

NEWS AND VIEWS

PERSPECTIVE

A hot topic: the genetics of adaptation to geothermal vents in *Mimulus guttatus*

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Identifying the individual loci and mutations that underlie adaptation to extreme environments has long been a goal of evolutionary biology. However, finding the genes that underlie adaptive traits is difficult for several reasons. First, because many traits and genes evolve simultaneously as populations diverge, it is difficult to disentangle adaptation from neutral demographic processes. Second, finding the individual loci involved in any trait is challenging given the respective limitations of quantitative and population genetic methods. In this issue of *Molecular Ecology*, Hendrick *et al.* (2016) overcome these difficulties and determine the genetic basis of microgeographic adaptation between geothermal vent and nonthermal populations of *Mimulus guttatus* in Yellowstone National Park. The authors accomplish this by combining population and quantitative genetic techniques, a powerful, but labour-intensive, strategy for identifying individual causative adaptive loci that few studies have used (Stinchcombe & Hoekstra 2008). In a previous common garden experiment (Lekberg *et al.* 2012), thermal *M. guttatus* populations were found to differ from their closely related nonthermal neighbours in various adaptive phenotypes including trichome density. Hendrick *et al.* (2016) combine quantitative trait loci (QTL) mapping, population genomic scans for selection and admixture mapping to identify a single genetic locus underlying differences in trichome density between thermal and nonthermal *M. guttatus*. The candidate gene, R2R3 MYB, is homologous to genes involved in trichome development across flowering plants. The major trichome QTL, Tr14, is also involved in trichome density differences in an independent *M. guttatus* population comparison (Holeski *et al.* 2010) making this an example of parallel genetic evolution.

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The challenge of evolutionary genetics

Due to their sessile lifestyle, plants are particularly tractable systems for discovering the genetic basis of local adaptation. Botanists have been empirically testing whether populations are locally adapted since the early 19th century when Clausen *et al.* (1941) performed their pioneering reciprocal transplant experiments. Due to similar studies across many species, we now know that local adaptation is ubiquitous in plants (reviewed in Hereford 2009). What still remains to be discovered is, Which traits and genes underlie local adaptation? Is local adaptation due to few loci of large effect or many loci of small effect? Are adaptive mutations primarily protein coding or regulatory in nature? Is parallel evolution due to parallel genetic changes? In order to address any of these questions, the individual genes responsible for adaptation to different local environments must first be identified. This is a difficult task as no one method of genetic analysis is ideal. Population genetic scans for selection effectively find loci that are outliers in terms of genetic differentiation, but because of population structure, these outlier loci could be divergent due to neutral processes rather than natural selection. On the other hand, QTL mapping breaks up loci linked by neutral demographic processes with controlled crosses, but due to the limited resolution of recombination over just a few generations of crossing, a QTL region is much larger than an individual causative locus. Additionally, while genes for putatively adaptive traits have been discovered in the laboratory, few studies have found the genetic basis of a phenotype that has been shown to be ecologically relevant in nature.

Mimulus guttatus is an excellent system in which to study the genetic basis of adaptation. This widespread wildflower occupies a diversity of environments across western North America including extreme soil types such as old copper mine tailings and serpentine soils (Wu *et al.* 2008). *Mimulus guttatus* is also one of the few plants able to grow on geothermal vents in Yellowstone National Park. These vents are extreme environments with soil temperatures reaching over 50 °C. However, because of these high soil temperatures, geothermal vents create a unique winter growing season for *M. guttatus*. While the rest of Yellowstone is blanketed in snow November through May, a narrow layer of warm air above the vent soil surface melts the snow and provides a temperate, moist growth environment for *M. guttatus* (Fig. 1A and C). By summer, the growing season of neighbouring non-thermal *M. guttatus* populations, soils in these vents have completely dried out.

