# A review on $Q_{ST}$–$F_{ST}$ comparisons of seed plants: Insights for conservation

Mi Yoon Chung[1], Juha Merilä[2], Yuseob Kim[3], Kangshan Mao[4], Jordi López-Pujol[5], and Myong Gi Chung[6]

[1]Chungnam National University College of Biological Sciences and Biotechnology
[2]University of Helsinki
[3]Ewha Womans University
[4]Sichuan University
[5]Botanic Institute of Barcelona
[6]Gyeongsang National University

November 21, 2022

## Abstract

Increased access to genome-wide data provides new opportunities for plant conservation. However, information on neutral genetic diversity in a small number of marker loci can still be valuable because genomic data are not available to most rare plant species. In the hope of bridging the gap between conservation science and practice, we outline how conservation practitioners can more efficiently employ population genetic information in plant conservation. We first review the current knowledge about the within-population genetic variation and among-population differentiation in neutral genetic variation (NGV) and adaptive genetic variation (AGV) in seed plants. We then introduce the estimates of among-population genetic differentiation in quantitative traits ($Q_{ST}$) and neutral markers ($F_{ST}$) to plant biology and summarize conservation applications derived from $Q_{ST}$–$F_{ST}$ comparisons, particularly on how to capture most AGV and NGV on both in-situ and ex-situ programs. Based on a review of published studies, we found that, on average, two and four populations would be needed for woody perennials ($n = 18$) to capture 99% of neutral and adaptive genetic variation, respectively, whereas four populations would be needed in case of herbaceous perennials ($n = 14$). On average, $Q_{ST}$ is about 3.6, 1.5, and 1.1 times greater than $F_{ST}$ in woody plants, annuals, and herbaceous perennials, respectively. We suggest using maximum $Q_{ST}$ rather than average $Q_{ST}$ among trait comparisons. Hence, conservation and management policies or suggestions based solely on inference on $F_{ST}$ could be misleading, particularly in woody species. We recommend conservation managers and practitioners consider this when formulating further conservation and restoration plans for plant species, and for woody species in particular.

*REVIEW ARTICLE*

[1]Department of Biological Sciences, Chungnam National University, Daejeon 34134, Republic of Korea

[2]Ecological Genetics Research Unit, Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, PO Box 65, FI-00014 University of Helsinki, Finland

[3]Area of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong SAR

1

[4]Division of EcoScience, Ewha Womans University, Seoul 03760, Korea

[5]Department of Life Science, Ewha Womans University, Seoul 03760, Korea

[6]Key Laboratory for Bio-resources and Eco-environment of Ministry of Education, College of Life Science, State Key Laboratory of Hydraulics and Mountain River Engineering, Sichuan University, Chengdu 610065, P. R. China

[7]Botanic Institute of Barcelona (IBB, CSIC-Ajuntament de Barcelona), Barcelona ES 08038, Catalonia, Spain

[8]Division of Life Science and RINS, Gyeongsang National University, Jinju 52828, Republic of Korea

**Correspondence**

Myong Gi Chung, Division of Life Science and RINS, Gyeongsang National University, Jinju 52828, Republic of Korea.

Email: *mgchung@gnu.ac.kr*

**Abstract**

Increased access to genome-wide data provides new opportunities for plant conservation. However, information on neutral genetic diversity in a small number of marker loci can still be valuable because genomic data are not available to most rare plant species. In the hope of bridging the gap between conservation science and practice, we outline how conservation practitioners can more efficiently employ population genetic information in plant conservation. We first review the current knowledge about the within-population genetic variation and among-population differentiation in neutral genetic variation (NGV) and adaptive genetic variation (AGV) in seed plants. We then introduce the estimates of among-population genetic differentiation in quantitative traits ($Q_{ST}$) and neutral markers ($F_{ST}$) to plant biology and summarize conservation applications derived from $Q_{ST}$–$F_{ST}$ comparisons, particularly on how to capture most AGV and NGV on both in-situ and ex-situ programs. Based on a review of published studies, we found that, on average, two and four populations would be needed for woody perennials ($n = 18$) to capture 99% of neutral and adaptive genetic variation, respectively, whereas four populations would be needed in case of herbaceous perennials ($n = 14$). On average, $Q_{ST}$ is about 3.6, 1.5, and 1.1 times greater than $F_{ST}$ in woody plants, annuals, and herbaceous perennials, respectively. We suggest using maximum $Q_{ST}$ rather than average $Q_{ST}$ among trait comparisons. Hence, conservation and management policies or suggestions based solely on inference on $F_{ST}$ could be misleading, particularly in woody species. We recommend conservation managers and practitioners consider this when formulating further conservation and restoration plans for plant species, particularly woody species.

**KEYWORDS**

Adaptive variation, conservation, genetic diversity, herbaceous plants, neutral variation, woody species

**TAXONOMY CLASSIFICATION**

Evolutionary ecology

## 1 | INTRODUCTION

Genetic diversity is a prerequisite for evolutionary change in all organisms; preservation of a species' genetic diversity likely increases its chances of surviving over evolutionary time when facing environmental changes.

Plant evolutionary biologists, foresters, and conservation geneticists have long been interested in the genetic differences among populations and the degree to which these may contribute to local adaptation (see Table 1 for the definition of population genetic terms cited in this mini review). This interest traces back to the common garden experiments of Turesson et al. (1922) and the reciprocal transplants of Clausen et al. (1941). For decades, common garden and reciprocal transplant experiments have been instrumental in advancing our understanding of how natural selection shapes geographic phenotypic variation (reviewed in Flanagan et al., 2018; Sork, 2018). As putatively neutral molecular genetic markers (i.e., allozymes and DNA-based dominant and codominant loci) became available, plant biologists were able to compare the levels of genetic diversity and the degree of divergence seen at phenotypic traits with those at single gene markers (Reed & Frankham, 2001; De Kort et al., 2013; Leinonen et al., 2013; Marin et al., 2020).

Applications of the knowledge of traditional marker-based neutral genetic variation (NGV hereafter) to the conservation and restoration of plant species have been somewhat controversial due to the assumed evolutionary neutrality of used markers and their limitations to be informative about the adaptive potential (García-Dorado & Caballero, 2021; Teixeira & Huber, 2021). Although levels of NGV might not be always predictive of adaptive genetic variation (AGV hereafter; Teixeira & Huber, 2021), it is possible that NGV under the current conditions may become AGV under changed environmental conditions. However, NGV, largely corresponding to within-population genetic variation from allozymes to nucleotide sequences as reflected in the percentage of polymorphic loci ($\%P$), allelic richness ($AR$), or gene diversity (Hardy-Weinberg expected heterozygosity, $H_e$), is regarded to be a poor "proxy" of levels of AGV in quantitative traits (i.e., narrow- and broad-sense heritabilities [$h^2$ and $H^2$]; Reed & Frankham, 2001; Depardieu et al., 2020).

The same applies to the relationship between measures of among-population genetic differentiation (e.g., Merilä & Crnokrak, 2001). The comparison between $F_{ST}$ ([Wright, 1951] or its analogs estimated from neutral genetic markers [Merimans & Hedrick, 2010]; see Holsinger & Weir [2009] for different definitions and interpretations of $F_{ST}$) and $Q_{ST}$ ($F_{ST}$ analog for quantitative traits; Spitze, 1993; Depardieu et al., 2020), i.e., $Q_{ST}-F_{ST}$ comparisons or relationships, was formalized with the adoption of $Q_{ST}$ in the 1990s. $Q_{ST}$ creates an explicit quantitative prediction of the expectation for quantitative traits under neutrality which, thus, solidified the inference that quantitative traits typically show greater genetic divergence among populations than expected under neutrality (Merilä & Crnokrak, 2001; De Kort et al., 2013; Leinonen et al., 2013). Assuming that the used genetic markers are neutral, this supports the view that the divergence of quantitative traits among populations is predominantly driven by natural selection. Although $F_{ST}$ is generally a poor predictor of $Q_{ST}$, many researchers still follow or in part support the assumption that levels of NGV would be indicative of those of AGV (e.g., Oostermeijer et al., 1994; Hamrick & Godt, 1996; Ottewell et al., 2016; DeWoody et al., 2021; García-Dorado & Caballero, 2021, but see Teixeira & Huber, 2021).

