

NEWS AND VIEWS

OPINION

 $Q_{ST} < F_{ST}$ As a signature of canalization

JEAN-BAPTISTE LAMY,^{*†‡} CHRISTOPHE PLOMION,^{*†} ANTOINE KREMER^{*†} and SYLVAIN DELZON^{*†}

^{*}Univ. Bordeaux, UMR 1202 BIOGECO, F-33400, Talence, France; [†]INRA, UMR 1202 BIOGECO, F-33610, Cestas, France; [‡]INRA, UMR 547 PIAF, F-63100, Clermont-Ferrand, France

Abstract

A key aim of evolutionary biology – inferring the action of natural selection on wild species – can be achieved by comparing neutral genetic differentiation between populations (F_{ST}) with quantitative genetic variation (Q_{ST}). Each of the three possible outcomes of comparisons of Q_{ST} and F_{ST} ($Q_{ST} > F_{ST}$, $Q_{ST} = F_{ST}$, $Q_{ST} < F_{ST}$) is associated with an inference (diversifying selection, genetic drift, uniform selection, respectively). However, published empirical and theoretical studies have focused on the $Q_{ST} > F_{ST}$ outcome. We believe that this reflects the absence of a straightforward biological interpretation of the $Q_{ST} < F_{ST}$ pattern. We here report recent evidence of this neglected evolutionary pattern, provide guidelines to its interpretation as either a canalization phenomenon or a consequence of uniform selection and discuss the significant importance this issue will have for the area of evolutionary biology.

Keywords: Canalization, diversifying selection, evolutionary stasis, phylogeny signal, Q_{ST}/F_{ST} comparison, stabilizing selection, uniform selection

Received 10 January 2012; revised 27 July 2012; accepted 31 July 2012

Introduction: comparison of Q_{ST} and F_{ST} and inferences

The relative contributions of genetic drift and natural selection to evolutionary change have long been debated in evolutionary biology (Galpern 2000; McKay & Latta 2002; Hansen & Houle 2004; Leinonen *et al.* 2008; Meirmans & Philip 2011). Comparisons of the differentiation of phenotypic traits (as measured by Q_{ST}) with that of neutral molecular markers (as measured by F_{ST}) provide one of the

most accessible frameworks and universal tools for inferring the role of natural selection in population differentiation for quantitative traits (DeWoody *et al.* 2010).

Underlying assumptions for comparison of Q_{ST} and F_{ST}

Comparisons of Q_{ST} and F_{ST} are based on the rationale that F_{ST} values at neutral markers are estimators of the degree of population differentiation only due to the interplay between genetic drift and migration, assuming that mutation rates are negligible in comparison with migration rates (Spitze 1993; Merilä & Crnokrak 2001). If the quantitative traits are exposed only to the same neutral evolutionary forces as neutral genetic markers and they are genetically controlled by purely additive genes (without pleiotropy), then their level of differentiation between populations would be expected to be equal to that for neutral loci (*i.e.* $Q_{ST} = F_{ST}$). The comparison of these two quantities (Q_{ST} and F_{ST}) can therefore be used to detect the effects of selection, including the effect of cumulative past selection events in the absence of current selection (Whitlock 2008).

Inferring the action of natural selection on wild species

In comparisons of Q_{ST} and F_{ST} , three outcomes are possible, for which a different inference can be drawn. If the trait is neutral and additively determined, then Q_{ST} should be equal to F_{ST} . By contrast, $Q_{ST} > F_{ST}$ is predicted under conditions of diversifying (or divergent) selection for different local optima and $Q_{ST} < F_{ST}$ is predicted under conditions of uniform selection (also called homogeneous, spatially homogenizing, convergent or stabilizing selection across populations). Hereafter, we refer to ‘uniform selection’, to distinguish this situation from that of stabilizing selection (see Glossary) within a population.

