

Review: Redefining Domestication: Adaptive Introgression during Crop Expansion

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The process of domestication was once thought to be rapid and geographically constrained, with crops originating from a wild progenitor within one or more geographically defined centers followed by expansion to the modern-day extent of cultivation. *will need citation for this* However, archaeological and genetic evidence are beginning to reveal that, in many cases, domestication has been temporally protracted and more diffuse [1, 2, 3, 4]. This new conception of domestication emphasizes the role of beneficial gene flow (*i.e.*, adaptive introgression) from locally adapted wild relatives during crop expansion after 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 [5, 6]. 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 removal of undesirable wild background. To date, literature on crop-wild gene flow has focused on the risk of introgression of transgenes from domesticated crops into wild relatives (for a review, [7]) and on modern plant breeding efforts to introgress desired traits from wild relatives (for a review, [8, 9, 10]). *cite one paper here...the best, most recent and comprehensive review* The history of natural 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. Emerging results suggest a need for reevaluation of the existing domestication paradigm.

In this review, we will: 1) briefly describe recently developed methods for detecting adaptive introgression and provide a summary of their application for detecting crop-wild introgression, 2) review evidence supporting the hypothesis that wild-to-crop introgression has conferred local adaptation, 3) consider how the prevalence of this introgression alters traditional concepts 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

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 ($\delta a \delta i$) [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 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.

abrupt transition here to Gmin equation...can you smooth this into the text? I am not much of a fan of Gmin, as we applied this method and it is not good. I am wondering if we just give the equation of RNDmin, in order to focus readers attention on the later.

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

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]).

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 has conferred Müllerian

mimicry *I would explain a bit more here...wing coloration loci, protects against predation...* 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

Over the last few years, several high-profile publications based on genome-wide data have documented introgression between crops and their wild relatives outside putative domestication centers. Recent empirical studies have revealed that introgression has occurred in many of the world’s most important crops (**Table 2**).

1. Maize:

The relationship between maize (*Zea mays* ssp. *mays*) and the teosinte *Zea mays* ssp. *mexicana* (hereafter referred to as *mexicana*) offers a prime case study of adaptive wild-to-crop introgression. Maize was domesticated from (*Zea mays* ssp. *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 wild *mexicana*. Introgression from *mexicana* to maize in the Central Plateau has long been reported based on both morphological [33, 34, 35] and molecular [36, 37, 38, 39, 40] data. However, [41] 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 showed evidence of *mexicana* introgression based on local ancestry deconvolution using HAPMIX and results from the linkage model of STRUCTURE (Figure 1). These introgressed segments showed low diversity and overlapped QTL that had previously been found to control anthocyanin content and leaf macrohairs [34], traits known to be important in high elevation adaptation. 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 Mexico, yet maize has colonized and adapted to high elevation in a number of other regions. A recent study [3] 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 maize landraces with *mexicana* introgression 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.

2. Asian Rice:

The story of Asian rice domestication is still debated. A recent investigation pointed to a single domestication occurring 8,200-13,500 BP in the Yangtze Basin in China from the wild species *Oryza rufipogon*, with later divergence of the two prominent varietal groups, indica and japonica [42]. On the other hand, both genetic and archaeobotanical evidence point toward independent domestications of japonica and indica in the Yangtze Basin and the Indian Ganges plain respectively [43]. An alternative explanation, as described by [?], suggests an initial domestication of japonica in China followed by formation of the indica

group through hybridization of japonica and local *O. rufipogon* populations in Southern and South-eastern Asia. As suggested by [?], gene flow between domesticated Asian rice and its wild relatives outside of the Yangtze Basin could have imparted locally adaptive traits. Adaptive introgression may in fact be the signal interpreted as independent domestications.

