

# Adapting genomics to study the evolution and ecology of agricultural systems

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In the face of global change, agriculture increasingly requires germplasm with high yields on marginal lands. Identifying pathways that are adaptive under marginal conditions is increasingly possible with advances at the intersection of evolutionary ecology, population genetics, and functional genomics. Trait-based (reverse ecology) approaches have connected flowering time in *Arabidopsis thaliana* to single alleles with environment-specific effects. Similarly, genetic dissection of rice flooding tolerance enabled the production of near-isogenic lines exhibiting tolerance and high yields. An alternative gene-forward (forward ecology) approach identified candidate genes for local adaptation of *Arabidopsis lyrata* to heavy-metal rich soils. A global perspective on plant adaptation and trait correlations provides a foundation for breeding tolerant crops and suggests populations adapted to marginal habitats be conservation priorities.

## Addresses

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## Introduction

Understanding the distribution and abundance of plant species, while historically the purview of ecology, is increasingly urgent as we strive to meet the demands of a growing global population. We are experiencing the loss and degradation of agricultural land through multiple anthropogenic changes including irrigation-induced salinization, contamination by industrial processes, urban and suburban expansion, and global change in temperature and precipitation patterns [1]. Thus, plant production is being shifted to marginal land where we lack the resources to conduct green revolution agriculture with high fertilizer and water inputs. One strategy to

facilitate the use of these lands involves identifying plant germplasm with traits that are adapted to these conditions and breeding to combine these attributes with characteristics valued in elite germplasm. Studying natural populations that occur in marginal habitats from the combined perspective of evolutionary ecology and functional genomics can elucidate the molecular, physiological, and ecological ways by which plants adapt to these environments. We review examples at the intersection of evolutionary ecology and functional genomics from the past two years that are relevant to the development of germplasm for marginal lands.

## Local adaptation and phenotypic plasticity

Evolutionary ecology provides a conceptual framework that can be fruitfully tied to molecular genetics to yield insight into design principles for adaptation to marginal habitats. Two major ways plants adapt to their environment are local adaptation and phenotypic plasticity. ‘Local adaptation’ occurs when increasing fitness in one environment causes a fitness decrease when grown in other environments, that is, there is a ‘fitness trade-off’ between environments. These fitness trade-offs can lead to adaptive diversification and ultimately speciation [2–4]. Adaptive variation can also be caused by ‘phenotypic plasticity’, where the same genotype exhibits different phenotypes depending on the environment. Whether a species evolves fixed strategies (local adaptation), phenotypic plasticity, or a combination of fixed and plastic strategies depends on the costs and evolutionary constraints [5–7]. Molecular and physiological work is the only way to understand what limits plasticity in natural plants and to guide breeding efforts. Genotypes that bear a low cost of plasticity are ideal crops, as they can tolerate a broad range of habitats. On the other hand, phenotypes with fundamental constraints on plasticity may be best attained by breeding for adaptive variation that mimics local adaptation. For example, if improved sodium tolerance in a crop could simply come from upregulating cation-specific transporters involved in exclusion or sequestration under saline conditions, plastic expression would work well; if sodium tolerance through altered cation channel kinetics results in sensitivity to potassium or calcium levels, then channel configuration would need to be designed for particular  $\text{Na}^+/\text{K}^+/\text{Ca}^{2+}$  levels [8,9].

## Phenotypic trade-off axes

Macro-ecological studies comparing species across habitats and taxonomic groups have identified multiple phenotypic axes that represent fundamental phenotypic

**Glossary**

**Forward genetics:** The approach of dissecting the genetic basis of a known trait through controlled crosses or association mapping.

**Forward ecology:** The approach of trying to infer the ecological relevance of alleles identified as targets of local adaptation or recent selection through genome scans.