Although there is already an ongoing transition from conservation genetics to conservation genomics (Allendorf et al., 2010; Sork, 2018), genomic data for many rare plants are still scarce, and hence, conservation managers and practitioners need to continuously utilize information on NGV, if any, to support their decision making. Comparative (i.e., $Q_{ST}-F_{ST}$ comparisons) and, particularly, theoretical studies of NGV and AGV within and among populations in a variety of organisms are very abundant in the literature (e.g., Reed & Frankham, 2001, 2003; Hendry, 2002; McKay & Latta, 2002; Leinonen et al., 2013 and references therein; Li et al., 2019). So far, however, there have been few studies that have applied $Q_{ST}-F_{ST}$ comparisons to conservation, even though several such applications are possible (Reed & Frankham, 2003; but see McKay et al., 2001; Petit et al., 2001; Gravuer et al., 2005; Rodríguez-Quilón et al., 2016).

As a different issue from the above, there have been increasing recommendations in lowering the gap between conservation science and practice (sometimes coined as "the conservation genetics gap", "the research-implementation gap", or "the science-practice gap") (Taylor et al., 2017; Britt et al., 2018; Dubios et al., 2019; Fabian et al., 2019; Holderegger et al., 2019). It is agreed that conservation researchers should communicate with practitioners to integrate their genetic findings into conservation implementation (Ottewell et al., 2016; Chung et al., 2021). To achieve this, a generally and clearly written narrative covering $Q_{ST}-F_{ST}$ in seed

plants might be needed to lower the threshold for plant conservation practitioners to employ population genetics information in conservation practice.

With this in mind, we first introduce the current knowledge about within-population genetic variation and among-population differentiation both in NGV and AGV in seed plants to highlight the distinction between the approaches used for each system to identify NGV and AGV. Next, we introduce the known general application of $Q_{ST}$–$F_{ST}$ comparisons to plant biology. We also provide management suggestions as to how to capture germplasms (e.g., seeds) covering most AGV and NGV based on the analyses of molecular and quantitative trait data.

## 2 | COMPARISON OF WITHIN-POPULATION GENETIC VARIATION: NEUTRAL MARKERS VERSUS ADAPTIVE TRAITS

As neutral genetic markers reflect demographic processes (including past demographic histories) within local populations, they are informative for the management and conservation of genetic purposes. Small populations are generally susceptible to the loss of NGV and less adaptive to novel environments due to the loss of AGV through genetic drift (Reed & Frankham, 2003). The degree of individuals' heterozygosity (estimated as the number of loci for which each individual is heterozygous) is often correlated with fitness (Oostermeijer et al., 1994; Reed & Frankham, 2003). Even when there is a real relationship between an individual's heterozygosity and fitness, this does not imply that there should be a relationship between $H_e$ and $h^2$ at the population level. These are determined by somewhat different processes.

In a meta-analysis of 71 (60 out of these with allozymes) published datasets, $H_e$ is only weakly correlated with $h^2$ or $H^2$: $r = 0.217$ (–0.88 to 0.90, SD $\pm$ 0.433), indicating that neutral marker-based measures only explain 4% of the variation in quantitative traits (Reed & Frankham, 2001). In addition, the correlation between allozyme $H_e$ and $h^2$ for 17 metric characters in seven populations of the annual *Phlox drummondii* is highly variable, ranging from $r = -0.714$ to $r = 0.355$ (recalculated from Schwaegerle et al., 1986). Likewise, the correlation between microsatellite $H_e$ and $H^2$ of five phenotypic traits in seven populations of the endangered herb *Psilopeganum sinense* ranges from $r = -0.707$ to 0.261 (Ye et al., 2014). However, caution is needed because, at a degree of freedom of five with seven populations, the critical value of $r$ for $\alpha = 0.05$ is very high at $r = 0.75$, giving a very low power; when Bonferroni correction is applied across the five phenotypic traits, this becomes even higher at $r = 0.87$. Similar results revealing a weak correlation between NGV and AGV are available from other wild plant species as well: the rare perennial herb *Scabiosa canescens* and its common congener *S. columbaria* (allozymes, $H_e$ vs. $H^2$; Waldmann & Andersson, 1998); the annual *Clarkia dudleyana* (allozymes, $H_e$ vs. $CV_G$, coefficient of genetic variation of quantitative traits; Podolsky, 2001), the annual *Hordeum spontaneum* (allozymes, $H_e$ vs. $H^2$, Volis et al., 2005), and the selfing annual *Senecio vulgaris* (amplified fragment length polymorphisms [AFLPs], $H_e$ vs. $H^2$; Steinger et al., 2002).

These studies suggest that NGV has a limited ability to predict AGV within populations. Reed & Frankham (2001) listed six factors that could be responsible for the low correlation between NGV and AGV. Namely, these are differential selection, non-additive genetic variation, different mutation rates ($\mu$), low statistical power, environmental effects on quantitative characters, and impact of regulatory variation. In addition, various forms of natural selection affecting the level of neutral polymorphism at linked sites may also contribute to the lack of a relationship between NGV and AGV. The most dramatic effect on neutral variation occurs when beneficial alleles at loci contributing to AGV spread into a population, a process known as a "selective sweep" (Nielsen, 2005; Stephan, 2019). Selective sweep leads to a dramatic reduction of local $H_e$ and $AR$ along the chromosome segment (Kreitman, 2001). $H_e$ and $AR$ for non-neighboring or unlinked neutral regions are likely not affected by such events (Nielsen, 2005) because linkage disequilibrium between NGV and AGV decays gradually under the influence of recombination.

It should be noted that, however, invoking selective sweep as a factor that lowers the correlation between NGV and AGV could be problematic. The sweeping of one beneficial allele means that the AGV in that gene also disappears. Therefore, since AGV and NGV can be both high when a selective sweep does not

occur, but they are both reduced after a sweep, a positive correlation between AGV and NGV can be still maintained. Therefore, we need to ask whether there are other forms of natural selection in which NGV is lowered without reducing AGV. One such scenario, the hitchhiking effect of fluctuating selection, was provided by Barton (2000): fluctuating environment causing the adaptive alleles to oscillate between low and high frequencies, thus maintaining AGV without fixation or loss, is expected to reduce the levels of the surrounding NGV. The feasibility of such an evolutionary scenario is receiving growing attention, as fitness is indeed found to fluctuate rapidly and widely in natural populations (Bell, 2010; Messer et al., 2016) and population genomic studies have revealed seasonal oscillations of allele frequencies at a large number of sites (Bergman et al., 2014; Machado et al., 2021).

Under balancing selection, different alleles affecting fitness are maintained via heterozygote advantage, rare-allele advantage, or temporally/spatially heterogeneous selection. By definition, such loci harbor high levels of AGV (Aguilar et al., 2004; Charlesworth, 2006). The level of NGV is also expected to be elevated at sites closely linked to the loci of stable balanced polymorphism (Charlesworth, 2006). However, only very closely neighboring neutral sites may experience such an increase in polymorphism because meiotic recombination quickly erodes linkage disequilibrium around the selected loci (Fijarczyk & Babik, 2015). This suggests that a high level of AGV can be maintained by balancing selection without a proportional increase in NGV on the genomic average. Therefore, balancing selection should also contribute to the lack of a positive correlation between NGV and AGV.