The wild relatives rufipogon and nivara are both phenotypically diverse and show evidence of local adaptation. Rufipogon reproduction can be either primarily sexual or vegetative. Whereas rufipogon is adapted to forested wetland environments, nivara is adapted to dryer conditions and has life cycle adaptations to survive grazing pressure. Likewise, cultivated rice varieties display phenotypic differences important for fitness. In particular, two of the cultivated rice deepwater varieties (rayada and ashwina) are said to be selected for the environment along the Ganges river. Gene flow between these wild and cultivated rices is common, producing nuisance weedy hybrids in when the two are grown in sympatry. However, during early domestication, introgression may have been even more prevalent 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. 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. Introgression into indica is expected to be more likely than japonica, due to the higher degree of sympatry between indica and its wild relatives. The high genetic diversity within domesticated rice is likely due to introgression from wild relatives both within the domestication center(s) and in new environments where rice has dispersed [44].

3. Barley:

Domesticated and wild barley belong to the same species, *Hordeum vulgare*, and are capable of producing viable offspring via hybridization [45]. Barley (*Hordeum vulgare* subsp. *vulgare*) is believed to have been domesticated at least twice roughly 10,000 BP, once from wild subsp. *spontaneum* in the Fertile Crescent and once from subsp. *spontaneum* var. *agriocrithon* in Tibet [46, 47, 48, 49, 50]. *the source morrell2007genetic will be used to update this paragraph once we've worked out for sure that the second domestication of barley was in the Zargos mountains, rather than Tibet. Also, this paper puts the earliest archaeological samples of barley at closer to 8500 calibrated years ago.* However, details of barley domestication are still disputed.

There has been little genetic investigation into spontaneous barley/*spontaneum* hybrids [51]. Barley/*spontaneum* hybrids are fertile, and morphologically intermediate (putatively hybrid) barleys are found when wild and domesticated barleys are grown in sympatry, but hybrids of other wild relatives generally exhibit greatly diminished fertility [51, 52]. Even when the two are not grown immediately adjacent to one another, introgression from wild to domesticate has been shown to happen over distances of more than a kilometer [53].

The barley domestication process has reduced the number of alleles in the domesticate to only 40% of that found in wild barley, though there remains a great deal of phenotypic diversity among the wild barleys [54]. The authors of [?] used STRUCTURE to look for patterns of introgression from wild relatives in a dataset of 803 landraces, and found a high amount of variability in the amount of contribution from wild relatives, as well as its location in the genome, within barley populations. This is indicative of contribution from numerous wild populations. Furthermore, the authors found that wild introgression contribution is generally greatest from geographically-proximate populations, and that introgressed regions might be combined from geographically-separate wild populations. Low linkage disequilibrium and small blocks of identity by state indicate that these introgressed regions are old, perhaps

dating back to the beginning of barley domestication. As landraces and nearby wild relatives share similar genomic sequences, the introgressed regions that are exclusive to that landrace are more likely to contain adaptive alleles. Such alleles were not identified specifically, though wild-domesticate breeding experiments have shown that wild barleys have alleles for several important agronomic phenotypes, including powdery mildew resistance, brittleness, flowering time, plant height, lodging, and yield [55, 56?].

4. Sunflower:

The common sunflower (*Helianthus annuus*) shows evidence of domestication in eastern United States [57, 58] with additional evidence of a possible second origin of domestication in Mexico [59]. Pre-Columbian *H. annuus* distribution spanned much of the Great Plains, from what is now north-central Texas up to and through Montana and North Dakota (see figure 1 of [?]).

Domesticated sunflower has long lived in sympatry with wild relatives like *H. petiolaris* and *H. bolanderi* and forms stable hybrid populations [60, 61, 62]. Many wild sunflowers are locally-adapted, and weedy hybrid populations share these adaptations [63]. However, the most striking example of adaptive introgression within *Helianthus* is that of the cucumberleaf sunflower, *H. debilis* ssp. *cucumerifolius*. Cucumberleaf sunflower is endemic to south-central Texas, and exhibits several adaptations to the region. Introgressive hybridization imparted locally-adapted alleles from *H. debilis* to *H. annuus* via introgressive hybridization [64]. These introgressed hybrids formed a new lineage of sunflower (*H. annuus* ssp. *texanus*, *H. a. texanus* hereafter) which displays *H. debilis*-like traits adaptive to south-central Texas climate and ecology. These adaptive *debilis*-like traits include resistance to herbivorous pests and an increased branching plant architecture, as well as higher overall fitness than *H. annuus* (as measured by higher seed production [?]). Although *H. annuus* and *H. a. texanus* are interfertile, *H. a. texanus* displays persistent phenotypic differences from *H. annuus* [?].

