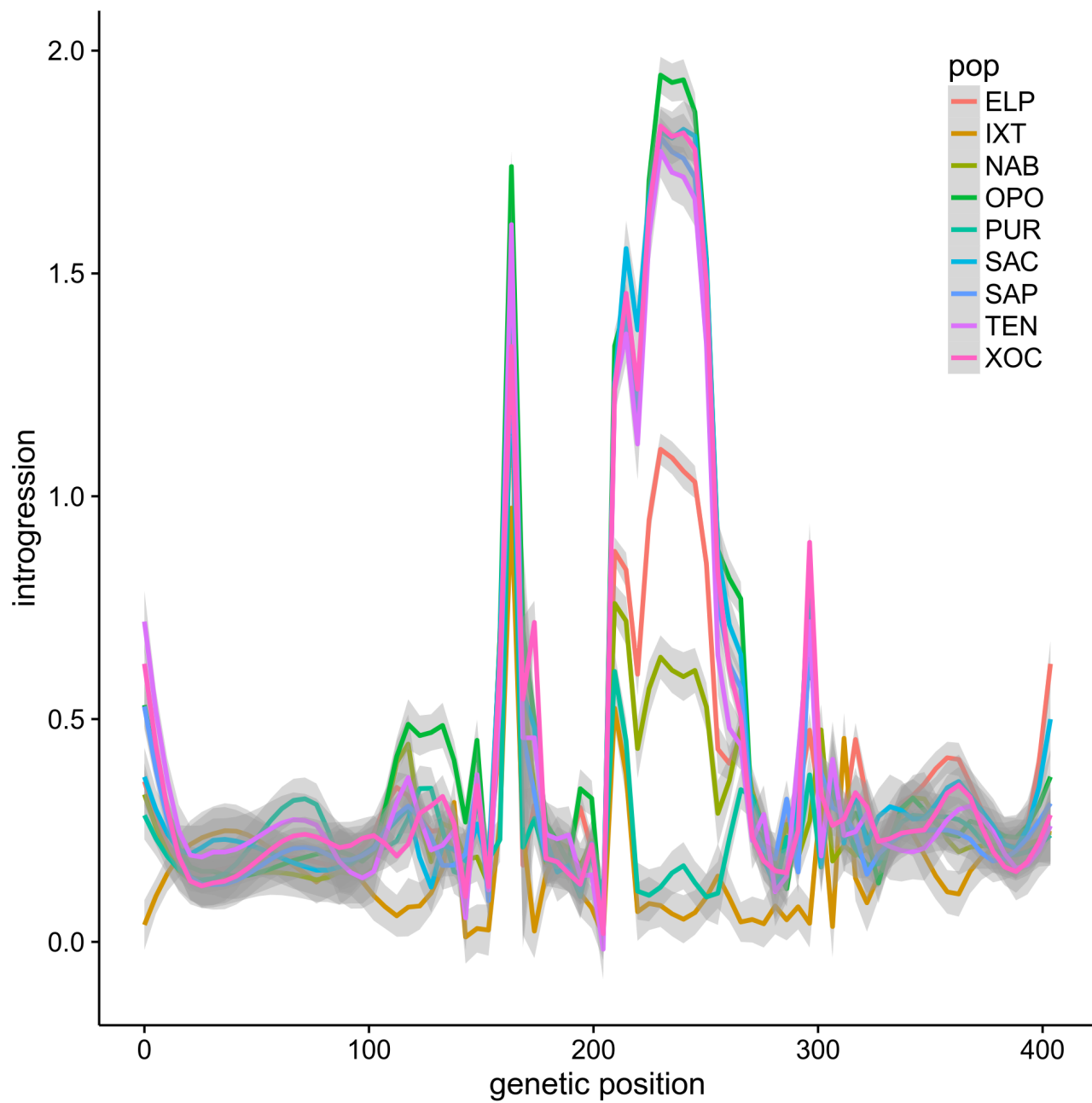


Figure 1: Li's caption here.

