

Population genomics of parallel adaptation

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Parallel evolution is one of the striking patterns in nature. The presence of repeated evolution of the same phenotypes, suites of traits, and adaptations suggests a strong role for natural selection in shaping biological diversity. The reasoning is straightforward: each instance of repeated evolution makes it less likely that these features evolved neutrally or due to stochastic forces in each population or species. With the growing sequencing capability, we are now poised to examine the genetic basis of parallel evolution in model and nonmodel systems. On pages 4102–4117 of this issue of *Molecular Ecology*, van Boheemen and Hodgins (2020) provide an exemplar study of this kind, using common ragweed (*Ambrosia artemisiifolia*; Figure 1a). Their study is noteworthy and ambitious in many respects, and we think will serve as a model for studying parallel adaptation, even in nonmodel species.

KEYWORDS

adaptation, cline, ecological genetics, invasive species, population genomics

Resolving the genetic basis of adaptive phenotypes can help distinguish between competing views of evolution and constraint (see Chevin et al., 2010; Conte et al., 2012; Orr, 2005; Rosenblum et al., 2014; Storz, 2016; Yeaman et al., 2018). For example, if evolution frequently uses unique genes or mutations to produce an adaptive phenotype, that suggests genetic redundancy in producing both phenotypes and high fitness genotypes. Independent genetic bases for the same adaptive phenotype might be expected when adaptation is occurring from new mutations, or when those phenotypes are highly polygenic traits, each influenced by many loci throughout the genome. In contrast, if evolution frequently uses the same genes or mutations to produce a convergent phenotype, that suggests a model of either adaptation from a shared pool of standing variation or pleiotropic constraint. If alternative mutations or genetic routes to produce a phenotype have pleiotropic costs, either on fitness or other ecologically important traits, we are less likely to observe them. Consequently, widespread pleiotropy can limit or bias the genes or mutations observed as responsible for adaptive phenotypes, out of a universe of larger potential genetic mechanisms.

1 | PARALLEL ADAPTATION OF RAGWEED ON THREE CONTINENTS

Common ragweed, *Ambrosia artemisiifolia* is an outcrossing wind-pollinated annual, commonly found in recently disturbed habitats. Native to North America, it has been introduced to Europe and Australia (van Boheemen et al., 2017; Chauvel et al., 2006). van Boheemen and Hodgins (2020) explored parallel evolution in the North American, Australian and European ranges. They sampled from 84 locations across these three ranges and raised 853 individuals in a common garden. With over 83k SNPs obtained from double-digest genotyping-by-sequencing, 19 phenotypes measured, and 22 environmental variables included, they tested the repeatability of rapid genomic and phenotypic adaptation. Their results suggest repeated patterns of climate adaptation, despite different demographic histories, which is consistent with previous studies (e.g., McGoey et al., 2020).

A highlight of this study is the application of several complementary population genomic approaches to study adaptation, in a rigorous statistical fashion. The authors used phenotype–environment

associations, F_{ST} -like outlier analysis ($X^T X$ of Günther & Coop, 2013), genotype–environment associations and genotype–phenotype associations. First, they identified patterns of phenotype–environment associations within ranges, and then examined whether these were shared across continents. They next tested for genomic outliers, by estimating $X^T X$ scores and genotype–environment and genotype–phenotype associations. Finally, van Boheemen and Hodgins estimated local linkage disequilibrium in SNPs among the ranges, and formally tested whether there was more overlap in the loci detected from these methods than expected by chance. Collectively, this is a comprehensive, thorough and creative examination of a rich data set, in an agriculturally and economically important species.

What did they find? van Boheemen and Hodgins found 42 phenotype–environment associations, 20 of which were replicated in more than 1 range, indicating widespread parallel phenotypic evolution. Among those shared across ranges were clines in flowering time, size, growth and sex function, several of which have been described previously for ragweed (van Boheemen et al., 2018; McGoey et al., 2020). Interestingly, the authors also found parallel patterns of genetic differentiation, with $X^T X$ scores, which measure differentiation within a range, showing strong correlations across continents. The authors found that the repeatability of outlier windows in the genome was higher than expected by chance, with 134 genomic windows showing multiple signatures of selection from population genetic analyses, 35 of which were shared in at least two ranges and 6 of which were significant in all three geographic ranges. Taken together, these results paint a portrait of parallel clinal evolution of phenotypes and genotypes in ragweed on three continents, with ~ 17%–26% of candidate adaptation loci showing evidence of repeatability across multiple ranges (Figure 1b).

2 | CONCLUSIONS, CHALLENGES AND PROSPECTS

How do these results fit into an emerging picture of the genetics and genomics of parallel adaptation? Empirical study in a wide range of systems (*Arabidopsis*, stickleback, maize, *Drosophila*, *Populus*, conifers) suggests some intriguing patterns.