The genome of the common sunflower has been greatly influenced by introgression from wild relatives, due to both natural outcrossing events and concerted breeding efforts in crop improvement. *Helianthus* has several genes for downy mildew resistance, and each imparts resistance to one or more races of *Plasmopara halstedii*, one of the most agronomically important diseases in sunflower cultivation [65]. Some of these downy mildew resistance genes were found in wild relatives (including *H. argophyllus*, *H. tuberosus*, and *H. praecox*) and have been successfully bred into modern *H. annuus* [66]. PIArg, an allele found in wild silverleaf sunflowers (*H. argophyllus*, inbred line Arg1575-2), confers resistance to all known (20 or more) races of downy mildew [67] while others (PI1-PI11) are effective for one or more types [68]. Silverleaf sunflower has also been the focus of drought resistance breeding efforts [69] and *Phomopsis* resistance breeding efforts [70]. *H. annuus* shows signs of persistent introgressive hybridization with *H. petiolaris* with evidence of positive selection driving some of the genetic differentiation between the two species [71].

Recent investigations into the history of *Helianthus* introgression have implemented genomic methods. [?] analyzed transcriptome sequence variation on cultivated and wild *H. annuus*, *H. petiolaris*, and *H. argophyllus*. Using STRUCTURE, these authors found that introgressions from wild relatives exist on every chromosome in at least one modern line, covering over 10% of the genome. Of particular note is the modern line RHA 274, a modern line which was bred with *H. a. texanus* in the 1970s to restore a branching plant body architecture, which allows the plant to produce pollen for a longer period of time, increasing seed production. RHA 274 has several large introgression from *H. a. texanus*, including one at the site of

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 2011
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
population structure related		
fineStructure	phased haplotype	Lawson et al. 2012
Globetrotter	phased haplotype	Hellenthal et al. 2014

HaGNAT, the domestication gene associated with branching. These introgressed regions are not found in the non-branching lines Sunrise and VNIIMK8931, further suggesting that the *H. a. texanus* introgressed regions are causative.

Re-evaluating concepts of domestication

A framework in which crops were domesticated from a single population or even a single species is, in several instances, an oversimplification. An history of introgression during diffusion appears to be the rule for crops rather than the exception. Theory suggests that colonizing species will overwhelmingly be recipients of introgression from locally-adapted native species [?]. Crops, given their frequent history of diffusion from defined centers of origin, are therefore potential recipients of adaptive introgression.

With this in mind, certain aspects of crop evolution must be re-evaluated:

* Estimates of the initial domestication bottleneck may be skewed when introgression is not considered. Chromosomal regions experiencing introgression may have an altered effective population size (N_e) relative to non-introgressed regions depending on diversity within the donor taxon. For example, introgression from wild taxa with historically high N_e will lead to underestimates of the strength of the domestication bottleneck. Conversely, if the donor population has a relatively small effective population size, the opposite bias may be imposed upon bottleneck estimations. In most cases, the effective population size of the domesticated crop will be lower than that of the wild progenitor and wild relative populations.

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	[72]
Asian Rice (<i>Oryza sativa</i>)	<i>O. rufipogon</i>	X	X	X	[?]
Barley (<i>Hordeum vulgare</i>)	<i>H. v.</i> subsp. <i>spontaneum</i>	X	X	X	[?]
Sunflower (<i>Helianthus annuus</i>)	<i>H. argophyllus</i> , <i>H. bolanderi</i> , <i>H. debilis</i> , <i>H. petiolaris</i>	X	X	X	[?]
Cassava (<i>Manihot esculenta</i>)	<i>M. glaziovii</i>	X	X	X	[?]
Potato (<i>Solanum tuberosum</i>)	many	X	X	X	[73]
Tomato (<i>Solanum lycopersicum</i>)	<i>S. pimpinellifolium</i>	X	X	X	[74]
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		[?]
Soybeans (<i>Glycine max</i>)	<i>G. soja</i>	X	X		[75]
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		[76]
Grapes (<i>Vitis vinifera</i> subsp. <i>vinifera</i>)	<i>V. v.</i> subsp. <i>sylvestris</i>	X	X		[?]
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		[77]
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		[78]
Apple (<i>Malus domestica</i>)	<i>M. sylvestris</i> , <i>M. orientalis</i> , <i>M. baccata</i> , <i>M. sieversii</i>	X	X		[?]