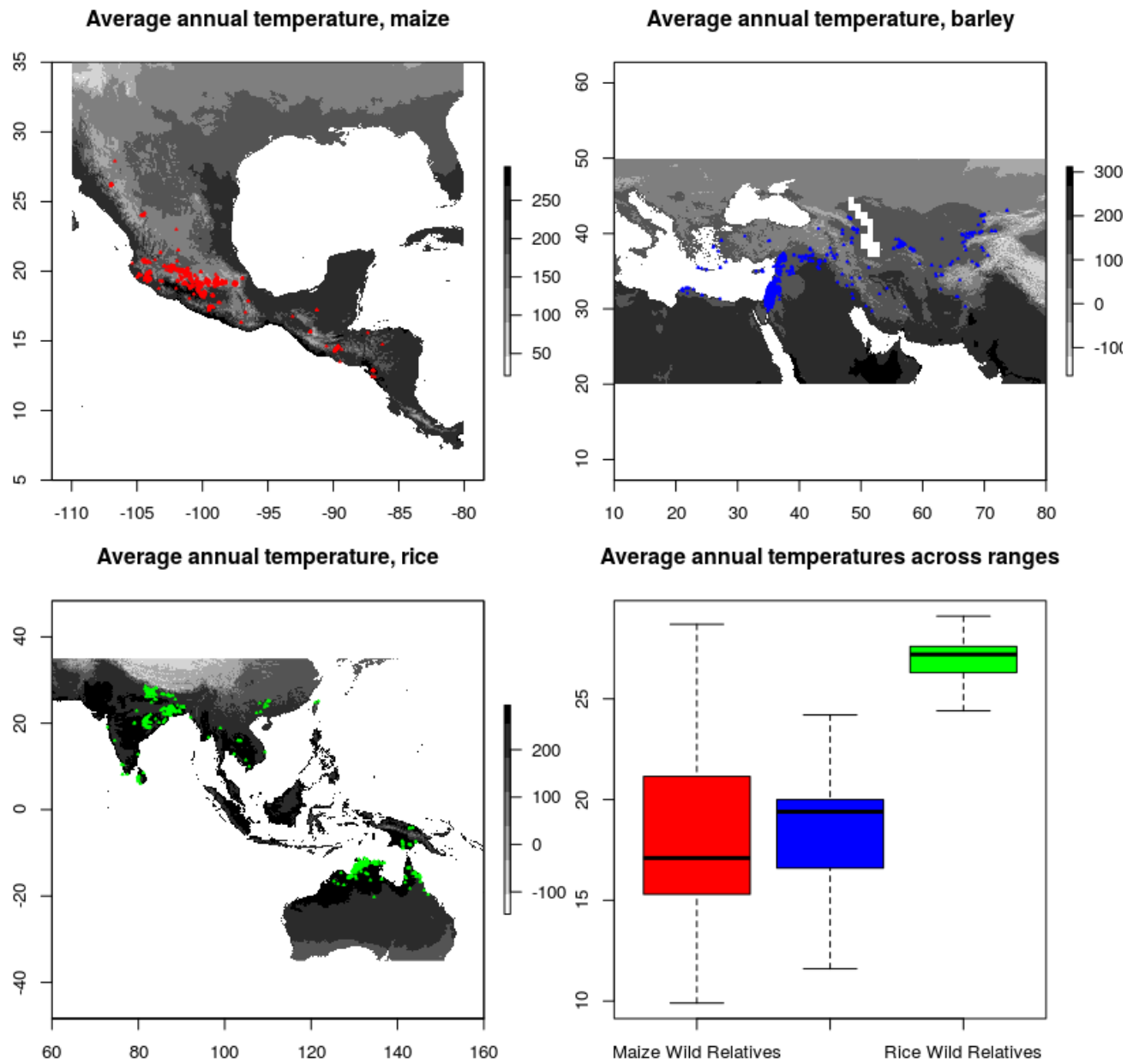


Figure 2: Map of the natural ranges of wild relatives of three domesticated crops, overlaid with average annual temperature. The distribution of average annual temperature experienced in the geographic home ranges of wild relatives interfertile with four crops