Uniform selection is conceptualized and modelled as *n* stabilizing selection events acting within *n* different populations with the same selection optimum for each population (Fig. 1), despite the partial genetic isolation (assessed by determining F_{ST}) (Le Corre & Kremer 2003; Whitlock & Guillaume 2009). This process reproduces trait conservatism and eventually leads to stasis (see Glossary), but unfortunately, this model does not provide suggestions for the biological hypothesis constraining the local selective optima across populations or subspecies living in different environments. In evolutionary ecology, most of the literature is oriented towards the explanation of the variation between populations (or related species), but discard experimental results leading to the absence of trait differentiation despite the great variability of environment. Therefore, it does not seem that the explanation for trait conservatism (and stasis) can lie only in selection regimes;

Correspondence: Sylvain Delzon, Fax: 33 (0)5 40 00 36 57; E-mail: sylvain.delzon@u-bordeaux1.fr

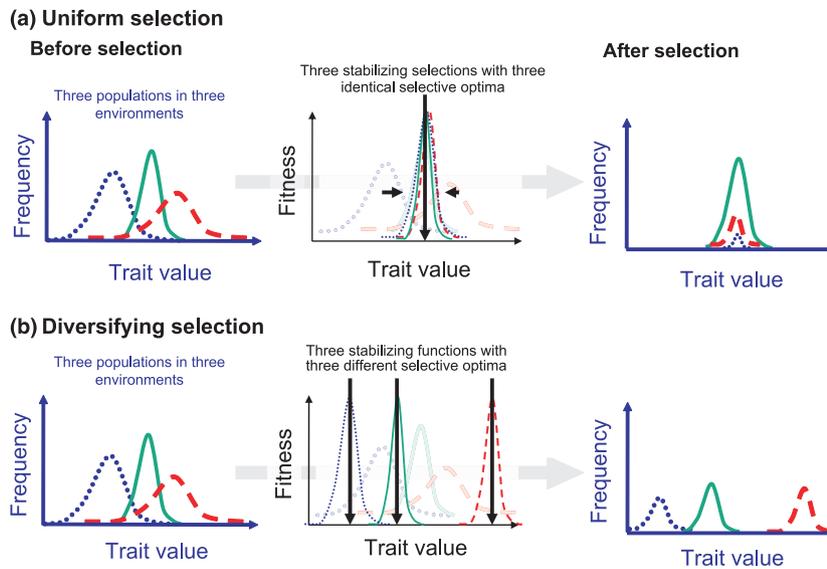


Fig. 1 Conceptual relationship between uniform or diversifying selection and stabilizing selection. On the left part, there are three populations inhabiting different environments across the species distribution range, symbolized by blue, green and red colours; they represent three different trait distributions. The central part shows the relationship between the fitness and the trait value (selection function). In the background of the selection function, we also reported the initial trait distribution. The horizontal black arrow illustrated the location of selective optima, while the vertical one symbolized the selective intensity of the selection function. (a) The upper panel shows the conceptual relationship between stabilizing selection and uniform selection. Uniform selection is the joint effect of n stabilizing selection events within n populations centred on the same selective optimum. Following this uniform selection event, populations exhibit the same mean trait value and a reduced variance. This selection process decreases the between-population variance. (b) The lower panel shows the conceptual relationship between stabilizing selection and diversifying selection. Diversifying selection could be modelled through stabilizing selections or other selection functions (disruptive, directional and divergent) with different selective optima between populations. Within-population consequences of diversifying selection depend on the selection function, but this selection process generally leads to increased between-population variance.

constraints due to genetic architecture are too readily dismissed (Bradshaw 1991; Brent Burt 2001; Merilä & Crnokrak 2001; Hansen & Houle 2004).

Methodological limits of comparison of Q_{ST} and F_{ST}

The empirical estimation of Q_{ST} is labour intensive [(O'Hara & Merilä 2005; Navarro *et al.* 2005; Goudet & Buchi 2006; Whitlock & Guillaume 2009) recommend >20 populations \times five families \times five progenies], and rigorous statistical comparisons between Q_{ST} and F_{ST} are not simple to perform. On the one hand, estimates of Q_{ST} and F_{ST} are subject to statistical and evolutionary stochasticity. The first leads to estimation error, while the second which is due to the randomness of evolutionary processes has not always been dealt with appropriately, particularly in comparisons between Q_{ST} and F_{ST} . Approaches for comparing these two parameters taking both types of error into account have only recently been developed, for univariate (Whitlock & Guillaume 2009; Lamy *et al.* 2011) and multivariate tests (Martin *et al.* 2008; Ovaskainen *et al.* 2011). On the other hand, the use of F_{ST} values estimated for neutral markers with rates of mutation higher than those for quantitative traits has been criticized, as it could potentially lead to spurious inferences of diversifying selection (Kronholm *et al.*

2010; Edeelar & Björklund 2011; Meirmans & Philip 2011; Whitlock 2011). Another extreme situation is presented by small populations with very low levels of gene flow, which is not the most appropriate situation for comparisons of Q_{ST} and F_{ST} (high neutral variance compared to putative selective variance, see Kremer & Le Corre 2012). Q_{ST} estimations are also subject to various sources of bias [reviewed by Whitlock (2008)]. For instance, Cano *et al.* (2004) demonstrated experimentally that Q_{ST} could be influenced by genotype \times environment interactions, suggesting that such an impact of phenotypic plasticity on Q_{ST} and F_{ST} estimator should be tested more often. Bearing these methodological problems in mind, we aim here to provide guidelines for the interpretation of the $Q_{ST} < F_{ST}$ pattern.