* Estimates of the timing of domestication based on levels of sequence divergence may be affected when introgressed haplotypes are included. The directionality of this effect is likewise dependent on N_e of the donor population.

* Loci under selection during domestication are often identified based on signatures of substantially-reduced nucleotide diversity in the domesticated taxon relative to the wild progenitor and high allele frequency differentiation between these taxa. Introgression may alter these signatures and confound detection of domestication loci.

* When highly-introgressed or hybrid populations are selected for domestication (as in the case of potato and tomato), identification of original progenitor(s) and domestication centers is difficult. Determining whether a crop Crops arising from highly-interfertile complexes of wild relatives

Future studies in crop-wild introgression

Research has so far shown that adaptive crop-wild introgression has played a significant role in the domestication histories of many agronomically-important crops. However, the dynamics of the process in these cases are not yet fully understood. To what extent does the level of introgression across taxa depend on divergence time and/or mutation load between donor and recipient taxa? Can colonizing species and/or hybrid swarms serve as bridges for gene flow between previously allopatric taxa? At what geographic scale does adaptive introgression occur? Is introgression frequently restricted to very local populations, or is it often seen over broad geographic ranges? To what extent does this depend on the slope of environmental gradients such as temperature, precipitation, and elevation? How did the conscious, subconscious, and unconscious decisions of early farmers facilitate or hinder adaptive introgression into their crops during early domestication? How do the practices of contemporary farmers affect the process of adaptive introgression today?

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 clearly tied to a specific environment may include beneficial alleles that can be utilized in crop breeding.

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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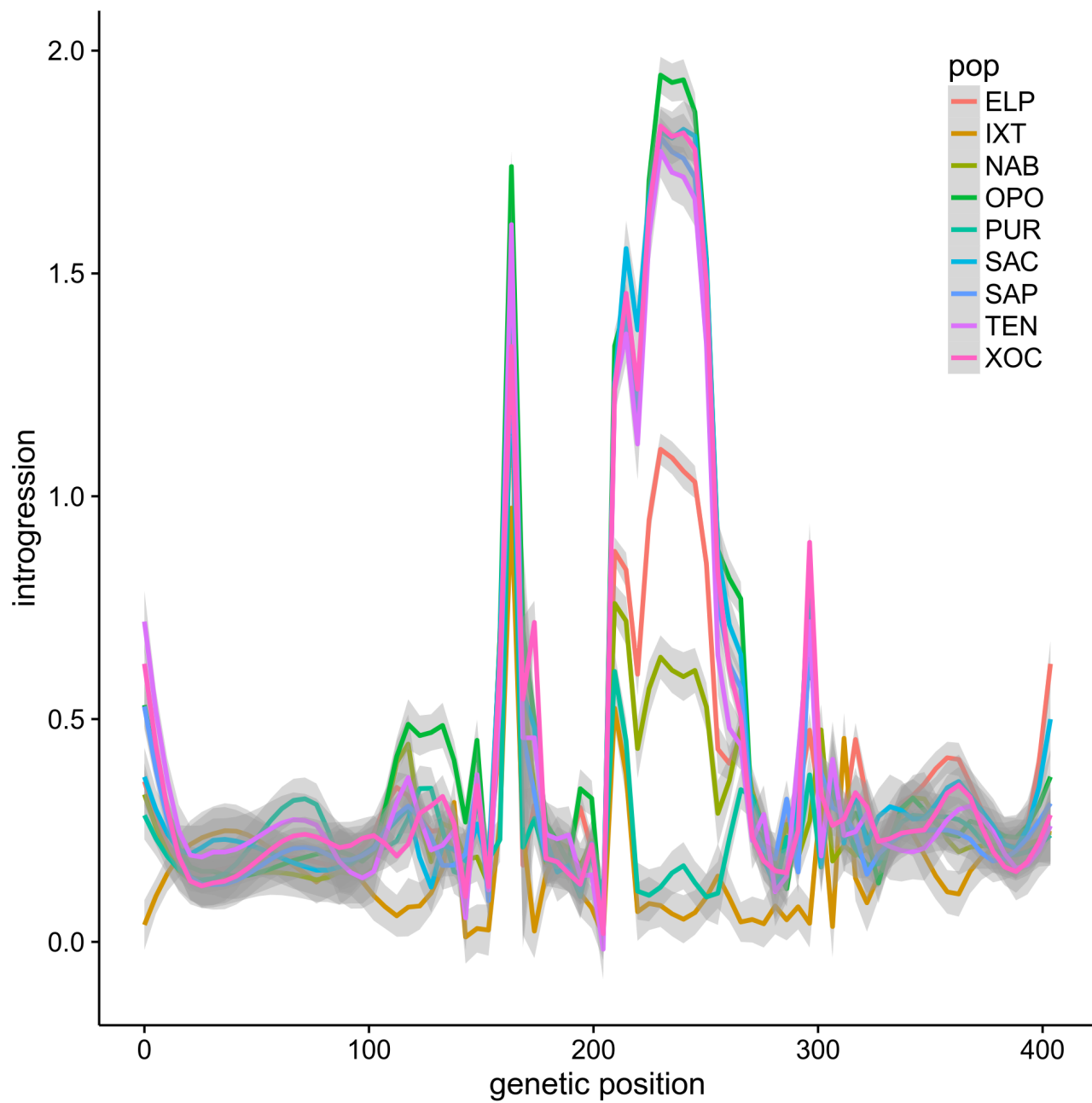


