

## Commentary

### Local adaptation in The model plant

Studies of local adaptation are among the most compelling sources of evidence for the role of natural selection in the evolution of divergence within species. The long-standing gold standard to test the hypothesis that populations are locally adapted is the reciprocal transplant experiment. The basic approach of a reciprocal transplant experiment is to test the performance (fitness) of individuals both in their native habitat and simultaneously in a foreign habitat. Local adaptation is determined to have occurred if native individuals have greater fitness than foreign transplants in any given habitat. Adaptation is often thought to come at a cost, such that local adaptation to one habitat leads to lower fitness in foreign habitats and results in a pattern of reciprocal home-site advantage (Fig. 1). Since the famous mid-twentieth century reciprocal transplant experiments of Clausen *et al.* (1940), numerous other researchers have found reciprocal home-site advantage in transplant studies (Leimu & Fischer, 2008; Hereford, 2009; Anderson *et al.*, 2011). These widespread results suggest that habitat-mediated natural selection plays a pervasive role in the maintenance of genetic variation and evolution of plant species. Given the abundant evidence for habitat-mediated selection, it is surprising that reciprocal transplant experiments have yet to provide strong evidence for reciprocal home-site advantage in *Arabidopsis thaliana*. However, this is no longer the case. In this issue of *New Phytologist*, Ågren and Schemske (pp. 1112–1122) report the highly anticipated results of a multi-year reciprocal transplant experiment between populations of *A. thaliana* that clearly demonstrates reciprocal home-site advantage in this important model system.

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Ågren and Schemske’s work is a landmark and sure to be highly cited. Beyond the glamour of their accomplishment in a widely studied plant species lies a well-executed study that is among the best reciprocal transplant experiments in any organism. Their experiment extended almost to the limits of the

European range of *A. thaliana*, with one of the populations in Italy and the other in Sweden. Given the distance involved, it is remarkable that the study was conducted over five different years and carefully designed to examine the impact of local environmental conditions on multiple life-history stages.

One of the most striking aspects of the study is how variable the results of the experiments were over the five seasons. At the Italian field site, the local Italian plants outperformed the Swedish plants anywhere from 3.1- to 22.2-fold depending on the year. And while local survival was greatest in both sites over 5 yr, overall fitness of local plants in Sweden was significantly greater in only three out of the five seasons. Such variation demonstrates how precious long-term studies are to our understanding of local adaptation and suggests that researchers cannot rule out reciprocal home-site advantage from a single season of research.

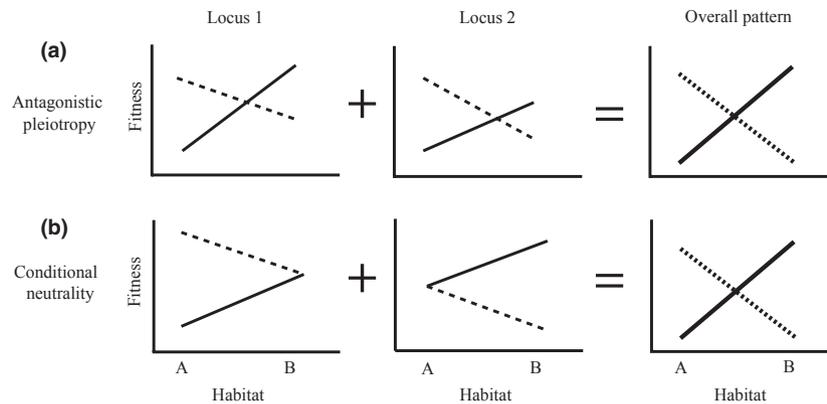
Their study also does a good job of linking the patterns of adaptation to the environmental variables responsible for local natural selection. For example, Ågren and Schemske found that the survival of local Swedish plants was greatest relative to the Italian plants in years when the minimum soil temperatures were lowest in Sweden, thus suggesting the relative benefits of cold adaptations in Swedish populations depend on winter conditions. Further, Italian plants flowered over a month earlier than Swedish plants in Italy, which may reflect adaptations to escape from the summer drought of the Mediterranean climate.

#### A golden age for local adaptation in *Arabidopsis*

Ågren and Schemske’s study comes on the heels of two excellent papers in *Science* that contributed an exciting new population genomic understanding of local adaptation in *A. thaliana*. Fournier-Level *et al.* (2011) conducted a genome-wide association study (GWAS) on fitness differences among accessions planted in four common gardens across Europe. Their study detected a number of single nucleotide polymorphisms (SNPs) associated with fitness in the field. They then found that many of those fitness SNPs were also associated with climatic variation across the continent. In an inversion of that approach, Hancock *et al.* (2011) first identified a set of climate associated SNPs across 948 accessions and then used those findings to predict the relative fitness of accessions grown in a common garden in France. Both studies display the immense potential of population genomic approaches and provide a template for merging association studies with field experimentation to understand how adaptive alleles are distributed across the natural landscape.

#### The loci of local adaptation

Many *Arabidopsis* biologists may be tempted to treat Ågren and Schemske’s results as sufficient evidence that reciprocal home-site



**Fig. 1** Two hypotheses of how an overall pattern of reciprocal home-site advantage can emerge from underlying locally adaptive loci. (a) Antagonistic pleiotropy (adaptive trade-offs), where individuals with the A allele (dashed line) have the highest fitness in habitat A and individuals with the B allele (solid line) do best in habitat B. (b) Conditional neutrality, where A and B alleles are superior in their native habitat but have no effect in the foreign habitat. Conditionally neutral alleles could sum over multiple loci to result in an overall pattern of reciprocal home-site advantage without trade-offs at the individual locus level.

advantage occurs in *A. thaliana*, and feel no need to conduct reciprocal transplant experiments of their own. This would be a mistake. There is still much that can be learned from reciprocal transplant experiments, including which environmental factors drive local adaptation in *A. thaliana* across Eurasia and what phenotypic traits have evolved in response to that selection. Further, there have been surprisingly few studies on how individual genetic loci actually contribute to local adaptation across habitats.