To summarize, heterozygosity at adaptive and neutral loci is expected to be impacted by different evolutionary factors, which may explain why estimators of NGV are poor surrogates for AGV within plant populations.

## 3 | COMPARISON OF AMONG-POPULATION DIFFERENTIATION: NEUTRAL MARKERS VERSUS ADAPTIVE TRAITS

Since sessile plants are subject to spatially divergent selection, elucidating the effects of local adaptation on population differentiation has become more important in light of adaptation to changing environments, including global climate change (Ehrich & Raven, 1969; Savolainen, 2011; Colautti et al., 2012). A commonly used way to infer the impact of divergent selection on plant population differentiation is by comparing $Q_{ST}$ (reflecting differentiation caused by both neutral and selective forces) versus $F_{ST}$ estimates (reflecting differentiation due to neutral processes including genetic drift) (Whitlock, 2008). The neutrality expectation depends on the assumption that mutation rates ($\mu$) are substantially lower than migration rates ($m$) (Hendry, 2002). Neutral markers having high $\mu$ (e.g., microsatellites) are not recommended to be used in $Q_{ST}$–$F_{ST}$ comparisons (Hendry, 2002; Edelaar et al., 2011). However, Li et al. (2019) suggested the use of microsatellites by discarding the most variable loci (i.e., outliers).

The $Q_{ST}$–$F_{ST}$ comparisons (i.e., elucidation of the relative magnitudes of $Q_{ST}$ and $F_{ST}$) have already provided valuable insights into responses of plant traits to spatiotemporal environmental heterogeneity (Kremer et al., 1997; Merilä & Crnokrak, 2001; McKay & Latta, 2002; Volis et al., 2005; Savolainen et al., 2007; Leinonen et al., 2008, 2013). The $Q_{ST}$–$F_{ST}$ relationship can have three different outcomes that have different interpretations (Merilä & Crnokrak, 2001; Leinonen et al., 2008): $Q_{ST} > F_{ST}$, $Q_{ST}$ [?] $F_{ST}$, and $Q_{ST} < F_{ST}$. First, if $Q_{ST} > F_{ST}$, the observed trait differentiation exceeds neutral expectations and the fraction not explained by neutral processes is likely to have been caused by disruptive (divergent) selection. Second, if $Q_{ST}$ [?] $F_{ST}$, trait differentiation is indistinguishable from the effects of drift, and, thus, there is no evidence for selection (Lande, 1992). Finally, if $Q_{ST} < F_{ST}$, trait divergence among populations is less than expected due to genetic drift alone; this pattern is suggestive of spatially uniform or stabilizing selection (favoring average phenotypes) across populations.

Using several simple generalized linear models, Leinonen et al. (2008) carried out a meta-analysis of 55 animal and plant studies that used the same populations for both $F_{ST}$ and $Q_{ST}$ estimation. Their results confirmed the main conclusions of Merila & Crnokrak (2001), who found a low but significant positive correlation between $Q_{ST}$ and $F_{ST}$ (Spearman rank correlation, $r_s = 0.39$, $P = 0.017$; Leinonen et al., 2008),

and, on average, $Q_{ST} > F_{ST}$ ($P < 0.001$). Leinonen et al. (2008) suggested that genetic differentiation due to natural selection and local adaptation is the "norm," not the exception. The positive correlation between the degree of adaptive phenotypic divergence and differentiation at neutral loci is mainly caused by limited gene flow and enhanced local genetic adaptation, known as "isolation by adaptation" (Nosil et al., 2007). Leinonen et al. (2008) further found that the study design (*viz.*, wild, broad sense, and narrow sense), marker type (restriction fragment length polymorphisms, random amplified polymorphic DNAs, microsatellites, allozymes, and AFLPs), and trait type (morphological traits and life-history traits) rarely explain any significant variance in the $Q_{ST}$ data. Furthermore, Leinonen et al. (2008) pointed out two potential biases in finding that 70% of $Q_{ST}$ values exceed the associated $F_{ST}$ values. First, a sampling bias due to the deliberate selection of populations from contrasting environments to be investigated, as well as focus on populations previously known to be phenotypically divergent. Second, a publication bias favoring studies reporting $Q_{ST} > F_{ST}$ outcomes, possibly because of difficulties interpreting $Q_{ST}$ [?] $F_{ST}$ and $Q_{ST} < F_{ST}$ patterns. For example, $Q_{ST} < F_{ST}$ could be due to canalization, which is a process or tendency in which "species genetic backgrounds share the same genetic constraints" (Lamy et al., 2012) and "a fundamental feature of many developmental systems" (Hall et al., 2007). To partially distinguish canalization and uniform selection, Lamy et al. (2012) suggested "a bottom-up approach" that combines information from $Q_{ST}$–$F_{ST}$ comparisons and phylogenetic reconstruction. For a given trait, if $Q_{ST} < F_{ST}$ and phylogenetically closely related species occurring under different environmental conditions exhibit trait conservatism, then canalization could be inferred as an alternative to the classical uniform selection hypothesis (cf. fig. 3 in Lamy et al. [2012]). Well-known examples of canalization in plants are leaf shape in *Arabidopsis thaliana* and cavitation resistance found in all *Pinus* species (Hall et al., 2007; Lamy et al., 2011). The R package "driftsel" (Ovaskainen et al., 2011; Karhunen et al., 2013; 2014) can be used to differentiate between stabilizing selection, diversifying selection, and random genetic drift, allowing to circumvent a lot of the problems with the traditional $Q_{ST}$–$F_{ST}$ comparisons.

The study by De Kort et al. (2013) was the first meta-analysis of $Q_{ST}$–$F_{ST}$ comparisons (401 cases that included each $Q_{ST}$ value per trait for each entry) exclusively focusing on plants. The authors compiled 51 entries representing 44 plant species from 18 families covering 17 entries for annuals, 19 for herbaceous perennials, and 15 for woody species. De Kort et al. (2013) found that average $Q_{ST}$ values were significantly larger than the corresponding $F_{ST}$ values (0.345 versus 0.214, Wilcoxon signed-rank test, $P = 0.003$: paired $t$-test, $P = 0.000$, recalculated from original data from De Kort et al., 2013). The authors also found that the excess of $Q_{ST}$ relative to $F_{ST}$ was significantly negatively correlated with $F_{ST}$ ($\beta = -0.484$, $P < 0.01$). A weak but positive overall relationship between pairwise $Q_{ST}$ and $F_{ST}$ values ($r_s = 0.278$, $P = 0.048$; $\beta = 0.464$, $P = 0.003$, recalculated from De Kort et al., 2013) suggests that $F_{ST}$ in neutral markers could be to some degree predictive of $Q_{ST}$ in quantitative traits. These correlations are what one would expect because (i) $Q_{ST}$ reflects both neutral forces and natural selection caused by environmental differences and $F_{ST}$ only measures neutral processes including genetic drift and gene flow, (ii) $Q_{ST}$ and $F_{ST}$ estimates are based on the same (among-population) partition of total genetic variation, differing only in the data used in estimation—quantitative adaptive loci (the former) and neutral loci (the latter), and (iii) divergent selection that causes $Q_{ST}$ could also lead to the increase of $F_{ST}$ by restricting gene flow ("isolation by adaptation"; Nosil et al., 2007). In addition, De Kort et al. (2013) found a significant positive correlation between the average inter-population distance and their $Q_{ST}$–$F_{ST}$ difference values ($P < 0.05$), suggesting that isolation by distance plays an important role in adaptive evolution. The authors' meta-analysis suggests that plant species are generally differentiated by natural selection in various types of traits (*viz.*, fitness [reproductive and physiological traits] and non-fitness [biomass-related and phenological traits] both in early life and in the adult stage). For example, the authors detected a larger $Q_{ST}$–$F_{ST}$ difference values for non-fitness traits than for fitness traits, confirming the expectation that the former respond, in general, faster to directional selection than the latter (Merilä & Sheldon, 1999; Leinonen et al., 2008). Finally, De Kort et al. (2013) found slightly higher $Q_{ST}$–$F_{ST}$ difference values for annuals than perennials (0.143 versus 0.123), but the difference was not significant. This may not support the prediction (De Kort et al., 2013) that perennials can respond to selection slower than annuals.