Figure 1: Li's caption here.

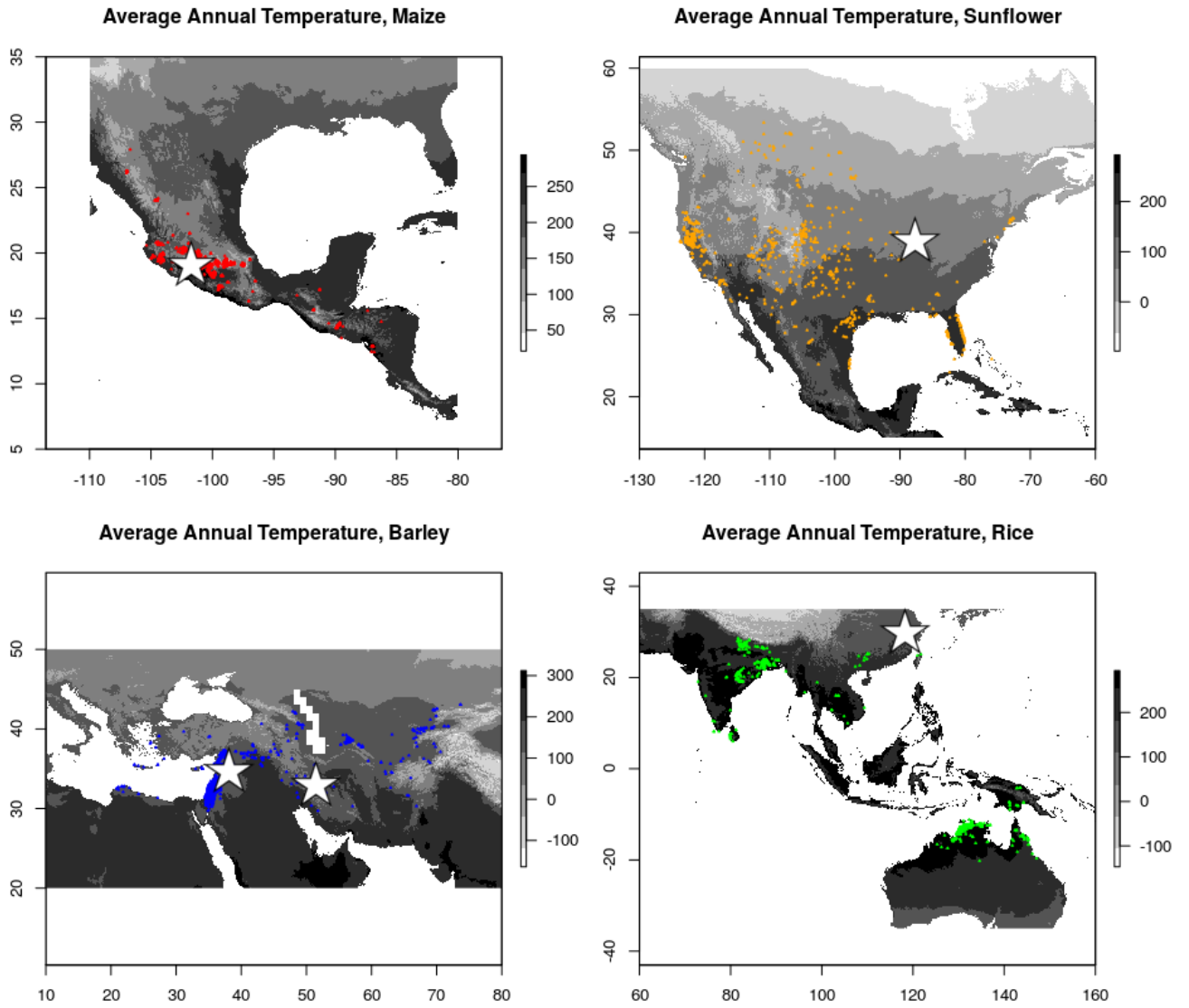


Figure 2: Map of the natural ranges of wild relatives of four domesticated crops, overlaid with average annual temperature.