$Q_{ST} < F_{ST}$: publication bias and cryptic published evidence

A recent review (Leinonen *et al.* 2008) showed that 70% of Q_{ST} values exceed the associated F_{ST} values (see Fig. 2 for an updated comparison). The authors pointed out two potential biases in such a pattern: (i) a sampling bias, due to the deliberate selection, by researchers, of populations from contrasting environments or based on prior knowledge of phenotypic divergence and (ii) a publication bias

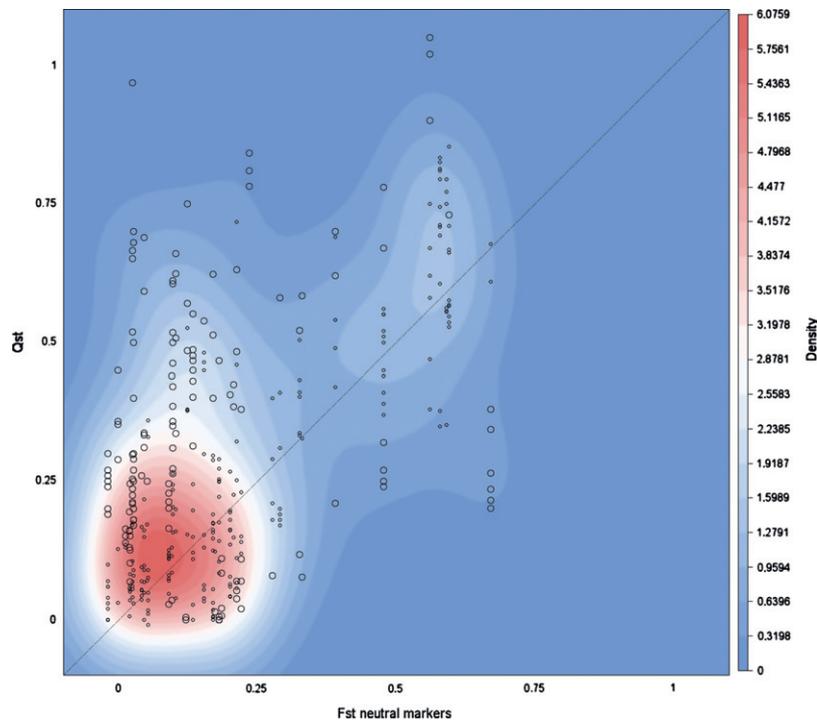


Fig. 2 Relationship between Q_{ST} and F_{ST} estimates from empirical published studies (based on and updated* from Leinonen *et al.* 2008 see Table S1 and Table S2). The thin dashed black line shows the 1:1 ratio. Circles represent Q_{ST} estimates of individual traits plotted against F_{ST} estimates for presumably neutral markers, small circles for no significant results, and large circles for significant results. It is worth noticing that statistical significance of Q_{ST} versus F_{ST} is diversified with different statistical power and robustness (P -value from the literature). For the sake of clarity, P_{ST} estimates were discarded because they do not control for the effect of the environment (Pujol *et al.* 2008; Brommer 2011); most were therefore located above the 1:1 line and close to zero on the F_{ST} axis. The contour plot highlights the nonuniform nature of the distribution of Q_{ST} and F_{ST} comparison results. *Updated references are Andersen *et al.* (2008); Badri *et al.* (2008a,b); Chenoweth & Blows (2008); Demont *et al.* (2008); Kinnison *et al.* (2008); Kohn *et al.* (2008); Olivieri *et al.* (2008); Vonlanthen *et al.* (2009); Yoshida *et al.* (2008); Chun *et al.* (2009a,b); Eroukhanoff *et al.* (2009); Liang *et al.* (2009); Meyer *et al.* (2009); Ramírez-Valiente *et al.* (2009); Yoshida *et al.* (2009); Antoniazza *et al.* (2010); Lind *et al.* (2010); Santure *et al.* (2010); Scheepens *et al.* (2010); Alberto *et al.* (2011); J. B. Lamy & S. Delzon, unpublished data.

favouring studies reporting an outcome $Q_{ST} > F_{ST}$ (Fig. 2), possibly due to the difficulties involved in interpreting a $Q_{ST} < F_{ST}$ pattern. These difficulties have epistemological and scientific foundations as selection is classically invoked to account for differences, rather than similarities, between populations and there is no widely accepted consensus concerning the most probable evolutionary interpretation of the ' $Q_{ST} < F_{ST}$ ' pattern.