In summary, these differences in $F_{ST}$ and $Q_{ST}$ are a product of the different evolutionary forces such as drift, gene flow, and selection (Slatkin, 1973), which are further complicated by potential biasing effects caused by phenotypic plasticity, environmental maternal effects, non-additive genetic interaction, pleiotropic effects, and, as mentioned above, different $\mu$ in $F_{ST}$ and $Q_{ST}$ (for more details see De Kort et al., 2013).

## 4 | APPLICATION OF $Q_{ST}$–$F_{ST}$ COMPARISONS TO PLANT BIOLOGY

Many $Q_{ST}$–$F_{ST}$ comparisons falling roughly into seven categories (*viz*. local adaptation, sexual selection, evolutionary stasis, human-induced evolution, artificial selection, biological invasions, and management and/or conservation) can be applied to plant biology, have been conducted to infer ecological and evolutionary processes. Perhaps the most commonly studied issue is to identify natural selection as a cause of broad-scale clinal variation in morphological and life-history traits (local adaptation, e.g., in *Campanulastrum americanum* [Prendeville et al., 2013], in *Helianthus maximiliani* [Kawakami et al., 2011], in two subspecies of *Antirrhinum majus* [Marin et al., 2020] or various tree species [Savolainen et al., 2007]). As an example of sexual selection, Yu et al. (2011) detected sex-specific selection as the cause of the evolution of sexual dimorphism in *Silene latifolia*. Using *Pinus pinaster* as a study species, Lamy et al. (2011) identified selective constraints explaining phenotypic uniformity across species distributions (evolutionary stasis, i.e., canalization or uniform selection).

Other examples are the demonstration of how human-induced habitat changes can either cause or impair adaptation (human-induced evolution, e.g., in *Thlaspi caerulescens* [Jiménez-Ambriz et al., 2007] and *Arabidopsis halleri* [Meyer et al., 2010]). In addition, studies on how selective breeding shapes diversification and population structuring of crop species (artificial selection) have been conducted in *Oryza sativa* (Sreejayan et al., 2011) and *Zea mays* (Pressoir & Berthaud, 2004). By performing $Q_{ST}$–$F_{ST}$ comparisons between the invasive species' native and invasive ranges (biological invasions), several researchers provided information on the evolution of invasiveness and the adaptive potential of invasive plant species such as *Hypericum canariense* (Dlugosch & Parker, 2007), *Ambrosia artemisiifolia* (Chun et al., 2011), *Lythrum salicaria* (Chun et al., 2009), and *Geranium carolinianum* (Shirk & Hamrick, 2014).

For management purposes, Gravuer et al. (2005) identified units or populations suitable for translocation in *Liatris scariosa*. Furthermore, some authors demonstrated that setting conservation priorities should not be based only on neutral marker diversity and that $Q_{ST}$–$F_{ST}$ comparisons can be used to identify populations that are suitable for translocation in *Arabis fecunda* (McKay et al., 2001) and *Araucaria araucana* (Bekessy et al., 2003). The last two issues, i.e., conservation and management, will be the focus of the next section.

## 5 | INSIGHTS INTO CONSERVATION AND RESTORATION DERIVED FROM $Q_{ST}$–$F_{ST}$ COMPARISONS

Because $F_{ST}$ estimates are significantly lower in trees than in most herbaceous perennials and annuals, Chung et al. (2020) recommended that conservation genetic strategies be designed differently for tree species versus other types of plant species. That is, seeds of most tree species (which generally show low values of $F_{ST}$) could be sourced from a few populations distributed across the species' range, whereas seeds of rare herbaceous species (often with high $F_{ST}$ values) should be taken from many populations to capture the highly localized genetic diversity. Based on a small body of available data on seed plant species (data from Lamy et al., 2012; De Kort et al., 2013; Leinonen et al., 2013), on average, $Q_{ST}$ is higher than $F_{ST}$ in common forest tree species, indicating that their quantitative traits have been subject to diversifying selection and local adaptation (Kremer et al., 1997; Savolainen et al., 2007). It has been suggested that more populations would be needed to preserve enough AGV for adaptively significant quantitative traits than for NGV, particularly in trees (McKay et al., 2001; Hamrick et al., 2006; Chung et al., 2020). More specifically, conservation practitioners may need information about how to capture most AGV and NGV based on known levels of NGV and AGV from population or conservation genetic studies.

Population(s) to be protected in situ or to be sampled for seed banking purposes could be estimated using the formulae: PNGV = 1 – $F_{ST}$ (or $G_{ST}$)$^N$ for NGV, where PNGV = proportion of NGV captured by sampling, $N$ = number of populations (Ceska et al., 1997; Hamrick et al., 2006) and PAGV = 1 – $Q_{ST}{}^N$

for AGV, where PAGV = proportion of AGV captured by sampling. However, one should be aware that if there are more than two alleles per locus for the neutral markers, then $Q_{ST}$ and $G_{ST}$ are on different scales, and the formulae PAGV $= 1 - Q_{ST}^N$ and PNGV $= 1 - F_{ST}^N$ cannot be interpreted in the same way (J. D. Nason, pers. comm.). For multi-allelic markers, it depends on $\mu$ whether this is problematic. In addition, as $\Phi_{ST}$ (a function of the among-population variance component and the within-population component, which is based on genetic distances among alleles for the neutral markers) is conceptually similar to $Q_{ST}$, it is advisable to use $\Phi_{ST}$ rather than $G_{ST}$, $F_{ST}$, or $\vartheta$ (Edelaar et al., 2011). The calculations for 99% capture of AGV and NGV can be key to figuring out ideal sample sizes, especially when resources are limited. Based on the average values of De Kort et al. (2013) for $F_{ST}$ and $Q_{ST}$ (annuals, $n = 19$, 0.308 versus 0.451 [i.e., $Q_{ST}$ is about 1.5 times greater than $F_{ST}$]; herbaceous perennials, $n = 14$, 0.267 versus 0.299 [$Q_{ST}$ is about 1.1 times greater]; woody perennials, $n = 18$, 0.074 versus 0.269 [$Q_{ST}$ is about 3.6 times greater]; recalculated from De Kort et al., 2013), to capture 99% of NGV and AGV for woody perennials, just two and four populations would be needed using the abovementioned formulae, respectively. On the other hand, on average, four populations of herbaceous perennials would be needed to secure 99% of NGV and AGV, respectively, because the average difference between $Q_{ST}$ and $F_{ST}$ is small (0.032). For annuals, on average, four and six populations are needed to secure 99% of NGV and AGV, respectively.

We apply this approach to a real-life example: for the widespread tree *Populus balsamifera*, Keller et al. (2011) reported a mean $\Phi_{ST}$ value of 0.067 estimated from 310 nuclear SNP loci and a mean $Q_{ST}$ value of 0.421 (range = 0.127–0.832) obtained from 13 ecophysiological and phenological traits originating from 20 populations across North America. To capture 99% of NGV, two populations of this tree would be needed using the above formula. When we apply the mean $Q_{ST}$ value to the formula, at least six populations would be necessary to capture the same level of AGV. However, the value of $Q_{ST}$ depends on the trait under consideration: for traits with a high $Q_{ST}$, more populations should be sampled than for traits with a low $Q_{ST}$. Given this, the prudent thing would be not to use the average $Q_{ST}$ but the maximum $Q_{ST}$ in these calculations. If this logic is applied to *P. balsamifera*, as for bud set $Q_{ST} = 0.832$, then up to 25 populations would need to be targeted to maintain enough variation for the trait. This does not mean that NGV is not essential; there is probably a reservoir of genetic variation in every population that is neutral now but may be selectively important if environmental conditions change. Furthermore, NGV can be very informative about the populations' past demography which is often of interest in conservation biology (Frankham, 2015; Allendorf, 2017; DeWoody et al., 2021; García-Dorado & Caballero, 2021).

