

# Review: Crop adaptation through historical introgression from wild relatives

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The traditional paradigm in crop domestication has been origin from a wild relative within one or more defined geographic centers followed by expansion to the modern-day extent of cultivation. Absent from this paradigm are the effects of hybridization between diffusing domesticates and closely-related, locally-adapted wild relatives outside the center of origin. New methods have recently been employed to detect genome-wide patterns of introgression in a number of species. In this review, we will: 1) briefly describe these methods and provide a summary of their recent application for detection of 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 recent applications

The recent availability of genome-wide resequencing and reduced-representation genotyping (*e.g.*, GBS and RAD-Seq) data combined with new analytical methods have facilitated comprehensive study of introgression across a number of species (**Table 1**).

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 to identify introgression across taxa [1, 2, 3].
2. In several instances, introgression has been found to be conserved across individuals and populations suggesting an adaptive role:
  - (a) Adaptive introgression has been discovered from Neanderthals and other archaic hominins into humans at loci controlling skin pigmentation, defense against pathogens, and tolerance of high altitude (reviewed in [4]).
  - (b) Introgression across butterfly species at protective color-pattern loci has conferred Müllerian mimicry ([5]; **Figure 1**).
  - (c) Adaptive introgression across mosquito species has spread insecticide resistance [6].
  - (d) Introgression across *Mimulus* (*i.e.*, monkeyflower) species has resulted in adaptation to pollinator preference and has contributed to speciation [7].
3. Identification of introgression across a wide range of taxa at loci controlling a variety of adaptive traits suggests it has been an important evolutionary force.

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

**Figure 1:** Wing coloration patterns in *Heliconius* and evidence for introgression across species based on Patterson’s  $D$ -statistic; adapted from [5].

## Crop adaptation through introgression

Over the last few years, several high-profile publications based on genome-wide data have documented introgression between crops and wild relatives outside putative domestication centers. A history of introgression during diffusion appears to be the rule for crops rather than the exception.

1. Crops, given their frequent history of diffusion from defined centers of origin, are ideal recipients of adaptive introgression. Theory suggests that such colonizing species will overwhelmingly be recipients rather than donors of introgression [8].
2. Empirical studies have revealed that introgression has occurred in many of the world’s most important crops (**Table 2**).
  - (a) Maize: As maize spread from a lowland center of origin into the Mexican highlands it received introgression from a highland-adapted wild relative [9].
  - (b) Sunflower: Domesticated sunflower has received substantial introgression from wild relatives post-domestication that has potentially reintroduced a branching morphology [10].
  - (c) Rice: Introgression appears to have played an important role in the history of rice. Japonica rice cultivars were likely domesticated first from wild rice populations in southern China, and indica cultivars later developed through hybridization of ancient japonica with new wild rice populations in south and southeast Asia [11].
  - (d) Barley: Landraces of barley show shared ancestry with geographically-proximate populations of wild relatives suggesting introgression [12].
  - (e) Olive: Hybridization between wild and domesticated olive has been prevalent throughout the Mediterranean Basin [13].
  - (f) Cassava: Substantial introgression from a closely-related wild species has been found in cassava, occurring both naturally and through a targeted breeding program for disease resistance [14].
3. Predictions regarding the likelihood of adaptive introgression in additional crops can be made through comparison of their centers of origin to both their current extent of cultivation and the distribution of wild relatives across environmental gradients (**Figure 2**).

**Table 2:** Overview of literature evaluating potential for crop-wild introgression in the world’s 15 most important crops including a column of references and a column summarizing major findings.

**Figure 2:** Multi-panel figure showing maps of crop centers of domestication, distributions of wild relatives, and current extent of cultivation across gradients of (a) temperature, (b) precipitation, and (c) elevation. This figure will illustrate the adaptive potential of wild-to-crop introgression.

## Reevaluating 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. A demography incorporating introgression from additional

sources appears to be more correct for many crops. With this in mind, certain aspects of crop evolution must be reevaluated:

1. The initial domestication bottleneck is most likely underestimated when introgression is not considered. Chromosomal regions experiencing introgression will potentially have increased effective population size relative to non-introgressed regions. Inferences regarding the strength of domestication bottlenecks should be revisited with this in mind.
2. The time since domestication based on levels of sequence divergence may be inflated when introgressed haplotypes from divergent taxa are included in estimates.
3. The influx of diversity through introgression may belie selection occurring on these genomic regions during domestication or local adaptation since one of the hallmarks of selection is reduced diversity.

## Future studies in crop-wild introgression

Additional study of introgression in agroecosystems could lead to advances in both basic and applied genetics:

1. Basic questions:
  - (a) To what extent does the level of introgression across taxa depend on divergence time between donor and recipient taxa?
  - (b) 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?
  - (c) To what extent have domesticates served as bridges for gene flow between previously allopatric taxa?
2. Applications:
  - (a) Loci underlying the domesticated phenotype that are potentially beneficial targets for crop improvement can be more clearly identified by removing the confounding population genetic signal of introgression.
  - (b) Adaptive introgression that is clearly tied to a specific environment may include beneficial alleles that can be utilized in crop breeding.

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