Quantitative trait locus (QTL) mapping studies in the context of a reciprocal transplant experiment have only been conducted in *Avena barbata* (Gardner & Latta, 2006), *Boechera stricta* (Anderson *et al.*, 2012), *Hordeum spontaneum* (Verhoeven *et al.*, 2008), and *Mimulus guttatus* (Hall *et al.*, 2010). In most cases, those studies found that individual loci had effects on fitness in one habitat, but no detectable effect in alternative habitats. Similarly, Fournier-Level *et al.* (2011) found that only 12 of their 797 top SNPs had associations with fitness at more than one of their four field sites. The pattern of fitness advantage in only one habitat is often referred to as conditional neutrality (Fig. 1). By contrast, theoretical models have often predicted individual loci underlying local adaptation will show a pattern of reciprocal home-site advantage (e.g. antagonistic pleiotropy) that mirrors (Fig. 1) the overall pattern of fitness of transplanted individuals because of presumed trade-offs involved in adaptation (Kawecki & Ebert, 2004). While such trade-offs have now been shown to occur at the individual locus scale in the case of a chromosomal inversion (Lowry & Willis, 2010), it has never conclusively been shown for an individual gene.

There are many challenges for studies examining the role of individual genes in local adaptation (Anderson *et al.*, 2011, 2012). The combination of genetic transformation with reciprocal transplant experiments would be the ultimate way to test the hypothesis of adaptive gene function, but such studies are prohibitive because of ethical and legal considerations. Therefore,

this kind of research will primarily have to rely on hybrid mapping populations and introgression lines for the foreseeable future. Perhaps the greatest challenge for understanding the genetics of local adaptation is that the effect size of many loci involved may be too small to detect in nature without an impossibly large field experiment (Rockman, 2012). It is now becoming increasingly clear that local adaptation involves numerous phenotypic traits, most of which have a complex genetic basis. This realization underlies one of the major challenges that will confront studies of adaptive evolution in the 21st century and suggests the benefits of studies that merge population genomics and field experimentation (e.g. Fournier-Level *et al.*, 2011). Even so, small effect alleles are likely to bedevil studies of local adaptation well into the future, especially when functional alleles are rare (Rockman, 2012).

## The future

One potential promising way forward is to take a systems biology approach and incorporate reciprocal transplant experiments with genetical genomics (i.e. Jansen & Nap, 2001). Expression QTL (eQTL) mapping and metabolomics should be integrated with future reciprocal transplant experiments to identify ‘modules’ involved in local adaptation and better understand the complexity of the process.

Finally, it is important to note that Ågren and Schemske’s study incorporated a large set of hybrid recombinant inbred lines, which will allow them to conduct QTL mapping to determine how individual loci contribute to adaptive traits and fitness between Italian and Swedish plant populations. Genetic mapping in this reciprocal transplant experiment will also provide the opportunity to address the relative roles of conditional neutrality and antagonistic pleiotropy for local adaptation in this important model system. I, for one, am very excited to see what those results will hold.

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## References

- Ågren J, Schemske DW. 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist* 194: 1112–1122.
- Anderson J, Lee CR, Rushworth C, Colautti CR, Mitchell-Olds T. 2012. Genetic tradeoffs and conditional neutrality contribute to local adaptation. *Molecular Ecology*. doi: 10.1111/j.1365-294X.2012.05522.x
- Anderson JT, Willis JH, Mitchell-Olds T. 2011. Evolutionary genetics of plant adaptation. *Trends in Genetics* 27: 258–266.
- Clausen J, Keck DD, Hiesey WM. 1940. *Experimental studies on the nature of species. I. Effect of varied environment on Western North American plants*. Washington, DC, USA: Carnegie Institution of Washington, Publications No. 520.
- Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM. 2011. A map of local adaptation in *Arabidopsis thaliana*. *Science* 334: 86–89.
- Gardner KM, Latta RG. 2006. Identifying the targets of selection across contrasting environments in *Avena barbata* using quantitative trait locus mapping. *Molecular Ecology* 15: 1321–1333.
- Hall MC, Lowry DB, Willis JH. 2010. Is local adaptation in *Mimulus guttatus* caused by trade-offs at individual loci? *Molecular Ecology* 19: 2739–2753.
- Hancock AM, Brachi B, Faure N, Horton MW, Jarymowycz LB, Sperone G, Toomajian C, Roux F, Bergelson J. 2011. Adaptation to climate across the *Arabidopsis thaliana* genome. *Science* 334: 83–86.
- Hereford J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173: 579–588.
- Jansen RC, Nap JP. 2001. Genetical genomics: the added value from segregation. *Trends in Genetics* 17: 388–391.
- Kawecki TJ, Ebert D. 2004. Conceptual issues in local adaptation. *Ecology Letters* 7: 1225–1241.
- Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3: e4010.
- Lowry DB, Willis JH. 2010. A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. *PLoS Biology* 8: e1000500.
- Rockman MV. 2012. The QTN program and the alleles that matter for evolution: all that's gold does not glitter. *Evolution* 66: 1–17.
- Verhoeven KJ, Poorter H, Nevo E, Biere A. 2008. Habitat-specific natural selection at a flowering-time QTL is a main driver of local adaptation in two wild barley populations. *Molecular Ecology* 17: 3416–3424.

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