The application of the above formulae to plants with different life forms, as well as the example of *Populus balsamifera*, suggests that conservation and management policies or actions based solely on $F_{ST}$ could potentially be misleading. Again, these findings stress that guidelines and conservation genetic strategies should be designed based on genetic information on both NGV and AGV together for tree and herbaceous (whether perennial or annual) species. In addition, managers or practitioners should design restoration and conservation strategies by knowing that, on average, $Q_{ST}$ is about 3.6, 1.5, and 1.1 times greater than $F_{ST}$ in woody plants, annuals, and herbaceous perennials, respectively.

To summarize, $F_{ST}$ estimates appear to be more closely related to AGV than within-population genetic diversity metrics (e.g., $H_e$, $\%P$, or $AR$) in seed plant species. Thus, $F_{ST}$ should be considered as a more predictable parameter for conservation and restoration purposes. Together with the metrics of $H_e$, $\%P$, or $AR$, the particular degree of $F_{ST}$ (i.e., low, moderate, or high) is important for prioritizing populations for collection and identifying appropriate sources for reintroductions (Hamrick & Godt, 1996; Ottewell et al., 2016; Chung et al., 2021). Thus, the importance of the proper consideration of $F_{ST}$ information (and $Q_{ST}$, if available) in conservation management cannot be overstated, particularly when it comes to annuals and herbaceous perennials.

## 6 | CONCLUSIONS AND PERSPECTIVE

Within-population genetic variation, both natural and restored, is crucial for the response to short-term environmental stresses and long-term evolutionary change. Although the levels of $H_e$ are often correlated with fitness (Oostermeijer et al., 1994; Reed & Frankham, 2003; Szulkin et al., 2010), $H_e$ of NGV is poorly

correlated with heritability ($h^2$ or $H^2$) of quantitative traits (AGV). As discussed above, the relationship of $H_e$ to $h^2$ or $H^2$ is often very weak, while the relationship between $F_{ST}$ and $Q_{ST}$ is comparatively stronger; thus, $F_{ST}$ could be considered a proxy of $Q_{ST}$. However, whenever logistically possible, common garden and/or transplant studies are strongly recommended to quantify patterns of adaptive genetic variation and differentiation (de Villemereuil et al., 2016; Sork, 2018; Capblancq et al., 2020). The most comprehensive studies conducted so far are generally those carried out with many commercially important tree species (e.g., eucalypts, oaks, poplars, pines, and spruces), as plants (including propagules) with well-adapted genotypes are used to replant clear-cut areas (Depardieu et al., 2020). Exemplifying this, 14 out of 18 entries for woody perennials (seven genera) used in our analyses belong to the eucalypt-oak-pine-spruce-poplar group (De Kort et al., 2013). More studies on $Q_{ST}$–$F_{ST}$ comparisons are needed, particularly on rare woody species and common herbaceous species, to avoid bias in the inferences, as well as to balance entries among the different life forms. Although the differences between herbaceous and woody plants regarding $F_{ST}$ were large in the data reviewed here, similar average values for $Q_{ST}$ were relatively common in the data set used (De Kort et al., 2013). With a larger dataset, one could also expect some generalizations to emerge concerning the $Q_{ST}$–$F_{ST}$ relationships regarding life history characteristics and morphological/anatomical traits. Such generalizations could aid conservation managers and practitioners in using neutral $F_{ST}$ estimates to predict approximate $Q_{ST}$ values and aid the conservation and restoration of plant species. Multiple approaches, including molecular markers (NGV), quantitative traits and/or quantitative trait loci coding for traits and contemporary genome-wide association approaches in the context of a common garden experiment, and environmental variation (e.g., designation of climatic zonation) are needed to gain comprehensive insights into conservation of herbs and trees (de Villemereuil et al., 2016; Rodríguez-Quilón et al., 2016; Sork, 2018).

## ACKNOWLEDGEMENTS

## CONFLICT OF INTEREST

All the authors state that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT

There was no new data created or analyzed for this manuscript.

## ORCID

Mi Yoon Chung https://orcid.org/0000-0002-8756-5367

Juha Merilä https://orcid.org/0000-0001-9614-0072

Yuseob Kim https://orcid.org/0000-0002-7975-6147

Kangshan Mao https://orcid.org/0000-0002-0071-1844

Jordi López-Pujol https://orcid.org/0000-0002-2091-6222

Myong Gi Chung https://orcid.org/0000-0002-1283-3574

## REFERENCES

Aguilar, A., Roemer, G., Debenham, S., Binns, M., Garcelon, D., & Wayne, R. K. (2004). High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mam-

mal.*Proceedings of the National Academy of Sciences of the United States of America* , *101* , 3490–3494. https//doi.org/10.1073/pnas.0306582101

Allendorf, F. W. (2017). Genetics and the conservation of natural populations: allozymes to genomes. *Molecular Ecology* , *26* , 420–430. https//doi.org/10.1111/mec.13948

Allendorf, F. W., Hohenlohe, P. A., & Luikart, G. (2010). Genomics and the future of conservation genetics. *Nature Reviews Genetics* ,*11* , 697–709. https//doi.org/10.1038/nrg2844

Bekessy, S. A., Ennos, R. A., Burgman, M. A., Newton, A. C., & Ades, P. K. (2003). Neutral DNA markers fail to detect genetic divergence in an ecologically important trait. *Biological Conservation* ,*110* , 267–275. https//doi.org/S0006-3207(02)00225-2

Bell, G. (2010). Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society B: Biological Sciences* , *365* , 87–97.*https://doi.org/10.1098/rstb.2009.0150*

Bergland, A. O., Behrman, E. L., O'Brien, K. R., Schmidt, P. S., & Petrov, D. A. (2014). Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila* . *PLoS Genetics* , *10* ,e1004775. https//doi.org/10.1371/journal.pgen.1004775

Britt, M., Haworth, S. E., Johnson, J.B., Martchenko, D., & Shafer, A. B. (2018). The importance of non-academic coauthors in bridging the conservation genetics gap. *Biological Conservation* , *218* , 118–123. https://doi.org/10.1016/j.biocon.2017.12.019

Capblancq, T., Fitzpatrick, M. C., Bay, R. A., Exposito-Alonso, M., & Keller, S. R. (2020). Genomic prediction of (mal)adaptation across current and future climatic landscapes. *Annual Review of Ecology, Evolution, and Systematics* , *51* , 245–269.*https://doi.org/10.1146/annurev-ecolsys-020720-042553*

Ceska, J. F., Affolter, J. M., & Hamrick, J. L. (1997). Developing a sampling strategy for *Baptisia arachnifera* based on allozyme diversity. *Conservation Biology* , *11* , 1133–1139.*https://doi.org/10.1046/j.1523-1739.1997.95527.x*

Charlesworth, D. (2006). Balancing selection and its effects on sequences in nearby genome regions. *PLoS Genetics* , *2(4)* , e64. https//doi.org/10.1371/journal.pgen.0020064

Chun, Y. J., Nason, J. D., & Moloney, K. A. (2009). Comparison of quantitative and molecular genetic variation of native vs. invasive populations of purple loosestrife (*Lythrum salicaria* L., Lythraceae). *Molecular Ecology* , *18* , 3020–3035. https//doi.org/10.1111/j.1365-294X.2009.04254.x

Chun, Y. J., Le Corre, V., & Bretagnolle, F. (2011). Adaptive divergence for a fitness-related trait among invasive *Ambrosia artemisiifolia* populations in France. *Molecular Ecology* ,*20* , 1378–1388. https//doi.org/10.1111/j.1365-294X.2011.05013.x

Chung, M. Y., Son, S., Herrando-Moraira, S., Tang, C. Q., Maki, M., Kim, Y.-D., López-Pujol, J., Hamrick, J. L., & Chung, M. G. (2020). Incorporating differences between genetic diversity of trees and herbaceous plants in conservation strategies. *Conservation Biology* , *34* , 1142–1151. https//doi.org/10.1111/cobi.13467

Chung, M. Y., Son, S., López-Pujol, J., Mao, K., & Chung, M. G. (2021). Plant conservation practitioners can benefit from neutral genetic diversity. *Diversity* , *13* , 552. https://doi.org/10.3390/d13110552

Clausen, J., Keck, D. D., & Hiesey, W. M. (1941). *Experimental studies on the nature of species I. Effect of varied environments on western North American plants* . Carnegie Institution of Washington Publication No. 520, pp. 1–452.