To date, there seem to be relatively few cases of an independent genetic basis to adaptive traits (Fang et al., 2020; Gould & Stinchcombe, 2017). In contrast, there are several recently described cases where there appears to be a parallel genetic basis (Holliday et al., 2016; Nelson & Cresko, 2018; Pool et al., 2017; Preite et al., 2019; Yang et al., 2018; Yeaman et al., 2016; Wang et al., 2020). Some of these are clear cases of independent evolution despite many years of separate evolutionary histories (e.g. conifers separated by ~ 140 million years; Yeaman et al., 2016), while others clearly implicate gene flow from nearby populations (Wang et al. 2020). For sticklebacks, genetic parallelism is seen on finer geographic scales (Alaska and the Pacific Northwest; e.g. Hohenlohe et al., 2010; Jones et al., 2012; Nelson & Cresko, 2018), but not globally, a pattern attributed to founder events and the loss of genetic diversity following colonization of the Atlantic (Fang et al., 2020). Such demographic forces will not automatically lead to independent genetic bases of adaptations. For example, Yang et al. (2018) detected parallel evolution of early flowering due to *FLC* variants in *Capsella rubella*, despite a genome-wide bottleneck accompanying the origin of that species through selfing. Likewise, van Boheemen and Hodgins show that Australian ragweed still shows signals of genetic parallelism, despite a severe bottleneck following introduction.

We are excited to see whether the tentatively emerging consensus of genetic parallelism is upheld in future studies, in a wider variety of species, life histories, and with varied geography and

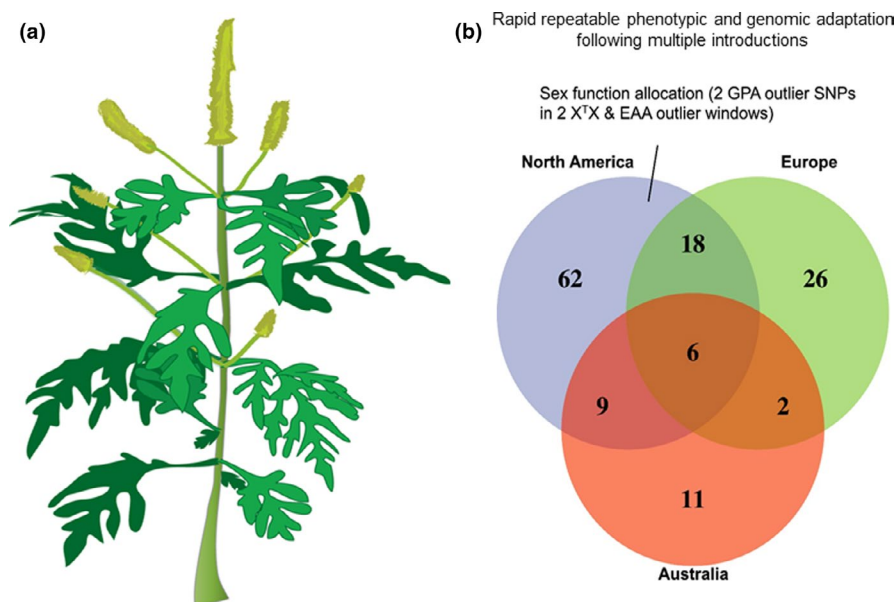


FIGURE 1 (a) Schematic illustration of ragweed. Image by Brechann McGoey, modified from McGoey et al. (2020). (b) Overlap of outlier windows from the three geographic ranges, which is higher than expected by chance. Modified from figure 3 of van Boheemen and Hodgins (2020)

adaptations. A particularly exciting future endeavour will be to distinguish whether genetic parallelism is due to evolution from a pool of shared standing variation, or true de novo evolution at the same genes. Even for cases in which parallel phenotypic evolution is not shared at the level of nucleotide substitutions or genes, we see merit in determining whether there is parallelism at other levels of biological organization (e.g. genetic pathways, developmental processes or hormonal signalling, different modification of the same morphological structures; Rosenblum et al., 2014; Wessinger & Hileman, 2020; Wang et al., 2020). Continued investigation on this front will reveal the degree of genetic lability and constraint in adaptation.

Finally, we are heartened to see the emergence of ragweed as a system for diverse studies of evolution and adaptation. Beyond its impact on hay-fever (allergy) and asthma sufferers, ragweed is an important agricultural weed, especially in the invaded range, and appears to have also adapted to urban environments in the USA (Gorton et al., 2018). The broad spectrum of tools in modern ecological genetics—crossing designs (McGoey et al., 2017), quantitative genetics (McGoey and Stinchcombe, 2018), manipulative experiments in the field (Gorton et al., 2019; Sun et al., 2020), genotyping by sequencing and population genetics (Martin et al., 2016; van Booheemen et al., 2017, 2018; van Booheemen & Hodgins, 2020; McGoey et al., 2020), transcriptomics (Hämälä et al., 2020)—is available in an annual plant that is of agricultural and health importance (Montagnani et al., 2017), and with a rich history of ecological investigation (e.g. MacDonald & Kotanen, 2010). We are excited to see future investigations of such a promising system in plant ecological genetics.

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