

Commentary

Adapting with the enemy: local adaptation in plant–herbivore interactions

Local adaptation by natural selection is a fundamental process in population differentiation and speciation. To determine if populations are adapted to local conditions, researchers use reciprocal transplant experiments: individuals are moved among populations to compare their performance in familiar (local) and foreign (nonlocal) conditions. These experiments are meant to evaluate whether adaptation to one environment comes at a cost (via fitness trade-off) to performing well in another (nonlocal) environment (Kawecki & Ebert, 2004). Multiple meta-analyses of these experiments confirm that local adaptation can be a common phenomenon (e.g. Lajeunesse & Forbes, 2002; Leimu & Fischer, 2008; Hoeksema & Forde, 2008; Hereford, 2009), but individual experiments often cannot distinguish which aspect of the environment (abiotic or biotic) populations are adapted to. In research exploring local adaptation to biotic factors, such as antagonist interactions between plants and herbivores, co-evolutionary theory plays an important role in forming predictions of when local adaptation should be observed (e.g. Gandon, 2002). One prediction is that populations will vary in who is ahead in the co-evolutionary ‘arms race’, and that this race is the primary driver of local adaptation. However, until Garrido *et al.* (pp. 445–453) in this issue of *New Phytologist*, no study had simultaneously examined local adaptation in both host plants and their herbivores, while controlling for the potential abiotic factors that mediate local adaptation.

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The study focuses on four genetically differentiated Mexican populations of jimson weed (*Datura stramonium*) and one of its main herbivores, the three lined potato beetle (*Lema trilineata*). To specifically assess local adaptation in a co-evolutionary framework, the authors took what might initially seem a counter-intuitive approach of removing the organisms from the local habitats

entirely. However, by controlling the abiotic habitat with common garden and laboratory experiments, they could single out the biotic component of local adaptation. Interestingly, herbivores were more likely to be locally adapted to their host plants than the plants themselves to herbivores, suggesting that factors other than herbivores are important drivers for local adaptation in plants (if these plants do exhibit local adaptation). This is not surprising for two reasons. First, the host plant is more likely to be the most significant component of an herbivores environment rather than the reverse. Second, despite the intuition that herbivory has negative effects on plants and anti-herbivore defenses are costly, these can be difficult to detect (e.g. Koricheva, 2002). For example, the combination of plant and herbivore origin was important for *D. stramonium* herbivore resistance (1 – % damage) but not fitness (seeds). However, in populations where herbivores showed local adaptation, the plants were not adapted or maladapted as predicted in a co-evolutionary arms race (Fig. 1). Thus, these results confirm major assumptions of co-evolutionary theory.

To fully show that local adaptation of plant–animal interactions shapes the evolution for the interacting species, estimates of the underlying processes of natural selection by the co-adapting partners are necessary. Results from a common garden experimental approach can be directly used to predict the evolutionary ecology of plant–herbivore interactions within populations. For example, if herbivores are locally adapted to their host plants (as was found here), then there should be little natural selection on plant consumption traits in herbivores within those populations because the herbivores have the co-evolutionary upper hand. Furthermore, if foreign, differentiated individuals are introduced (experimentally or via migration), then those traits should be under selection in the direction of the local herbivore phenotype. Thus, reciprocal transplants should reveal selection on the foreign rather than local phenotypes. By contrast, for host plants, when herbivores are locally adapted and thus presumably the plants are not, the prediction is that herbivore-mediated selection on plant traits will drive evolution of plant resistance, tolerance or possibly escape from herbivory (e.g. flowering time; Parachnowitsch & Caruso, 2008). However, if the reverse is true and plants are locally adapted to their enemies (examples reviewed in Garrido *et al.*), then selection should act on herbivores instead. Combining common garden experiments with *in situ* natural selection studies examines two crucial components of the importance of plant–insect interactions to population differentiation: the presence of local adaptation in co-evolving partners; and the mechanisms that drive it.

