As studies of  $F_{ST}$  and  $Q_{ST}$  accumulate, more studies will better meet these assumptions. Although sampling  $F_{\mathrm{ST}}$  and  $Q_{\rm ST}$  from separate populations is not ideal, studies are limited and if the correlation among species means has any generality, their inclusion should not introduce any systematic bias. All the studies that we included enabled a formal calculation of  $Q_{\rm ST}$  to be made. However, on review, we found an error in our calculation of  $V_{g(w)}$ for some studies. We have updated our data set with corrected values (http://www.dal.ca/~rglatta/QST/ McKayLatta.html gives an annotated summary of our calculations trait by trait and study by study) and recalculated our correlation (r = 0.369, P = 0.049logarithmic) again finding an  $r^2$  of <0.14.

Moreover, much of the observed relationship derives from the observation that  $Q_{\rm ST}$  is typically greater than  $F_{\rm ST}$  [1–3]. Although this enables us to infer the action of local selection, it also induces a spurious correlation. If pairs of random numbers are constrained such that 0<x<y<1, without any other relationship, the median correlation (1000 sets of 25) is r= 0.67. Thus, regardless of statistical significance, knowing marker  $F_{ST}$  enables little to be inferred about average  $Q_{ST}$ , save to suggest the lower limit representing the neutral case from which diversifying selection acts to increase  $Q_{ST}$ . Even less inference is possible about individual traits and certainly very little about the exact geographical patterns of adaptive population divergence within a species. We reiterate that, in simulations, diversifying selection on polygenic traits does not produce a response at neutral markers [5] such that markers cannot be expected to reflect adaptive differences. The stronger the local adaptation, the more  $Q_{\rm ST}$  differs from  $F_{\rm ST}$  and the weaker the association. However, marker  $F_{ST}$ could predict the distribution of alleles at quantitative trait loci underlying adaptive traits, as these are expected to behave differently from the traits that they influence [5]. In this light, we can only welcome further theoretical development [6] on the evolutionary forces shaping  $F_{\rm ST}$  and  $Q_{\rm ST}$ 

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Published online: 19 August 2002

# $Q_{\rm ST}>=\neq < F_{\rm ST}?$

In a recent review in TREE, McKay and Latta [1] examined the relationship between  $Q_{\rm ST}$  and  $F_{\rm ST}$  in natural populations. Here, I outline two issues that deserve further consideration in such comparisons.

The expectation that  $Q_{ST} = F_{ST}$  under neutrality [1-3] depends on the assumption that mutation rates  $(\mu)$  are considerably lower than migration rates (m). This assumption might be violated for some systems (e.g. low gene flow) and markers (e.g. microsatellites, where  $\mu \approx 0.0001$ ). For example,  $F_{\rm ST}$  was  $\geq$  0.30 for nine out of 29 studies in [1] and six out of 24 studies in Merilä and Crnokrak [2]. Under the island model (for simplicity),  $F_{ST} \ge 0.30$  would equate to  $N_{\rm e}(m+\mu) \le 0.583$  and  $(m+\mu)$  $\leq$ 0.00017 (if, for example,  $N_{e} = 5000$ ). Thus, for a wide range of plausible parameter space, mutation need not be appreciably lower than migration. Failing this assumption,  $Q_{\rm ST} = F_{\rm ST}$  under neutrality only if mutational inputs are similar across marker loci and quantitative traits. Unfortunately, this also might not be true. For example, when migration is low, the higher mutation rates for microsatellites than for allozymes should lead to higher heterozygosities and lower  $F_{\rm ST}$ s for the former [4]. Under these conditions,  $Q_{\rm ST}$ cannot simultaneously equal  $F_{ST}$ s that are estimated using different markers. Heterozygosity also varies among quantitative traits, perhaps because

they present different-sized targets for mutation [5]. Different quantitative traits might thus have different  $Q_{\rm ST}s$  even in the absence of selection.

The ability to detect differences between  $Q_{\rm ST}$  and  $F_{\rm ST}$  will vary through the course of evolution. Whitlock [3] argued that  $Q_{ST}$  might not exceed  $F_{ST}$  in young systems because selection has not had enough time to drive divergence. However, evidence from natural populations shows that substantial adaptive divergence can occur over very short periods of time [6]. Indeed, grayling Thymallus thymallus that colonized new sites from a common ancestral source had life-history  $Q_{\rm ST}{\bf s}$  that greatly exceeded microsatellite  $F_{\rm ST}$ s after only 11-22 generations [7]. I argue instead that it should become increasingly difficult to demonstrate that  $Q_{ST} > F_{ST}$  as divergence times increase. When migration and mutation are both low,  $F_{\rm ST}$ can approach unity at equilibrium, leaving little room for  $Q_{\rm ST}$  to exceed  $F_{\rm ST}$  even if the divergence of quantitative traits was driven by selection. In accordance with this prediction, the magnitude by which  $Q_{ST}$ exceeds  $F_{\rm ST}$  decreases with increasing  $F_{\rm ST}$ (see figures in [1,2]).

Owing to the issues raised here, and by other authors [1–3], the relationship between  $Q_{\rm ST}$  and  $F_{\rm ST}$  warrants further theoretical and empirical investigation.

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Published online: 11 September 2002