Studies dealing with several traits tend to focus on traits with a $Q_{ST} > F_{ST}$ pattern, and interpretation of traits for which $Q_{ST} < F_{ST}$ tends to be discreet or entirely absent. Nevertheless, some studies have provided cryptic, but well-supported examples of the $Q_{ST} < F_{ST}$ pattern. Chapuis *et al.* (2008) showed (with a randomization procedure and a highly replicated design) that early traits of freshwater snails, such as morphological characters measured before maturity, have the same population means between 17 populations from permanent or temporary ponds (i.e. $Q_{ST} < F_{ST}$). Two studies also found that copepod subspecies (*Eurytemora affinis* and *Tigriopus californicus*) displayed morphological stasis (see Glossary) for secondary sexual

and life history traits (Lee & Frost 2002; Edmands & Harrison 2003). In plant sciences, Lamy *et al.* (2011) showed that cavitation resistance, a physiological trait related to survival in conditions of extreme drought, displayed no differentiation between populations originating from contrasting climates. Other studies (Navarro *et al.* 2005; Yoshida *et al.* 2008; Chun *et al.* 2009a,b; Santure *et al.* 2010) reported that Q_{ST} values were significantly lower than F_{ST} values, for various types of trait (floral morphology, vegetative morphology, growth, competitive ability). There is therefore enough evidence of trait conservatism in changing environments to now pay more attention on the evolutionary underpinnings of stasis.

Theoretical expectation of $Q_{ST} < F_{ST}$

From a theoretical standpoint, occurrences of $Q_{ST} < F_{ST}$ have been explored by simulations under different evolutionary scenarios, with various levels of uniform selection, divergent selection and gene flow (Le Corre & Kremer 2003; Miller *et al.* 2008). Under uniform selection,

regardless of the level of gene flow and the strength of within-population selection, Q_{ST} is always lower than F_{ST} . Indeed, under uniform selection, negative covariance between genes effects (which may be seen as linkage disequilibrium, a nonrandom association of genes) builds up, decreasing the between-population variance to levels lower than those predicted on the basis of gene flow alone (Kremer & Le Corre 2012). It is also worth noting that a $Q_{ST} < F_{ST}$ pattern may occur under diversifying selection (Le Corre & Kremer 2012). Under strong genetic drift (small effective population under limited gene flow), the between-population variance due to drift can become larger than the between-population variance generated by the differences in local optima [for more explanation about the underlying process, see Kremer & Le Corre (2012) and Le Corre & Kremer (2012)].

Other simulations and theoretical studies have tested departure from two implicit hypotheses (i.e. single traits and additive genetic determinism) underlying comparisons of Q_{ST} and F_{ST} : multitrait approach and nonadditive genetic determinism of the underlying genes. Phenotypic traits are often correlated, due to pleiotropy (see Glossary), and the response of a single trait to selection could be slowed down by these correlation constraints (Kruuk *et al.* 2008). Several statistical methods have been proposed to take the whole additive genetic variance-covariance matrix (G) for Q_{ST} and F_{ST} comparison into account (Kremer *et al.* 1997; Martin *et al.* 2008; Ovaskainen *et al.* 2011). However, detecting $Q_{ST} < F_{ST}$ comparison in a multivariate framework is more complex than previously thought. Using a modelling approach, Guillaume (2011) showed that the interplay between migration and genetic correlations among phenotypic traits can generate substantial phenotypic divergence in traits under uniform selection, and this could lead to false case of diversifying selection.

The effect of genetic architecture (nonadditive effects: dominance and epistasis, see Glossary) on Q_{ST} has also been investigated. It has been shown that dominance generally leads to the $Q_{ST} < F_{ST}$ outcome, in at least two evolutionary scenarios [the island model, see Goudet & Buchi (2006) and the pure drift model, see Goudet & Martin (2007)]. Moreover, epistasis generally decreases Q_{ST} relative to F_{ST} in the island model (Whitlock 1999) and in a pure drift model (Lopez-Fanjul *et al.* 2003). These analytical studies thus demonstrate that a nonadditive genetic architecture can lead to $Q_{ST} < F_{ST}$ without the need for uniform selection.