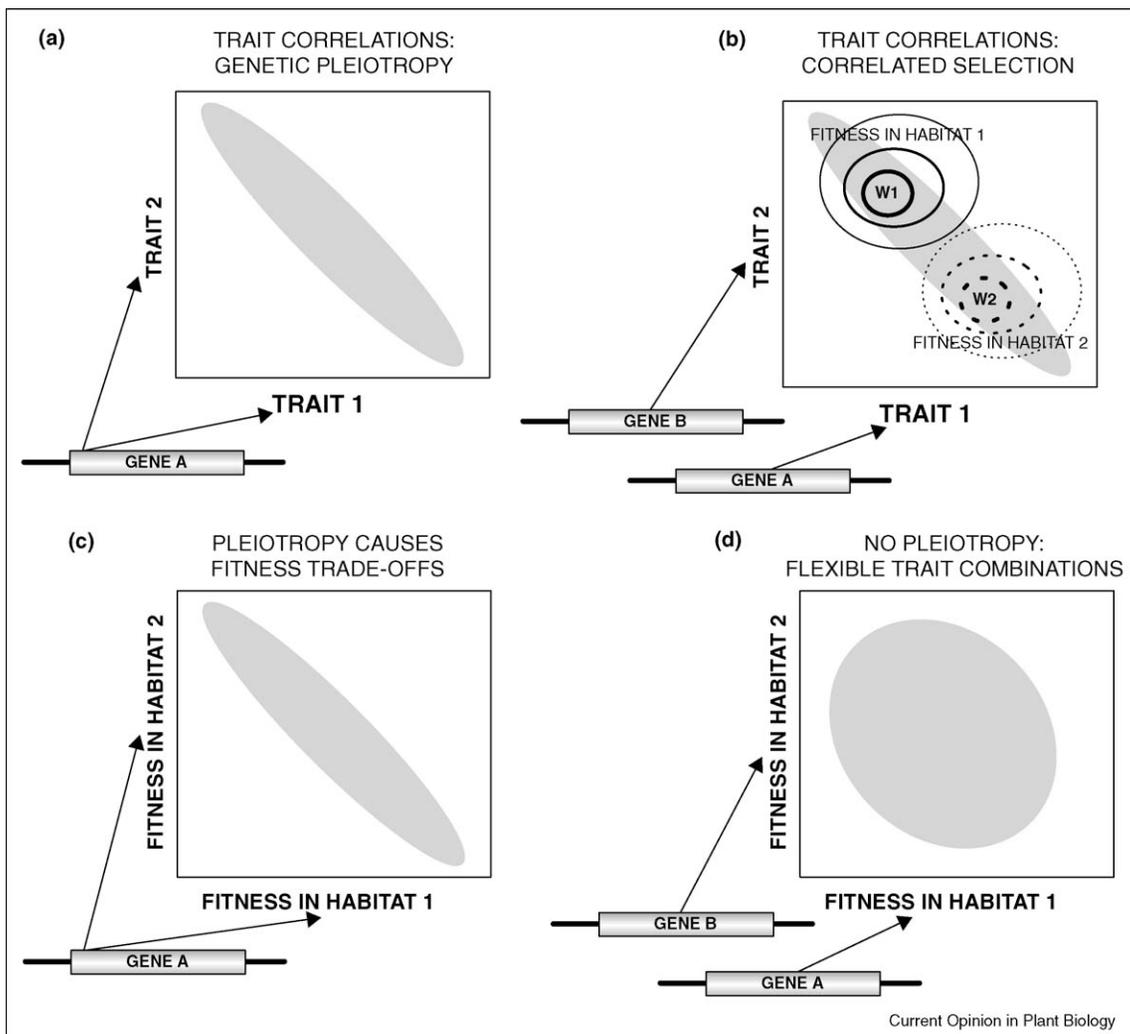
**Local adaptation:** The phenomenon where genotypes that occur in one habitat are more fit in that environment than in alternate environments.

**Phenotypic plasticity:** When a single genotype can produce different phenotypes in response to environmental cues.

**Pleiotropy:** When two traits are controlled by the same gene or pathway, such that altering the pathway to change one trait automatically changes the other.