From the plant’s perspective, reciprocal transplant and natural selection experiments could be further modified as recently suggested by Agrawal (2011). He advocates using factorial reciprocal transplant experiments where the presence of herbivores is also manipulated (for example through pesticides) to understand

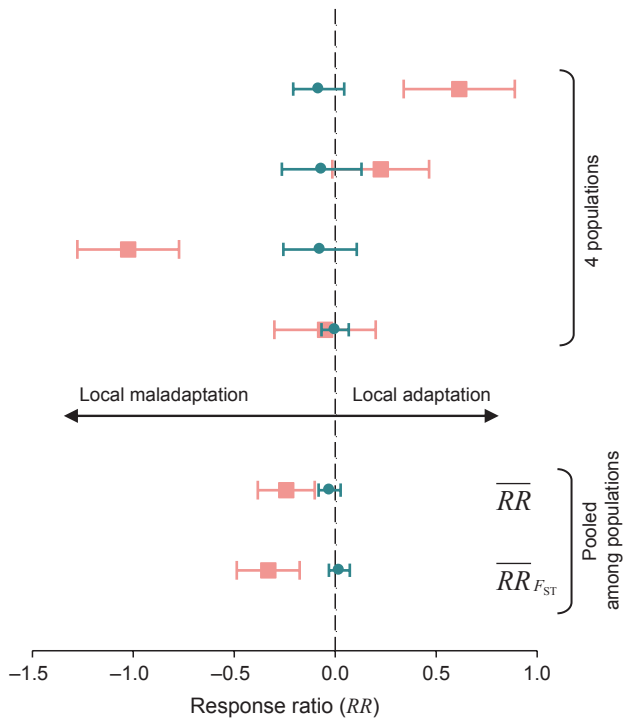


Fig. 1 Comparison of local adaptation in *Datura stramonium* (circles) and its herbivore *Lema trilineata* (squares) using the response ratio (RR) to quantify the ratio between sympatric (s) and allopatric performance (dashed line, zero effect). Here, RR is the weighted average (with 95% confidence interval) of $\log_e(\bar{X}_s/\bar{X}_i)$ for each *i*th allopatric group. RR differs from the coefficient of population differentiation (ϕ) in that calculations with \bar{X} with small sample sizes (*n*) are downweighted when averaged. For example, herbivore performance estimates based on *n* = 46 are given more weight than estimates from *n* = 4. Another way RR differs from ϕ is that it adjusts for redundancy of information arising from comparing a single sympatric performance estimate to multiple allopatric estimates (see Lajeunesse, 2011). This approach led to greater accuracy for detecting local (mal)adaptation and offers further support to the authors' findings. Co-evolutionary theory predicts that if the 'arms race' is symmetric between herbivores and plants (e.g. generation time is on par), then local adaptation will not be observed when multiple populations are averaged (Gandon, 2002). This average trend of no-local adaptation is evident for plants when assuming that populations are fully independent (\bar{RR}) or not independent using $(1 - F_{ST})$ as correlations to quantify the degree of population isolation ($\bar{RR}_{F_{ST}}$). However, averaging response ratios across herbivore populations with or without correlations indicated an overall trend of maladaptation. We caution that this is not truly a robust test for the hypothesis given that results are only pooled across four populations, and are particularly sensitive to the inclusion of a population with significant local maladaptation. We report this test as an illustrative example of what can be done with response ratios. We thank E. Garrido for providing data for these calculations. Population order (from top to bottom): Esperanza, Pedregal, Teotihuacan, and Tula.

the evolution of plant defenses. This design has the advantage of determining the relative role of herbivores vs other components of the environment in plant local adaptation and allowing for manipulation of the entire herbivore community rather than a single member. However, it is limited to understanding one partner of the interaction (the plant). If the results Garrido *et al.* found in *Datura stramonium* are common, then we would predict that it is these other factors rather than herbivores that are

more often important for local plant adaptation, despite the predicted herbivore-mediated selection. Given that plants are often consumed by several herbivore species occupying multiple guilds (functional feeding groups) and may have diffuse rather than pairwise co-evolution with their enemies (Strauss *et al.*, 2005), Agrawal's experimental design is feasible at the community scale. Furthermore, temporal repeatability of these natural selection measures could assess whether plants are truly more likely to adapt to the nonherbivore environment or whether local adaptation to herbivores is hindered by temporal variation in herbivore-mediated selection.