While there is variable genetic structure between thermal and nonthermal populations, thermal *M. guttatus* have several phenotypes that allow them to occupy their extreme



Fig. 1 (A) An image of *M. guttatus* growing on geothermal vents surrounded by snow in Yellowstone National Park in winter, (B) an image of a nonthermal *M. guttatus* population flowering in the summer in Yellowstone National Park, (C) an image of thermal-adapted *M. guttatus* rosettes covered with trichomes and snowmelt, (D) an image of smooth-leaved nonthermal *M. guttatus* rosettes. All images are credited to Margaret F. Hendrick.

environment: early flowering under short days, an annual life cycle, dwarfism, greater allocation to reproduction and increased trichome density (Lekberg *et al.* 2012). Trichomes, hairs that occur on a plant's surface, have many important functions. In addition to commonly known advantages such as plant defence against herbivores, increased trichome density decreases leaf wettability (Brewer *et al.* 1991). Having low leaf wettability is advantageous in cold and high precipitation environments as wet leaves freeze more easily (Aryal & Neuner 2010) and have less efficient photosynthetic gas exchange (Brewer *et al.* 1991). Therefore, having increased trichome density should allow thermal *M. guttatus* to both avoid freezing and maintain photosynthetic efficiency during their cold snowy growing season.

Combining approaches advances the field

To identify the genetic basis of differences in trichome density between thermal and nonthermal *M. guttatus* populations, Hendrick *et al.* (2016) combined QTL mapping, population genomic and admixture mapping approaches. First, plants were collected from thermal and nearby nonthermal Yellowstone populations and grown in a common greenhouse environment. Controlled crosses were performed to create an F_2 QTL mapping population. F_2 individuals were genotyped at previously detected *M. guttatus* trichome QTL (Holeski *et al.* 2010). This approach identified a single major effect QTL on chromosome 14, Tr14, which controlled ~50% of the segregation variance in trichome density. To narrow the QTL region, Hendrick *et al.* (2016) next pooled wild individuals from the thermal and nonthermal populations and examined genomewide genetic differentiation (F_{st}). Within the Tr14 region, the

authors found a small area of elevated F_{st} spanning six genes. One of these highly differentiated loci, an R2R3 MYB transcription factor, is a strong functional candidate. R2R3 MYBs are involved in trichome development in many species of flowering plants including *Arabidopsis*, cotton, poplar and *Anthirrinum*. To further establish whether this functional candidate gene was involved in trichome differentiation, Hendrick *et al.* (2016) collected admixed *M. guttatus* populations showing segregating variation in trichome density located between thermal and nonthermal sites. Admixture mapping is a powerful tool for refining QTL location because it takes advantage of the many generations of recombination that have occurred in a wild hybrid population. Individuals from admixed populations were grown in a common garden and genotyped at markers spanning the Tr14 QTL region. The authors observed a strong association between genotype at the candidate R2R3 MYB locus and trichome density in the admixed individuals. Although the authors have not yet confirmed this candidate locus with functional tests, their combined mapping approach provides multiple strong lines of evidence that the R2R3 MYB controls differences in nonthermal and thermal *M. guttatus* trichome density.

With a candidate trichome locus in hand, exciting questions about the general workings of natural selection that were posed at the beginning of this article can now begin to be answered. In this study, a trait involved in adaptation to an extreme microenvironment is due to a single locus of large effect rather than many loci of small effect. The locus is a transcription factor and therefore involved in gene regulation, but further work will be necessary to determine whether the causal mutations are protein coding or *cis*-regulatory. A previous QTL study found that Tr14 controls

differences in trichome density between two different and geographically distant *M. guttatus* populations (Holeski *et al.* 2010). Given differences in the life history and ecology of these populations, it is most likely that trichome density evolved independently in these two studies (Hendrick *et al.* 2016). Therefore, parallel trichome evolution within *M. guttatus* is due to parallel genetic changes at the level of the QTL.

The future of the genetics of adaptation

Hendrick *et al.*'s (2016) study illustrates the power of an integrative genetic mapping approach to identify genes involved in local adaptation. By combining population and quantitative genetics, the authors went from a QTL region hundreds of kilobases wide to a single strong candidate locus. Although generating multiple kinds of genetic mapping data is labour-intensive, it is clearly the future of the field. The next step in understanding the genetic basis of adaptation is to functionally test candidate genes detected using combined mapping approaches. With the advent of revolutionary functional genetic techniques such as CRISPR-Cas9, this will become possible in more and more systems as time goes on.

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