Colautti, R. I., Lee, C. R., & Mitchell-Olds, T. (2012). Origin, fate, and architecture of ecologically relevant genetic variation. Current Opinion in Plant Biology, 15, 199–204. https//doi.org/10.1016/j.pbi.2012.01.016

De Kort, H., Vandepitte, K., & Honnay, O. (2013). A meta-analysis of the effects of plant traits and geographical scale on the magnitude of adaptive differentiation as measured by the difference between $Q_{ST}$ and $F_{ST}$. *Evolutionary Ecology* , *27* , 1081–1097. https//doi.org/10.1007/s10682-012-9624-9

Depardieu, C., Girardin, M. P., Nadeau, S., Lenz, P., Bousquet, J., & Isabel, P. (2020). Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate. *New Phytologist* , *227* , 427–439. https//doi.org/10.1111/nph.16551

de Villemereuil, P., Gaggiotti, O. E., Mouterde, M., & Till-Bottraud, I. (2016). Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity* , *116* , 249–254. *https//dx.doi.org/10.1038/hdy.2015.93*

DeWoody, J. A., Harder, A. M., Mathur, S., & Willoughby, J. R. (2021). The long-standing significance of genetic diversity in conservation. *Molecular Ecology* , *30* , 4147–4154. https//doi.org/10.1111/mec.16051

Dlugosch, K. M., & Parker, I. M. (2007). Molecular and quantitative trait variation across the native range of the invasive species *Hypericum canariense* : evidence for ancient patterns of colonization via pre-adaptation? *Molecular Ecology* , *16* , 4269–4283. https//doi.org/10.1111/j.1365-294X.2007.03508.x

Dubois, N.S., Gomez, A., Carlson, S., & Russell, D. (2019). Bridging the research-implementation gap requires engagement from practitioners. *Conservation Science and Practice* , 2, e134. https//doi.org/ 10.1111/csp2.134

Edelaar, P., Burraco, P., & Gomez-Mestre, I. (2011). Comparisons between $Q_{ST}$ and $F_{ST}$—how wrong have we been? *Molecular Ecology* , *20* , 4830–4839. https//doi.org/10.1111/j.1365-294X.2011.05333.x

Ehrlich, P. R., & Raven, P. H. (1969). Differentiation of populations. *Science* , *165* , 1228–1232. https//doi.org/ *10.1126/science.165.3899.1228*

Fabian, Y., Bollmann, K., Brang, P., Hein, C., Olschewski, R., Rigling, A., Stofer, S., & Holderegger, R. (2019). How to close the science-practice gap in nature conservation? information sources used by practitioners. *Biological Conservation* , *235* , 93–101. *https://doi.org/10.1016/j.biocon.2019.04.011*

Fijarczyk, A., & Babik, W. (2015). Detecting balancing selection in genomes: limits and prospects. *Molecular Ecology* , *24* , 3529–3545. https//doi.org/10.1111/mec.13226

Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., & Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evolutionary Applications* , *11* , 1035–1052. https//doi.org/10.1111/eva.12569

Frankham, R. (2015). Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology* , *24* , 2610–2618. https//doi.org/10.1111/mec.13139

García-Dorado A, & Caballero A. (2021). Neutral genetic diversity as a useful tool for conservation biology. *Conservation Genetics* , *22* , 541–545. https://doi.org/10.1007/s10592-021-01384-9-9

Gravuer, K., von Wettberg, E., & Schmitt, J. (2005). Population differentiation and genetic variation inform translocation decisions for *Liatris scariosa* var. *novae-angliae* , a rare New England grassland perennial. *Biological Conservation* , *124* , 155–167. https//doi.org/10.1016/j.biocon.2005.01.021

Hall, M. C., Dworkin, I., Ungerer, M. C., & Purugganan, M. P. (2007). Genetics of microenvironmental canalization in *Arabidopsis thaliana* . *Proceedings of the National Academy of Sciences of the United States of America* , *104* , 13717–13722. https//doi.org/10.1073/pnas.0701936104

Hamrick, J. L., & Godt, M. J. W. (1996). Conservation genetics of endemic plant species. In J. C. Avise, & J. L. Hamrick (Eds.), *Conservation Genetics: Case Histories from Nature* (pp. 281–304). Chapman & Hall.

Hamrick, J. L., Godt, M. J. W., & Gonzales, E. (2006). Conservation of genetic diversity in old-growth forest communities of the southeastern United States. *Applied Vegetation Science* , *9* , 51–57. https://doi.org/10.1111/j.1654-109X.2006.tb00655.x

Hendry, A. P. (2002). $Q_{st} > = \neq < F_{st}$? *Trends in Ecology & Evolution*, *17*, 502. *https://doi.org/10.1016/S0169-5347(02)02603-4*

Holderegger, R., Balkenhol, N., Bolliger, J., Engler, J. O., Gugerli, F., Hochkirch, A., Nowak, C., Segelbacher, G., Wider, A., & Zachos, F. E. (2019). Conservation genetics: linking science with practice. *Molecular Ecology*, *28*, 3848–3856. https://doi.org/10.1111/mec.15202

Holsinger, K. E., & Weir B. S. (2010). Genetics in geographically structured populations: defining, estimating and interpreting $F_{ST}$. *Nature Reviews Genetics*, *10*, 639–650. https://doi.org/10.1038/nrg2611

Jiménez-Ambriz, G., Petit, C., Bourrié, I., Dubois, S., Olivieri, I., & Ronce, O. (2007). Life history variation in the heavy metal tolerant plant *Thlaspi caerulescens* growing in a network of contaminated and noncontaminated sites in southern France: role of gene flow, selection and phenotypic plasticity. *New Phytologist*, *173*, 199–215. https://doi.org/10.1111/j.1469-8137.2006.01923.x

Karhunen, M., Merilä, J., Leinonen, T., Cano, J. M., & Ovaskainen, O. (2013). DRIFTSEL: an R package for detecting signals of natural selection in quantitative traits. *Molecular Ecology Resources*, *13*, 746–754. *https://doi.org/10.1111/1755-0998.12111*

Karhunen, M., Ovaskainen, O., Herczeg, G., & Merilä, J. (2014). Bringing habitat information into statistical tests of local adaptation in quantitative traits: a case study of nine-spined sticklebacks. *Evolution*, *68*, 559–568. https://doi.org/10.1111/evo.12268

Kawakami, T., Morgan, T. J., Nippert, J. B., Ocheltree, T. W., Keith, R., Dhakal, P., & Ungerer, M. C. (2011). Natural selection drives clinal life history patterns in the perennial sunflower species, *Helianthus maximiliani*. *Molecular Ecology*, *20*, 2318–2328. https://doi.org/10.1111/j.1365-294X.2011.05105.x

Keller, S. R., Soolanayakanahally, R. Y., Guy, R. D., Silim, S. N., Olson, M. S., & Tiffin, P. (2011). Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *American Journal of Botany*, *98*, 99–108. https//doi.org/10.3732/ajb.1000317

Kreitman, M. (2001). "Selective sweep." In S. Brenner, & J. H. Miller (Eds.), *Encyclopedia of Genetics* (pp. 1803–1804). Academic Press.

