

Can laboratory evolution experiments teach us about natural populations?

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The ability to predict how natural populations will evolve and adapt to major changes in environmental conditions has long been of interest to evolutionary biologists and ecologists alike. The reality of global climate change has also created a pressing need for advancement in this particular area of research, as species are increasingly faced with rapid shifts in abiotic and biotic conditions. Evolutionary genomics has the potential to be incredibly useful as we move forward in addressing this need and in particular, evolve and resequence (E&R) studies—where researchers combine experimental evolution with whole-genome sequencing—have an important role to play. However, while E&R studies have shown a great deal of promise in tackling fundamental questions regarding the genetics of adaptation (Long et al., 2015; Schlötterer et al., 2014), it is unclear whether results from laboratory experiments can be directly translated to natural populations. In a From the Cover article in this issue of *Molecular Ecology*, Hsu et al. (*Mol Ecol*, **29**, 2020) explicitly contend with this issue by examining the overlap between genes implicated in thermal adaptation in a *Drosophila melanogaster* E&R study and genes identified by comparing natural populations from different latitudinal clines. They report significant correlations between the two sets of temperature-adaptive genes and ultimately conclude that E&R studies can indeed generate insights applicable to populations inhabiting complex natural environments. While more work is needed to assess the generality of these conclusions, Hsu and Belmouaden (*Mol Ecol*, **29**, 2020) contribute an important precedent.

KEYWORDS

adaptation, experimental evolution, gene expression

Among evolutionary biologists, there exist fundamentally different approaches to the empirical study of adaptation. While some researchers favour examining patterns of genetic variation within and between natural populations living in different environments, others rely on laboratory experiments where they can exert direct control over environmental variables and study evolutionary responses to specific selective pressures (Bailey & Bataillon, 2016). Those who favour studying adaptation in nature sometimes argue that laboratory experiments are too oversimplified and contrived to be representative of evolution in the wild. And conversely, those working in the

laboratory sometimes argue that field-based studies have limited power due to confounding environmental variables and incomplete knowledge of the evolutionary history of focal populations. Within this broader context, studies like Hsu et al. (2020) are incredibly valuable as they present experimental data that bridge this divide.

In their core analysis, Hsu et al. (2020) compare gene expression profiles between groups of experimentally evolved *Drosophila melanogaster* population subjected to either hot or cold selection regimes for dozens of generations. They compare results from experimental populations to one another, and to reconstituted ancestral

populations created by crossing inbred lines, to characterize expression patterns within and across regimes. They ultimately identify 541 genes that show similar shifts in expression regardless of selection regime (i.e. adaptation to common laboratory conditions) and 203 genes that exhibit temperature-specific responses. They then compare their list of temperature-specific candidates to genes differentially expressed across latitudinal clines in *D. melanogaster* populations sampled from nature—one along the North American continent (Panama vs. Maine; Zhao et al., 2015), and another in Europe and Africa (Zimbabwe vs. the Netherlands; Hutter et al., 2008)—and find significant correlations between the sets of candidate genes. Synthesizing these correlations, they conclude that well-designed evolution experiments can in fact predict how populations will respond to specific selective pressures in nature.

It is interesting to consider the lists of genes returned by each comparison in this work. Naively, one might expect that if laboratory experiments were truly predictive, they would reveal the same individual genes as those observed to diverge in nature. Figure 1 provides a snapshot of the raw gene lists compared in this study. Among the genes implicated as having differential expression (i.e. increased expression at one temperature/latitude and decreased expression at a contrasting temperature/latitude), few of them overlap. The authors point out that while individual gene lists are modestly concordant, applying a more integrative perspective yields more power and insight. They assigned genes that co-occur in regulatory networks into “modules” and showed that differentially expressed genes along each latitudinal cline were significantly correlated with differentially expressed genes from the laboratory experiment. The results presented in Figure 1 are thought-provoking for a few reasons. First, it is notable that the natural populations themselves, collected from

different continents, share few differentially expressed genes. Of course, the underlying genetic variation in the populations of each cline differs such that direct comparisons between them are complicated. In light of this, it is rather remarkable that the laboratory experiment recapitulates any differentially expressed genes observed in natural populations at all, especially in the cline from which it shares no ancestry (the laboratory experiment was initiated by flies collected in Portugal). Second, this work highlights the utility of applying a combined approach in the analysis between laboratory and natural experiments. Leveraging the power of the *Drosophila* genetics toolkit enables the modular comparisons made by the authors, which was informative in this case. And so, they show the inherent value in integrating laboratory experiments using model (or emerging model) systems with field-based surveys.