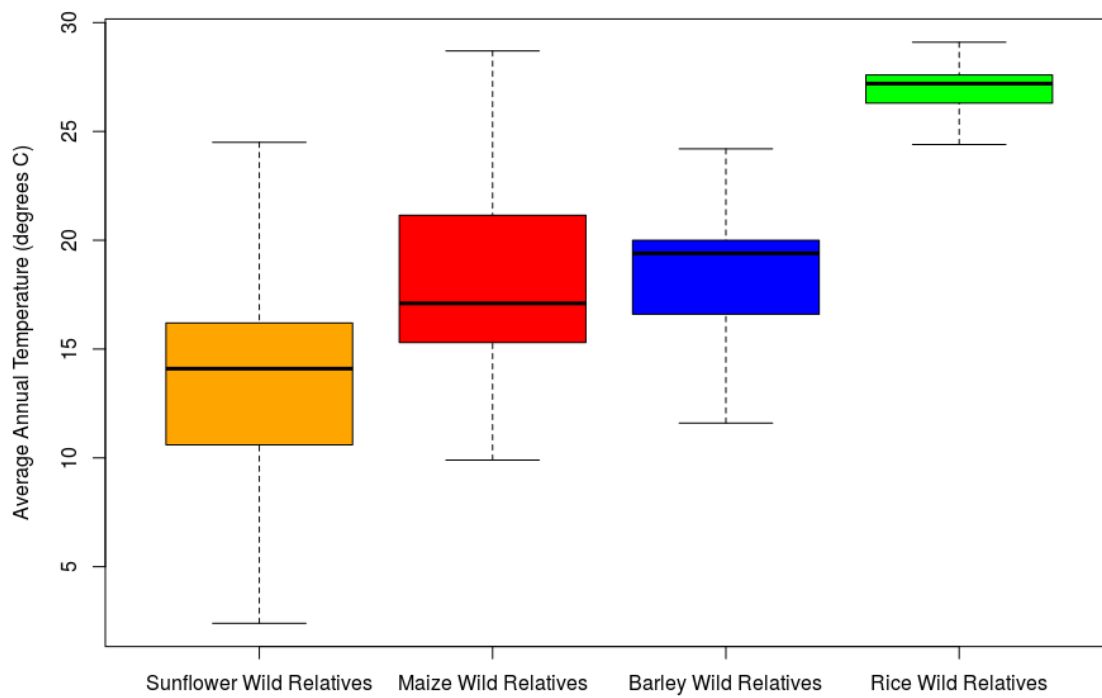


Figure 3: The distribution of average annual temperature experienced in the geographic home ranges of wild relatives interfertile with four crops