Kremer, A., Zanetto, A., & Ducousso, A. (1997). Multilocus and multitrait measures of differentiation for gene markers and phenotypic traits. *Genetics*, 14, 1229–1241. https://doi.org/10.1093/genetics/145.4.1229

Lamy, J.-B., Plomion, C., Kremer, A., & Delzon, S. (2012). $Q_{ST} < F_{ST}$ as a signature of canalization. *Molecular Ecology*, *21*, 5646–5655. https//doi.org/10.1111/mec.12017

Lamy, J.-B., Bouffier, L., Burlett, R., Plomion, C., Cochard, H., & Delzon, S. (2011). Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS ONE*, *6(8)*, e23476. https//doi.org/10.1371/journal.pone.0023476

Lande, R. (1992). Neutral theory of quantitative genetic variance in an island model with local extinction and recolonization. *Evolution*, *46*, 381–389. https://doi.org/10.1111/j.1558-5646.1992.tb02046.x

Le Corre, V., & Kremer, A. (2012). The genetic differentiation at quantitative trait loci under local adaptation. *Molecular Ecology*, *21*, 1548–1566. https//doi.org/ 10.1111/j.1365-294X.2012.05479.x

Leinonen, T., O'Hara, R. B., Cano, J. M., & Merilä, J. (2008). Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology*, *21*, 1–17. https//doi.org/10.1111/j.1420-9101.2007.01445.x

Leinonen, T., McCairns, R. J. S., O'Hara, R. B., & Merilä, J. (2013). $Q_{ST}-F_{ST}$ comparisons: evolutionary and ecological insights from genomic heterogeneity. *Nature Reviews Genetics*, *14*, 179–190. https//doi.org/10.1038/nrg3395

Li, Z., Löytynoja, A., Fraimout, A., & Merilä, J. (2019). Effects of marker type and filtering criteria on $Q_{ST}$-$F_{ST}$ comparisons. *Royal Society Open Science*, *6(11)*, 190666. *https://dx.doi.org/10.1098/rsos.190666*

Machado, H. E., Bergland, A. O., Taylor, R., Tilk, S., Behrman, E., Dyer, K., Fabian, D. K., Flatt, T., González, J., Karasov, T., Kim, B., Kozeretska, I., Lazzaro, B. P., Merritt, T. J. S., Pool, J. E., O'Brien, K., Rajpurohit, S., Roy, P. R., Schaeffer, S. W., Serga, S., Schmidt, P., & Petrov, D. A. (2021). Broad geographic sampling reveals the shared basis and environmental correlates of seasonal adaptation in *Drosophila*. *eLife*, *10*, e67577. https//doi.org/10.7554/eLife.67577

Marin, S., Gibert, A., Archambeau, J., Bonhomme,V., Lascoste, M., & Pujol, B. (2020). Potential adaptive divergence between subspecies and populations of snapdragon plants inferred from $Q_{ST}$–$F_{ST}$ comparisons. *Molecular Ecology*, *29*, 3010-3021. https://doi.org/10.1111/mec.15546

McKay, J. K., Bishop, J. G., Lin, J.-Z., Richards, J. H., Sala, A., & Mitchell-Olds, T. (2001). Local adaptation across a climatic gradient despite small effective population size in the rare Sapphire Rockcress. *Proceedings of the Royal Society B: Biological Sciences*, 268, 1715–1721. https//doi.org/10.1098/rspb.2001.1715

McKay, J. K., & Latta, R. G. (2002). Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, *17*, 285–291. https//doi.org/10.1016/S0169-5347(02)02478-3

Merilä, J., & Sheldon, B. C. (1999). Genetic architecture of fitness and nonfitness traits: empirical patterns and development of ideas. *Heredity*, *83*, 103–109. https://doi.org/10.1046/j.1365-2540.1999.00585.x.

Merilä, J., & Crnokrak, P. (2001). Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, *14*, 892–903. https://doi.org/10.1046/j.1420-9101.2001.00348.x

Merimans, P., & Hedrick, P. W. (2010). Assessing population structure: $F_{ST}$ and related measures. *Molecular Ecology*, *11*, 5–18. http//doi.org/10.1111/j.1755-0998.2010.02927.x

Messer, P. W., Ellner, S. P., & Hairston, N. G. Jr. (2016). Can population genetics adapt to rapid evolution? *Trends in Genetics*, *32*, 408-418. https//doi.org/10.1016/j.tig.2016.04.005.

Meyer, C. L., Kostecka, A. A., Saumitou-Laprade, P., Créach, A., Castric, V., Pauwels, M., & Frérot, H. (2010). Variability of zinc tolerance among and within populations of the pseudometallophyte species *Arabidopsis halleri* and possible role of directional selection. *New Phytologist*, *185*, 130–142. https//doi.org/10.1111/j.1469-8137.2009.03062.x

Nielson, R. (2005). Molecular signatures of natural selection. *Annual Review of Genetics*, *39*, 197–218. https://doi.org/10.1146/annurev.genet.39.073003.112420

Nosil, P., Egan, S. P., & Daniel, J. (2007). Heterogeneous genomic differentiation between walking-stick ecotypes: "isolation by adaptation" and multiple roles for divergent selection. *Evolution*, *62*, 316–336. https//doi.org/10.1 I 11/j.1558-5646.2007.00299

Oostermeijer, J. G. B., van Fijek, M. W., & den Nijs, J. C. M. (1994). Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe*. *Oecologia*, *97*, 289–296. https//doi.org/10.1007/BF00317317

Ottewell, K. M., Bickerton, D. C., Byrne, M., & Lowe, A. J. (2016). Bridging the gap: a genetic assessment framework for population-level threatened plant conservation prioritization and decision-making. *Diversity and Distributions*, *22*, 174–188. https//doi.org/10.1111/ddi.12387

Ovaskainen, O., Karhunen, M., Zheng, C. Z., Arias, J. M. C., & Merilä, J. (2011). A new method to uncover signatures of divergent and stabilizing selection in quantitative traits. *Genetics*, *189*, 621–632. https//doi.org/10.1534/genetics.111.129387

Petit, C., Fréville, H., Mignot, A., Colas, B., Riba, M., Imbert, E., Hurtrez-Boussés, I., Virevaire, M., & Olivieri, I. (2001). Gene flow and local adaptation in two endemic plant species. *Biological Conservation*, *100*, 21–34. https//doi.org/10.1016/S0006-3207(00)00204-4

Podolsky, R. H. (2001). Genetic variation for morphological and allozyme variation in relation to population size in *Clarkia dudleyana* , an endemic annual. *Conservation Biology* , *15* , 412–423. https//doi.org/10.1046/j.1523-1739.2001.015002412.x

Podolsky, R. H., & Holtsford, T. P. (1995). Population structure of morphological traits in *Clarkia dudleyana* . I. Comparison of $F_{ST}$ between allozymes and morphological traits.*Genetics* , *140* , 733–744. https//doi.org/10.1093/genetics/140.2.733

Prendeville, H. R., Barnard-Kubow, K., Dai, C., Barringer, B. C., & Galloway, L. F. (2013). Clinal variation for only some phenological traits across a species range. *Oecologia* , *173* , 421–430. https//doi.org/10.1007/s00442-013-2630-y

Pressoir, G., & Berthaud, J. (2004). Population structure and strong divergent selection shape phenotypic diversification in maize landraces.*Heredity* , *92* , 95–101. https://doi.org/10.1038/sj.hdy.6800388

Reed, D. H., & Frankham, R. (2001). How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* , *55* , 1095–1103. https://doi.org/10.1111/j.0014-3820.2001.tb00629.x

