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Commentary

Local adaptation or foreign advantage? Effective use of a single-test site common garden to evaluate adaptation across ecological scales

Since the groundbreaking work of Turesson (1922) and Clausen and colleagues (e.g. Heisey *et al.*, 1942; Núñez-Farfán & Schlichting, 2001), local adaptation of plant populations has been assessed in plant species with a variety of life histories and habitats. Several reviews and quantitative syntheses have determined that local adaptation is pervasive, although not universal, across plant species (e.g. Hoeksema & Forde, 2008; Hereford, 2009), even in recently introduced invasive taxa (Oduor *et al.*, 2016). Local adaptation may often be a consequence of fitness trade-offs between habitats (Kawecki & Ebert, 2004), but can also be affected by demographic factors such as drift, gene flow and mutation-rate variation. Although widely acknowledged as important, determining the best definition, and best measures of local adaptation particularly across diverse life histories remain a source of disagreement and a challenge; there is a need for models where fitness components are evaluated across life stages. In this issue of *New Phytologist* Peterson *et al.* (pp. 345–356) expertly surmount complications of measuring local adaptation in common-garden experiments using several populations of the geographically widespread monkey flower, *Mimulus guttatus* with variable life histories and ecologies.

‘Common-garden studies such as this can help target the most informative comparisons of populations and focal traits.’

Local adaptation is commonly operationally defined in two ways: ‘local vs foreign’, where individuals from a focal population or habitat outperform conspecific individuals transplanted from other populations or habitats, or as ‘home vs away’, (or sympatric vs allopatric) where a focal genotype performs better in its habitat of origin than it does in another habitat (Blanquart *et al.*, 2013). Experiments that use reciprocal-transplant designs can result in a

variety of outcomes, with local germplasm performing best in all sites, only in some sites, or in none. Furthermore, sometimes a population may perform better at home than elsewhere, and sometimes not. Specific patterns, of course, depend on the architecture of adaptations, costs and trade-offs to local performance, the relative fertility or toxicity of sites, and the ecological history of the seed source. Reciprocal-transplant experiments have been the gold standard for dissecting these effects since the work of Clausen and colleagues. However, with multiple sites such designs rapidly become sufficiently daunting logistically that compromises are required. In some cases, such as when there are multiple hierarchical scales of adaptation (i.e. to specific sites, habitat types, and climatic regions), experimental designs become so large they are unable to simultaneously detect local adaptation between habitat types as well as between sites within a habitat. For some aspects of local adaptation, single-site common-garden experiments may provide a more manageable experimental approach where it is possible to delve deeper into patterns. The work from Peterson *et al.* is just such an example.

Mimulus guttatus occurs in a wide geographic and ecological range of habitats from coastal bluffs to serpentine seeps and montane stream banks. It also has two life-history races, annual and short-lived perennial, that are partially reproductively isolated by a chromosomal inversion (Nesom, 2012). This diversity of life-history strategies and variation across diverse habitats make comparing life forms in the same experiment across multiple sites complicated. Typically, two habitat types of *Mimulus* have been compared (e.g. Ivey *et al.*, 2004; Hall & Willis, 2006; Lowry *et al.*, 2008), but none have used more than a small number of populations. To examine more populations together across a gradient of life histories from the *M. guttatus* species complex, Peterson *et al.* used a single montane site with detailed measurements and life-history matrix modeling to expand their scope. They planted several different ecotypes of the *M. guttatus* species complex from 11 different populations into a stream site. Over two growing seasons they tracked survival, different aspects of reproduction, and recruitment, and then integrated across the lifespan by calculating population growth rates (λ) which are more appropriate fitness measures than a measure of a single fitness component such as seed set. This approach is particularly useful when lifespan varies so extensively, from annual to perennial, but would be generally useful for dissection of differences in fitness. Employing life-table response experiments (Caswell, 2001) allowed Peterson *et al.* to evaluate which components of fitness most contribute to increased performance. By comparing performance of the 10 foreign populations to the native population, inference about local adaptation vs foreign advantage was possible. As populations varied in life forms (annual vs perennial) and habitat types (coastal, inland, low elevation, high elevation) hierarchical levels of ecological variation could be examined.

This article is a commentary on Peterson *et al.*, 211: 345–356.

Peterson *et al.* find mixed evidence for local adaptation, consistent with the complex hierarchy of variation that many have observed in *Mimulus*. Annual populations performed poorly in this site, where a perennial form is native. The contribution of rosettes overwintering gave perennial forms an advantage in the common garden montane stream-bank site, showing the poor match of annuals to this type of habitat. Among perennial populations, there was a foreign advantage. Lower elevation perennial forms had greater fecundity of both seedlings and rosettes, and less investment in belowground rhizomes. These patterns persisted despite variation in weather between the two years, with a strong drought in 2013 and a lesser one in 2014. This foreign advantage could be influenced by local inbreeding in the focal site, climate change shifting the geographic range of the climate match, variation in ecological history of populations, or a combination of factors.

The *Mimulus* system pursued by Peterson *et al.* is especially interesting because of the diversity of species within the clade (Beardsley *et al.*, 2004; Barker *et al.*, 2012) and the ongoing research in the taxonomic (e.g. Nesom, 2012) and systematic relationships. Systems with gradients of variation in traits and ecological diversity of habitat types as in *Mimulus* provide opportunities to investigate the complexity of environment population interactions, while allowing for an evaluation of continuous variation in life history within a single clade. Studies in systems with hierarchies of form can provide models for investigation of specific traits associated with potential for range shifts (Wu *et al.*, 2008) and species boundaries.

With two years of sampling and detailed measurements of fitness contributions throughout the lifespan, Peterson *et al.* effectively used a common-garden study to dissect hierarchical levels of local adaptation and foreign advantage in *Mimulus*. Although in many ways a model of a well-designed experiment, this does not minimize the need for reciprocal-transplant experiments. For particular focal comparisons, reciprocal-transplant experiments will remain the gold standard for showing trade-offs in performance among sites and through time. More importantly, reciprocal-transplant experiments are far more powerful for specifically examining plasticity of traits. In certain circumstances, the plasticity of traits is the primary mechanism by which an organism adapts to local environmental conditions. It has been seen in *Mimulus* that trichome density (Holeski, 2007; Colicchio *et al.*, 2015) and the amount and timing of seed germination (Vickery, 1983) are plastic traits; with each trait responding differently to distinct ecological settings. Reciprocal-transplant experiments allow for the ability and range of such plastic traits to be more easily tested in true multivariate environmental conditions. Similarly, lifespan, one of the major life-history traits that vary across the *Mimulus* complex, could still be tested in multiple sites over multiple years to examine environmental conditions in which annual or perennial behavior is favored.

Common-garden studies such as this can help target the most informative comparisons of populations and focal traits. Similarly, studies like this one demonstrate the need to pair sequencing studies, which may look for outliers or other signatures of selection based on patterns of molecular variation alone (Savolainen *et al.*, 2013), with detailed common-garden studies (e.g. de Villemereuil *et al.*, 2016).

Carefully designed and executed common-garden studies, such as the one performed by Peterson *et al.* can illuminate the key patterns of differentiation among populations, showing which particular life stages or developmental allocations differ most among them. Addressing these challenges will benefit from joint investigations of systematists, molecular geneticists, and evolutionary ecologists, and may shed new light on old questions in agriculture and forestry.

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