**Reciprocal transplant:** An experimental design to test for local adaptation in which genotypes from multiple habitats are grown through a common garden generation and then planted back into all sampled habitats.

trade-offs shaping plant diversity [10,11\*]. The three most well-supported dimensions are: (i) firstly, leaf mass per area versus leaf lifespan, (ii) secondly, seed number versus seed size and subsequent seedling survival, and (iii) lastly, plant height at maturity versus early growth rate and shade tolerance. These trait axes can influence many aspects of plant biology. For example, plant height enables increased competitive ability under light limiting conditions, but investing in stems reduces resources for reproduction [12], can increase the risk of mechanical damage [13], and reduces tolerance to water shortage [14]. These trait correlations can arise in two distinct ways and have implications for adaptation (Figure 1). First, there can be immediate physiological changes in two traits simultaneously due to ‘pleiotropy’ when a common pathway underlies both characters. Second, the fitness

**Figure 1**

Conceptual diagram of the implications trait correlations have for adaptation and breeding efforts. Trait correlations can arise due to (A) pleiotropy, where one gene affects multiple traits or (B) correlated selection, where different habitats select for different optimum trait combinations that induce correlations. Pleiotropy can have direct consequences for fitness trade-offs across habitats, as shown in (C). On the other hand, if trait correlations are due to correlated selection rather than pleiotropy, then breeding can uncouple fitness in different habitats without facing trade-offs (D).

consequences of changing one trait can impose selection on another trait. If traits are genetically correlated due to pleiotropy they impose hard constraints to adaptation and breeding efforts will be unable to decouple them (but see [15]). On the other hand, traits that are correlated because of natural selection may be manipulated independently of one another to attain preferred trait combinations. For example, if sodium tolerance in a cultivar is due to altered cation channel dynamics that affect potassium or calcium metabolism, the constraints are hard, while Na<sup>+</sup>-specific vacuolar exclusion through a specific transporter and osmotic tolerance through plastic deployment of osmoprotectants can likely be bred together [8,9].

### Reciprocal transplant experiments

The key to connecting phenotypic trade-offs with fitness trade-offs is to understand how traits are related to plant fitness across different environments. To determine which traits are adaptive in a given context, experiments measuring plant fitness must be performed under realistic conditions, preferably in the field. The canonical ‘reciprocal transplant’ experiment takes genotypes from multiple habitats and grows each genotype in each habitat [16,17<sup>••</sup>]. Fitness traits, such as seed production, are then regressed upon multiple phenotypes to determine how natural selection acts on these traits in different habitats [18,19]. Recently, coastal and inland ecotypes of the yellow monkey flower *Mimulus guttatus* were reciprocally transplanted to show strong differential selection on flowering time that favored local genotypes [20<sup>••</sup>]. There was also evidence of differential salt spray tolerance between coastal and inland ecotypes. Once adaptive traits are identified by regressing fitness onto phenotypes, genetic tools can be used to dissect their molecular basis. An alternative to the transplant experiment is Fst–Qst comparisons (reviewed recently in [21]), though this suffers from severe power limitations under realistic sampling designs and biological scenarios [22].