Reed, D. H., & Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conservation Biology* , *17* , 230–237. https://doi.org/10.1046/j.1523-1739.2003.01236.x

Rodríguez-Quilón, I., Santos-del-Blanco, L., Serra-Varela, M. J., Koskela, J., González-Martínez, S. C., & Alía, R. (2016). Capturing neutral and adaptive genetic diversity for conservation in a highly structured tree species. *Ecological Applications* , *26* , 2254–2266. https://doi.org/10.1002/eap.1361

Savolainen, O., Pyhäjärvi, T., & Knürr, T. (2007). Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics* , *38* , 595–619. https//doi.org/10.1146/annurev.ecolsys.38.091206.095646

Savolainen, O. (2011). The genomic basis of local climatic adaptation.*Science* , *334* , 49–50. https//doi.org/10.1126/science.1213788

Schwaegerle, K. E. K., Garbutt, K., & Bazzaz, F. A. (1986). Differentiation among nine populations of *Phlox* . I. Electrophoretic and quantitative variation. *Evolution* , *40* , 506–517. https//doi.org/*10.1111/j.1558-5646.1986.tb00503.x*

Shirk, R. Y., & Hamrick, J. L. (2014). Multivariate adaptation but no increase in competitive ability in invasive *Geranium carolinianum*L. (Geraniaceae). *Evolution* , *68* , 2945–2959. https://doi.org/10.1111/evo.12474

Slatkin, M. (1973). Gene flow and selection in a cline. *Genetics* ,*75* , 733–756. https//doi.org/10.1093/genetics/75.4.733

Sork, V. L. (2018). Genomic studies of local adaptation in natural plant populations. *Journal of Heredity* , *109* , 3–15. https://doi.org/10.1093/jhered/esx091

Spitze, K. (1993). Population structure in *Daphnia obtusa* : quantitative genetic and allozyme variation. *Genetics* ,*135* , 67–374. https://doi.org/10.1093/genetics/135.2.367

Sreejayan, Kumar, U. S., Varghese, G., Jacob, T. M., P., & Thomas, G. (2011). Stratification and population structure of the genetic resources of ancient medicinal rice (*Oryza sativa* L.) landrace Njavara.*Genetic Resources and Crop Evolution* , *58* , 697–711. https://doi.org/10.1007/s10722-010-9613-1

Steinger, T., Haldimann, P., Leiss, K., & Müller-Schärer, H. (2002). Does natural selection promote population divergence? A comparative analysis of population structure using amplified fragment length polymorphism markers and quantitative traits. *Molecular Ecology* ,*11* , 2583–2590. https://doi.org/10.1046/j.1365-294x.2002.01653.x

Stephan, W. (2019). Selective sweeps. *Genetics* , *211* , 5–13. https://doi.org/10.1534/genetics.118.301319

Szulkin, M., Bierne, N., & David, P. (2010). Heterozygosity-fitness correlations: a time for reappraisal. *Evolution*, *64*, 1202–1217. https//doi.org/10.1111/j.1558-5646.2010.00966.x

Taylor, H. R., Dussex, N., & van Heezik, Y. (2017). Bridging the conservation genetics gap by identifying barriers to implementation for conservation practitioners. *Global Ecology and Conservation*, *10*, 231–242. https://doi.org/10.1016/j.gecco.2017.04.001

Teixeira, J. C., & Huber, C. D. (2021). The inflated significance of neutral genetic diversity in conservation genetics. *Proceedings of the National Academy of Sciences of the United States of America*, *118(10)*, e2015096118. https://doi.org/10.1073/pnas.2015096118

Turesson, G. (1922). The genotypical response of the plant species to the habitat. *Hereditas*, *3*, 211-350. https://doi.org/10.1111/j.1601-5223.1922.tb02734.x

Volis, S., Yakubov, B., Shulgina, I., Ward, D., & Mendlinger, S. (2005). Distinguishing adaptive from nonadaptive genetic differentiation: comparison of $Q_{ST}$ and $F_{ST}$ at two spatial scales. *Heredity*, *95*, 466–475. https://doi.org/10.1038/sj.hdy.6800745

Waldmann, P., & Andersson, S. (1998). Comparison of quantitative genetic variation and allozyme diversity within and between populations of *Scabiosa canescens* and *S. columbaria*. *Heredity*, *81*, 79–86. https://doi.org/10.1046/j.1365-2540.1998.00379.x

Whitlock, M. C. (2008). Evolutionary inference from $Q_{ST}$. *Molecular Ecology*, *17*, 1885–1896. https//doi.org/10.1111/j.1365-294X.2008.03712.x

Wright, S. (1951). The genetical structure of populations. *Annals of Eugenics*, *1*, 323–354. https//doi.org/10.1111/j.1469-1809.1949.tb02451.x

Ye, Q., Tang, F., Wei, N., & Yao, X. (2014). Molecular and quantitative trait variation within and among small fragmented populations of the endangered plant species *Psilopeganum sinense*. *Annals of Botany*, *113*, 79–86. https//doi.org/10.1093/aob/mct255

Yu, Q., Ellen, E. D., Wade, M. J., & Delph, L. F. (2011). Genetic differences among populations in sexual dimorphism: evidence for selection on males in a dioecious plant. *Journal of Evolutionary Biology*, *24*, 1120–1127. https//doi.org/10.1111/j.1420-9101.2011.02245.x

**TABLE 1** Definitions of terms used in this mini review

| Term | Definition |
|---|---|
| Adaptation | A trait that increases the ability of a population or an organism to survive in its env |
| Allelic richness ($AR$) | A measurement of the number of alleles per locus with rarefaction adjusting for diff |
| Balancing selection | A process in which more than one allele is maintained at a locus at a frequency high |
| Broad-sense heritability ($H^2$) | The ratio of total genetic variance to total phenotypic variance within a population. |
| Common garden experiment | A traditional experiment in which genotypes from different populations (provenance |
| Conservation genetics | A branch of (population) genetics aimed to reduce the risk of population and specie |
| Conservation genomics | The use of genome-scale data with the same aims of conservation genetics, i.e., ensu |
| $F_{ST}$ | The probability of identity by descent (*ibd*; describing the pair of homologous DNA |
| $G_{ST}$ | The proportion of total genetic diversity found among populations averaged over all |
| Gene diversity ($H_e$) | Hardy-Weinberg expected heterozygosity both at monomorphic and polymorphic loc |
| Gene flow | The movement of alleles from one population to another population, which for plant |
| Genetic drift | A change in allele frequencies in a population over time resulting from a random sam |
| Genetic markers | Any type of neutral (see below) genetic information (e.g., allozymes, amplified fragm |
| Isolation by distance | A process by which geographically restricted gene flow results in a genetic differenti |
| Linkage disequilibrium | A state in which genes are combined in a dependent manner (i.e., linkage). It arises |
| Local adaptation | A situation in which resident genotypes have a relatively higher fitness in their local |
| Narrow-sense heritability ($h^2$) | The ratio of additive genetic variance to the phenotypic variance in a trait within a |
| Neutral | Molecular markers that do not affect fitness, i.e., individuals with different genotype |

15

| | |
|---|---|
| Non-additive genetic variation | Results from interactions between an allele at the same locus (dominance) or at diff |
| Percentage of polymorphic loci ($\%P$) | A measure used to quantify genetic diversity. |
| $Q_{ST}$ | The proportion of total additive genetic variance that is due to among-population d |
| $Q_{ST}$–$F_{ST}$ comparison experiment | The comparison of the degree of genetic differentiation in quantitative traits ($Q_{ST}$) |
| Reciprocal transplant experiment | A traditional experimental approach in which living organisms from two different en |
| Translocation | The deliberate (human-mediated) transfer of plants (entire plants, seeds, or propagu |