Hsu et al. (2020) provide an illustrative proof of concept that experimental evolution, despite its inability to fully capture the complexity of natural environments, can indeed inform our understanding of adaptation in nature. However, not all such efforts are so successful. In fact, a recent, very similar article recently published in *Molecular Ecology* concluded that E&R results from experiments with the harlequin fly (*Chironomus riparius*) were not relevant to the study of thermal adaptation in natural populations of this species (Pfenninger & Foucault, 2020). Here, the authors found no evidence of temperature-specific changes in patterns of genetic variation across selection treatments (control, intermediate and high temperature) and concluded their study could not provide direct insights into the potential for thermal adaptation in natural *C. riparius* populations. Comparing these studies and their outcomes, and others like them, is useful for highlighting important considerations for experimental design and the limitations of the E&R paradigm.

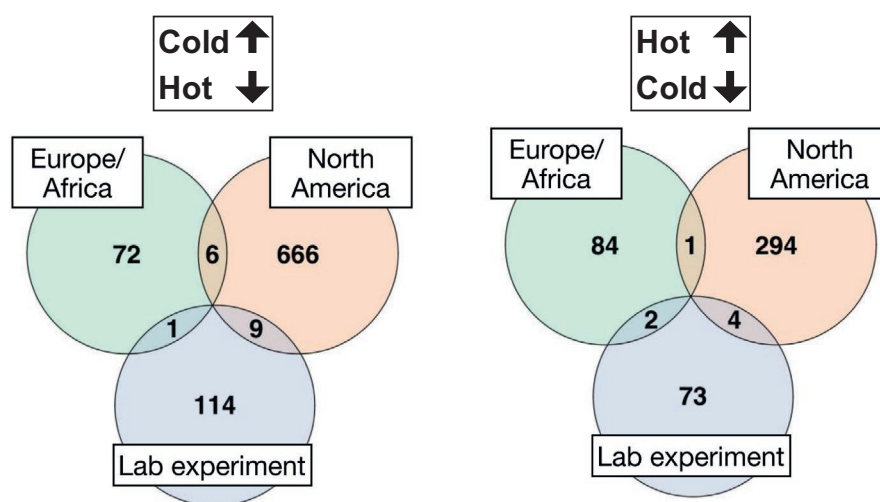


FIGURE 1 Differentially expressed genes in natural *Drosophila* populations, compared to the laboratory experiment. Green circles indicate comparisons between fly populations collected from Zimbabwe and the Netherlands; orange circles indicate comparisons between fly populations collected from Panama and Maine; blue circles indicate comparisons between hot- and cold-adapted experimental laboratory populations. Circles show number of genes that are either (left) highly expressed in temperate latitudes/cold adaptation and lowly expressed in tropical latitudes/hot adaptation, or (right) highly expressed in tropical latitudes/hot adaptation and lowly expressed in temperate latitudes/cold adaptation. While only the hot-adapted lines were significantly enriched for divergent genes observed in natural populations (right), a modular approach incorporating GO term enrichment and co-regulation provided more power to detect overlapping functional categories

Why does one study appear to reflect natural scenarios, while others do not? Certainly, there are many possibilities to consider. Perhaps genetic variation in laboratory populations is not representative of what is found in natural populations, at least in terms of functional variation for the trait under selection. Perhaps laboratory evolution experiments fail to comprehensively mimic the environments that natural populations encounter. Pfenninger and Foucault (2020) sought to use experimental evolution to assess the evolutionary potential for rapid thermal adaptation in natural *C. riparius* populations, but the general laboratory environment proved a much stronger selective agent than any of the thermal treatments. As such, they could only observe adaptation to common rearing conditions (e.g. increased larval density and water quality in the laboratory), which does not portend thermal adaptation in natural *C. riparius* populations. Finally, it is possible that applying powerful resources of model organisms like *Drosophila* will inherently increase an investigator's ability to extend results from the laboratory into the real world. Perhaps with the ability to apply a "modular" approach, seeking overlaps in functional categories of genes or regulatory networks comes a greater ability to identify patterns. Therefore, using E&R to address questions about adaptation in natural populations will inherently be more difficult in some species than others.

In summary, Hsu et al. (2020) provide a notable precedent for using laboratory E&R to further our understanding of adaptation in natural populations. As such, it belongs to a small but growing number of studies that bridge the divide between laboratory- and field-based studies of adaptation. Of course, there are many familiar roadblocks to translating findings from laboratory populations to nature, most related to experimental design choices that lead to poor imitations of nature. And yet, integrating laboratory-based and field-based research, particularly in nonmodel systems, holds tremendous promise for developing methods and models that will allow researchers to reliably predict how natural populations will respond to rapidly shifting environments across the globe.

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