### Forward genetics

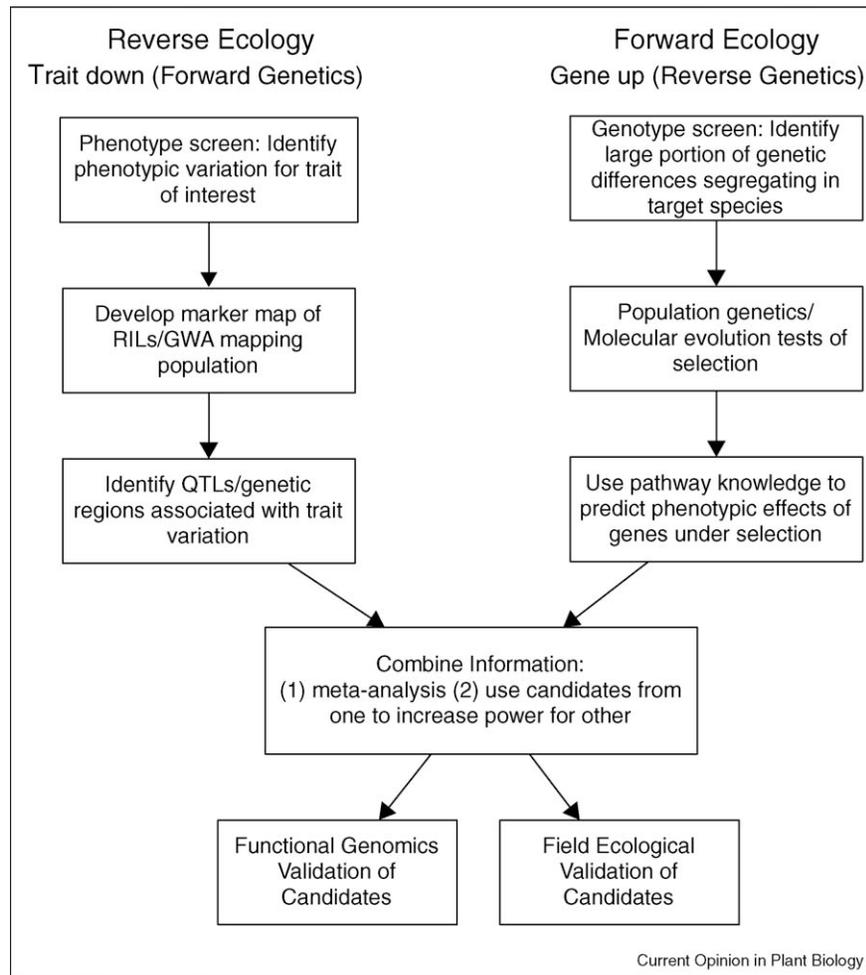
The traditional ‘forward genetic’ approach is to cross well-characterized homozygous parents to generate a population of recombinant inbred lines (RILs) that shuffle the parental alleles to identify loci correlated with quantitative traits (QTLs). In the *M. guttatus* example above, crossing coastal and inland genotypes enabled the genetic basis of salt tolerance to be mapped to several candidate loci [23]. Another recent example in *Avena barbata* found evidence for QTLs underlying trade-offs between allocations to vegetative versus reproductive biomass [24]. The precision of QTLs depends on the recombination breakpoints obtained in the crosses and the number of markers used to pinpoint them, sample size, and heritability of traits. Candidate QTLs require independent crosses or association mapping studies to cross-validate them. Genome wide association (GWA) mapping measures phenotypes in a diverse set of naturally occur-

ring genotypes that are typed at a large number of markers across the genome. Many markers, typically hundreds of thousands, are needed so that some will be linked to causal alleles. GWA mapping has the advantage of screening a wide variety of natural alleles, but the disadvantages that population structure can lead to a large number of false-positives and that the power to detect an allele depends on its frequency in the sample [25,26]. However, statistical techniques to address the issue of population structure are being developed and applied [27<sup>•</sup>,28]. In addition, imputation methods can enable different marker sets to be combined as well as missing data to be inferred from linked loci to facilitate meta-analysis [29,30]. Efforts to association map stress tolerance traits are underway in a number of crop plants and their near relatives (e.g. [31,27<sup>•</sup>]). A notable innovation is nested association mapping (NAM), which combines the strengths of QTL and association mapping approaches by creating multiple RIL populations using diverse cultivars as parents — this was recently carried out in maize to identify alleles for flowering time [32<sup>••</sup>,33]. Crosses and association mapping approaches are highly complementary approaches, since they can give independent information [34,27<sup>•</sup>]; for example, testing for the effects of candidate genes from a GWA study in an outbred mapping population in *Arabidopsis thaliana* enabled greatly increased power to detect potential causal alleles for flowering time variation [35].

All genetic mapping requires final confirmation through the manipulation of single genes or genetic regions. For example, Hanikenne *et al.* [36<sup>••</sup>] used RNAi to knock down candidate genes for heavy-metal accumulation of *Arabidopsis halleri* identified by previous QTL [37,38] and expression studies [39]. A complementary technique to gene knockouts or knockdowns is to develop near-isogenic lines (NILs) with the candidate allele introgressed into another genetic background. This has the benefit of studying the effect of a natural allele in a standard background. The introgression approach is essential to marker-assisted breeding and has recently been successful in transferring natural *snorkel1* and *snorkel2* [40<sup>••</sup>] and *sub1* [41] alleles present in deepwater rice varieties into high-yield rice cultivars to confer flooding tolerance.