As more elaborate experimental designs are developed in local adaptation research, the development of simple summary statistics of this research has not kept pace. In an effort to summarize their findings, Garrido *et al.* introduce the coefficient of population differentiation (ϕ), which quantifies the pooled outcome of multiple tests of local adaptation among several populations. Others have also argued that such a summary statistic is necessary (Kawecki & Ebert, 2004) or developed their own (Hereford, 2009). However, summary metrics like effect sizes – that quantify both the magnitude and direction of an experimental outcome – already exist in a meta-analytical context. In fact, effect sizes are routinely used to quantify the outcomes of local adaptation experiments for pooling research across multiple studies (see Hoeksema & Forde, 2008; Leimu & Fischer, 2008). Historically, however, the challenge has been to apply these study-outcome metrics to properly quantify multiple effects arising from a single experimental design – like those from factorial cross-population tests of local adaptation. Recent advances in effect size metrics such as the response ratio (for which ϕ is a variant) now allow for elaborate reciprocal transplant experiments to be quantified into a single summary statistic (see Fig. 1; Lajeunesse, 2011). The advantages of using effect sizes is that multiple within-study outcomes can be weighted by sampling error, the redundancy of using a common control can be avoided (typically there is only one sympatric group contrasted with several allopatric sources), or correlations among tests for local adaptation can be used to adjust the final pooled effect across populations. For example, Garrido *et al.* report F_{ST} estimates as evidence on how divergent the populations are genetically. Here, genetic divergence can be converted into correlations $(1 - F_{ST})$ and used to adjust the effect sizes based on how genetically independent the populations are to one another (see Fig. 1). These types of modifications may be especially valuable in a meta-population context where similarities among populations can diminish the strength of observations of local adaptation in nature – as predicted by the homogenizing effects of gene flow on local adaptation (Kawecki & Ebert, 2004). Thus, as an extension of Garrido *et al.*'s ϕ , we suggest that researchers adopt the response ratio to summarize their local adaptation experimental findings.

Another promising avenue of growth in research on local adaptation is to extend similar experimental designs and theory to mutualistic interactions. For example, Johnson *et al.* (2010) used this full factorial common garden approach to study local adaptation of plants and mycorrhizal fungi. In contrast to

plant–herbivore interactions, both plants and mycorrhiza showed local co-adaptation characteristic of a more mutualistic interaction. Furthermore, reciprocal transplants that also manipulate an agent of selection could be used to assess the effects of mutualistic as well as antagonistic interactions on local adaptation. For example, the importance of pollinators in floral local adaptation could be assessed through combining reciprocal transplants with hand-pollination treatments to determine the relative role of pollinators vs other environmental factors. Even more complicated designs that manipulate both herbivores and pollinators will add to our understanding of whether conflicting selection pressures alter the adaptive landscape.

In general, theories of plant–animal interactions, ranging from mutualistic to antagonistic, predict that these interactions are crucial to understanding the diversification of life (e.g. Ehrlich & Raven, 1964; Fenster *et al.*, 2004). Research employing a mixture of approaches such as those suggested here and elsewhere (e.g. Kawecki & Ebert, 2004) is likely best suited for studying these phenomena. Innovative experimental designs which not only test for local adaptation but also the mechanisms behind it, coupled with analytical tools to simplify interpretation of entire experiments, will go a long way in furthering our understanding of the mechanisms generating diversity. The results highlighted by Garrido *et al.* have put us one step further along that path, and we look forward to following the continued synthesis of ecological interactions and evolutionary theory.

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