$Q_{ST} < F_{ST}$: underlying mechanisms

The biological mechanisms resulting in the $Q_{ST} < F_{ST}$ pattern are generally skimmed over in scientific publications. We review here two evolutionary processes that might potentially account for this pattern.

True uniform selection and other selection-based hypotheses

An inference of uniform selection requires a demonstration that stabilizing selection drives independently each

population to the same selective optimum (Fig. 1). Stabilizing selection is documented in empirical literature (Kingsolver *et al.* 2001), but the variance of the associated phenotypic optima is less documented due to the difficulty in assessing these optima for life history and morphological traits. The demonstration of independent stabilizing selection (with the same selective optimum among populations) would require specific experimental designs, such as local measurements of selection on each population from contrasting environments, as described by Lande & Arnold (1983). These experiments would be very time-consuming and expensive, and the study of this type has therefore seldom been carried out. It must also be borne in mind that the explanation of stasis by uniform selection requires not only common stabilizing selection, but also the variation in selective optima within only a narrow range (Hansen & Houle 2004). Other selection-based hypotheses could be invoked to explain $Q_{ST} < F_{ST}$: for instance, DeWoody *et al.* (2010) showed by simulation that frequency-dependent selection applied in a multitrait framework maintains a high variance within populations. Extrapolating this mechanism to subdivided populations, this selection process will inflate variance within population relative to variance among populations, which might result in a $Q_{ST} < F_{ST}$ pattern. Sexually selected traits or traits involved in biotic relationship are prone to be targeted by frequency-dependent selection.

Simulation studies show that selection-based hypotheses are likely, but maybe not for all traits. For instance, cavitation resistance, which is a core fitness-related trait allowing plants to survive under extreme drought conditions (Maherali *et al.* 2004; Brodribb & Cochard 2009; Brodribb *et al.* 2010), is expected to diverge between populations from the most contrasted part of the species distribution range. Yet, despite high contrasted water-stress conditions (different selective optima), no difference between populations was reported for two angiosperm and conifer species with a broad distribution in Europe (Lamy *et al.* 2011; Wortemann *et al.* 2011) and Q_{ST} was significantly lower than F_{ST} (Lamy *et al.* 2011). For this drought-resistance trait, it is therefore less than likely that selection-based hypotheses would explain this pattern.

Canalization. Canalization (also called robustness, see Glossary) refers to any inheritable structure or process, adaptive or otherwise, reducing the sensitivity of a phenotype to changes or disturbances to the underlying genetic (mutation and recombination) and/or nongenetic (environmental variation) factors determining its expression [see Flatt (2005) for a complete review]. In the original meaning, a trait becomes canalized because the insensitivity to perturbations was considered to increase fitness (Waddington 1942, 1953; Wagner *et al.* 1997; Debat & David 2001). Nowadays, canalization concept is widely used in developmental sciences (Felix & Wagner 2008) and in the expanding evo-devo field (Carroll 2008). Such a concept should be taken into consideration in evolutionary ecology because, from a functional point of view, phenotype should be seen as a core of functions [*Bauplan*, see Gould & Lewontin

(1979) and Williams (1992)] inherited from the deep evolutionary history, and functions with more genetic variation allows for short-term adaptation.

Is it possible to infer canalization in the wild?

Canalization is a relative term that can be defined only in a comparative framework. It was first demonstrated in *Drosophila*, through comparisons of wild-type and modified inbred lines [based on artificial mutagenesis or abiotic stress, Waddington (1942) and Stearns (1994)]. However, Felix & Wagner (2008) proposed a comparative approach for the inference of canalization, by making use of the genetic variation naturally accumulating during evolution, and comparing the genetic variation between individuals or populations of the same species. These authors argued that the application of this approach 'in the wild' might be more powerful, as it would allow the comparison of genotypes that had accumulated genetic change over long periods of evolution, whereas laboratory experiments are much more short-term. Here, we propose the use of Q_{ST} and F_{ST} for such comparisons. As Q_{ST} is a standardized measure of genetic variation between populations (even between closely related species), then a $Q_{ST} < F_{ST}$ signature could be interpreted as the presence of a genetically canalized trait.