Ecological genomics combines evolutionary ecology with the forward genetic strategy to trace adaptation through plant traits down to causal alleles (Figure 2). This approach, which we term ‘reverse ecology’ because it goes from ecological factors to genes, has met with great success in the study of flowering time with the model plant *A. thaliana*. Both QTL and mutational studies identified candidate genes for flowering time that were subsequently found to vary latitudinally across populations [42], even after accounting for population structure [43,44,35]. GWA mapping using a global sample of genotypes successfully recovered some of these loci

Figure 2



Chains of inference in ecological genomics. Reverse ecology and forward ecology yield independent information that can be combined in the search for genes and pathways underlying adaptation.

despite a high false-positive rate [25]. Current work using ecotypes and mutants planted into multiple common garden field sites within *A. thaliana*'s native range suggests that these alleles exhibit local adaptation. Further refining the connection between genotype and environment, these studies enable the estimation of allele-specific fitness effects under different temperatures and day length regimes [45<sup>••</sup>]. Ultimately, the environment can be dissected into components such as moisture, temperature, and day length that can be used in the framework of niche modeling to determine which alleles are tracking which environmental variables [46,47].

### Forward ecology

In contrast to the well-established 'forward genetic' (reverse ecology) approach to ecological genomics, a 'forward ecology' (reverse genetic) strategy is increasingly possible in the era of high-throughput sequencing

(Figure 2). Population genetics provides models of genetic evolution that can be used to identify genes that are under directional or balancing selection without having to do any plant biology. For example, resequencing 121 candidate cold hardiness genes in Douglas Fir (*Pseudotsuga menziesii* var. *menziesii*) showed up to eight loci with the signature of natural selection after accounting for demography [48]. Increasingly, this approach can be taken on a genomic scale. For instance, genotyping *Arabidopsis lyrata* population samples originating from heavy-metal-rich serpentine soils and neighboring granitic outcroppings in North America has identified hundreds of candidate genes that differ in frequency between habitats using the *Arabidopsis* tiling array [49<sup>•</sup>]. Subsequent deep resequencing verifies that many of these genes differ in sequence in a larger number of lines from these populations [50]. Several of these candidates show evidence of differential natural selection across soil types in both the

screened populations and an independent set of populations from Scotland [50]. The challenge in this approach is to then relate candidate adaptation genes to phenotypic pathways; this requires screening a large number of phenotypes under multiple environmental conditions, for which we currently lack a standardized set of traits and growth conditions.

Both trait-down (forward genetics) and gene-up (forward ecology) approaches generate hypotheses for genetic pathways that are involved in ecological adaptation. However, the functional genomics tools to validate adaptive alleles are largely restricted to model and submodel organisms. For experiments in these species to be applicable to particular crops of interest, the generality of adaptive pathways needs to be understood. Pathways or physiological processes that are common to all plants likely are involved in the fundamental trade-offs that generate macro-ecological trait correlations; adaptation along these axes is likely to be readily generalized across taxa. Pathways that are restricted to particular taxonomic groups may represent adaptive traits that have not had time to evolve in species used for agriculture; these may be particularly fruitful targets for engineering novel adaptive trait combinations.

### Looking forward

Since adaptation through natural selection occurs through rare beneficial mutations increasing in frequency over tens to thousands of generations, natural populations of plants represent a precious resource. Despite advances in plant biology, we are unlikely in the near future to be able to predict which mutations will produce beneficial traits. Thus, adaptive alleles are one major target of conservation — germplasm of crops and crop relatives should be collected broadly and conserved for future genetic and phenotypic screening efforts [51]. However, populations are not fixed but continue to evolve on contemporary timescales. A second major target of conservation should therefore be habitats where plant species of interest are exposed to biotic and abiotic stresses that select for adaptive alleles. These protected populations, if properly managed, could provide a living reservoir of alleles that continually evolve in step with global change and novel pathogens. Increased understanding of the current distributions of genetic and phenotypic variation across agronomically relevant taxa in relation to ecological selection will provide a strong foundation for crop development in a limited and changing world.

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