Some traits are known from the literature to be invariant, that is, canalized traits, for example, the body temperature of mammalian, segmentation of blastoderm and wing shape (intersection veins position and the derived multivariate estimators) in *Drosophila* (Hansen & Houle 2004; Gilchrist & Partridge 2001; Manu *et al.* 2009; Williams 1992). Wing shape trait in *Drosophila* has been studied in developmental science and evolutionary quantitative genetics. For instance, Andersen *et al.* (2008) showed that populations from highland or lowland environments (contrasted atmospheric conditions) generally presented a low Q_{ST} (low genetic variance between populations), which is always lower than the F_{ST} . At this stage, it is difficult to define a threshold between uniform selection and canalization. But comparing the wing shape between species from the same genus (same *Bauplan* = same genetic architecture) but living in different ecological niches and having different geographical distributions (different selective optima) could give more clues about the underlying processes. Among 21 species of *Drosophila* with diverse ecological specialization (Table 1), Hansen & Houle (2004) noticed that wing shape trait in *Drosophila* species is a conserved trait ($CV_P = 8.1\%$, $n = 21$, see also Galpern 2000). Trait conservatism is classically explained by uniform selection, meaning that, for a given species, stabilizing selections must occur in all populations with nearly the same selective optima. However if a single global optimum does exist over contrasted conditions for *Drosophila*, why then would thousands of similarly-sized hymenopterans have such different wings? Surprisingly, little work has been devoted to this problem. The same reasoning could be applied to cavitation resistance in pine species. In *Pinus pinaster*, a significant $Q_{ST} < F_{ST}$ pattern was reported for this trait among

Table 1 Comparison of a well-known (wing traits in *Drosophila*) and a putative (cavitation resistance in *Pinus*) canalized trait

Species	<i>Drosophila buzzatii</i>	<i>Pinus pinaster</i>
Trait	Wing traits	Cavitation resistance
Interspecific level	In the <i>Drosophila</i> genus*	In the <i>Pinus</i> genus [†]
CV_P	8.1	13.0
Intraspecific level	Natural populations and hybrids (3 generations) [‡]	Natural populations [§]
Q_{ST}	0.06	0.02
F_{ST}	0.25	0.11

CV_P (%) is the coefficient of phenotypic variation for a given genus (*Drosophila* genus $n = 21$ and *Pinus* genus $n = 17$). Q_{ST} is the additive quantitative genetic variation between populations (phenotyped individuals: *Drosophila buzzatii* $n = 593$ and *Pinus pinaster* $n = 240$). F_{ST} is the neutral genetic difference between populations (number of loci: for *Drosophila buzzatii* $n = 10$ and for *Pinus pinaster* $n = 8$).

*Galpern (2000).

[†]Delzon *et al.* (2010).

[‡]Andersen *et al.* (2008).

[§]Lamy *et al.* (2011).

populations from extreme climatic origin (Lamy *et al.* 2011), while a high degree of conservation within the *pinus* lineage (36 species) showed that cavitation resistance strongly reflects phylogenetic history (strong evolutionary conservatism; S. Delzon, unpublished data). These examples might provide some clues that $Q_{ST} < F_{ST}$ could be also interpreted as canalization (genetic constraints) rather than only selection-based hypothesis.

However, selection-based and canalization hypotheses are not exclusives as demonstrated by some modelling studies in phylogenetic and evolutionary quantitative genetic fields. Over the very long term, assuming additive genetic model, canalization results from a phenomenon of stabilizing selection centred on the same selective optimum on average (Waddington 1942; Stearns & Kawecki 1995; Falconer & Mackay 1996; Bergman & Siegal, 2003; de Visser *et al.* 2003; Lande 2009). This scenario of apparition of canalization has been addressed and questioned by recent studies (Wagner *et al.* 1997; Zhang 2006): for instance, under fluctuating selection, Kawecki (2000) showed that modifier genes reducing phenotypic variance will be favoured leading to canalization. Adopting a new quantitative genetic formalism to described genetic architecture (Hansen & Wagner 2001b), Hansen and co-workers found the counterintuitive conclusion that the selection regime might be less important than the sign of functional epistasis (see Glossary) in determining the evolvability [for novel perspectives, see Hermisson *et al.* (2003); Carter *et al.* (2005); Hansen (2006)]. For instance, they showed that directional rather than stabilizing selection could lead to canalization if the underlying genes of a trait exhibit

negative directional epistasis (Carter *et al.* 2005). A task of future research is to further disentangle the complex relationship between these two phenomena.

Some guidelines to interpret $Q_{ST} < F_{ST}$

For nonmodel species, the use of classical methods (*i.e.* artificial mutagenesis or abiotic stress) for inferring canalization remains impracticable. This obstacle could be partially overcome by utilizing a bottom-up approach that combines information from Q_{ST}/F_{ST} comparisons and phylogenetic information (see Fig. 3). For a given trait, if Q_{ST} is lower than F_{ST} and closely related species living in different environmental conditions showed a trait conservatism, then canalization could be an alternative to the classical uniform selection hypothesis. Canalization could explain the constancy of a trait within species (low or lack of genetic variance between populations) and across species (evolutionary stasis). In other words, it means that species genetic backgrounds share the same genetic constraints (same *Bauplan*) rather than the same selective optima. This inference may be crucial for the identification of dimensions in which phenotype variation is constrained, impeding the

use of classical models for the prediction of past or future phenotypic evolution.

Future directions

Several future directions could be suggested: (i) Traits of known function and for which selective optima could be inferred a priori should be explored more extensively for their interpopulation differentiation. The comparison between the a priori selective optima and the inferred ones could give some clues about the underlying process (uniform selection or canalization). (ii) Recent genomic studies revealed that epistasis and pleiotropy seem to be the rule rather than exception (Hill *et al.* 2008; Weedon & Frayling 2008; Visscher 2008; Cheverud *et al.* 2004; Wagner *et al.* 2008; Wagner & Zhang 2011). However, Q_{ST} and F_{ST} comparisons are usually made in the traditional quantitative genetic context ignoring epistasis and pleiotropy. Therefore, more theoretical work is needed to quantify the impact of complex genetic architecture (for instance using Hansen's formalism) on the inference made from Q_{ST} and F_{ST} comparison. (iii) Multitrait approaches should be implemented more often to explore the effects of multivariate genetic

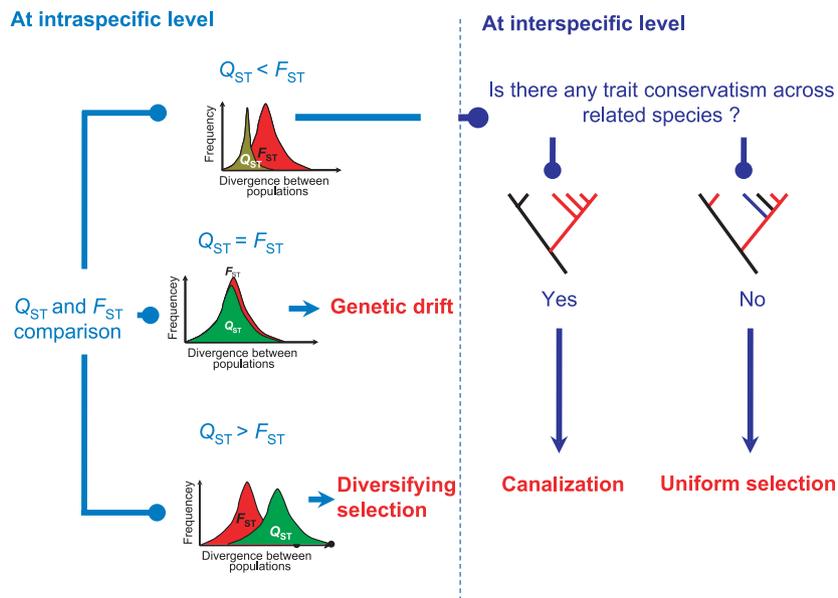


Fig. 3 Decision tree for the comparison of Q_{ST} and F_{ST} . This decision tree combines two levels of information for a given trait: (i) information relating to populations, based on comparisons of Q_{ST} and F_{ST} (light blue, left panel); (ii) the degree of evolutionary conservatism between closely related species living in different ecological conditions based on phylogenetic analyses. As indicated by the arrows and the red text, $Q_{ST} = F_{ST}$ and $Q_{ST} > F_{ST}$ are straightforwardly interpreted as genetic drift and diversifying selection, respectively. In the case of $Q_{ST} < F_{ST}$, more information is required for a robust inference indicated by the final circle and the blue text. Closely related species inhabiting different ecological niches (or any proxy which allows to assess a priori selective optima) and sharing the same value of trait (trait conservatism) provides clues about a potential canalization phenomenon (*i.e.* the genetic architecture narrows trait variability). It is worth noticing that trait conservatism concept excludes cases where trait evolution followed a Brownian model (an approximation of interspecific genetic drift motion). $Q_{ST} < F_{ST}$ associated with substantial variability between species for the studied trait could be interpreted as true uniform selection. Q_{ST} (in green) and F_{ST} (in red) are represented as distributions because these estimators are subjected to two types of errors (evolutionary and sampling errors).

constraints on phenotype evolution *in natura* (Martin *et al.* 2008; Ovaskainen *et al.* 2011).

Acknowledgements

We thank Stefan Andersson, Pascal Vonlanthen, Louis Bernatchez and Emmanuelle Porcher for kindly sharing published data. We thank Rémy J. Petit, Vincent Debat, Ivan Scotti and Maximilien Larter for helpful comments on the manuscript about quantitative genetics, canalization concepts and English syntax. This study has been carried out with financial support from the European commission under FP7 (FP7-211868 Novel-tree).

Glossary

Canalization

A trait is canalized if the underlying genetic architecture buffers its variation against all kinds of disturbance, being of genetic (mutation, hybridization, recombination) and/or environmental nature (Hansen & Houle 2004).

Directional epistasis

Functional epistasis (see definition of Epistasis) is said to be directional if genes systematically modify each other (genes effects) in particular patterns or directions in the phenotypic space. (i) Positive epistasis, where genes tend to reinforce each other's effects along the direction of selection, will accelerate the response, (ii) while negative epistasis, where genes tend to diminish each other's effects in the direction of selection, will reduce the response (Hansen & Wagner 2001a,b). Obviously, functional epistasis sign can lead to dramatic qualitative changes in evolutionary dynamics.

Epistasis

A phenomenon by which the effects of one gene are modified by one or several other genes. Despite this simple definition, there are several ways to conceptualize and quantify epistasis. A distinction should be made between statistical (Falconer & Mackay 1996; Lynch & Walsh 1998) and functional (or physiological) epistasis (Cheverud & Routman 1995; Hansen & Wagner 2001b). (i) Statistical epistasis refers to the standard quantitative genetic definition of epistasis as the third interaction terms in a regression of trait value on the presence of alleles. It is a population property and is a function of both allele frequencies and the biological interactions among genes. (ii) Functional epistasis refers to nonadditive interactions among loci in the mapping from specific genotypes to phenotype and is not a population property [see Hansen (2006) p126]. In other words, functional epistasis means that gene or genotype effects depend on the genetic background, suggesting that these effects might change due to selection, drift, mutation or any other

mechanisms. Both statistical and functional epistasis definitions are partially overlapping, but not univocal. Functional epistasis can contribute to additive and dominance genetic variance component, whereas statistical epistasis is associated only with the third interaction genetic component. In the present article, the use of epistasis alone means functional epistasis (epistatic effect of allele, gene or genotype).

Genetic architecture

The number of genes underlying the trait, their redundancy (gene duplication and alternate pathways) and/or the resulting network due to interallelic interaction (additive effect and dominance) and interloci interaction (epistasis).

Pleiotropy

Pleiotropy is due to two mechanisms: pleiotropic gene (gene affects more than one character) and linkage disequilibrium (the statistical associations between alleles at different loci). Pleiotropy is the underlying cause of genetic covariation between characters at the population level (Flatt 2005; Hansen 2006).

Stasis

Taxa, such as genera, species or populations, displayed the same value of trait despite significant genetic isolation and environmental distance between taxa. In evolutionary ecology field, stasis is, most of the time, assessed by a syn-chronic study through a comparative analysis.

Stabilizing selection

Selection-based process on the fitness value of an individual as it has been defined by Turelli (1984). In this model, the fitness is the function of selection intensity (ω^2), selection optimum (Z_{opt}) and trait value (Z). An individual has the higher fitness when its value of phenotypic trait equals to Z_{opt} , which does not imply it is the most abundant phenotype (Z).

References

- Alberto F, Bouffier L, Louvet J-M, Delzon S, Lamy J-B, Kremer A (2011) Adaptive responses for seed and leaf phenology in natural populations of sessile oak along an altitudinal gradient. *Journal of Evolutionary Biology*, **24**, 1442–1454.
- Andersen HD, Pertoldi C, Loeschcke V, Cavicchi S, Scali V (2008) Divergence at neutral and non-neutral loci in *Drosophila buzzatii* populations and their hybrids. *Evolutionary Ecology*, **22**, 593–605.
- Antoniazza S, Burri R, Fumagalli L, Goudet J, Roulin A (2010) Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution*, **64**, 1944–1954.

- Badri M, Zitoun A, Houcine I, Huguet T, Aouani ME (2008a) Morphological and microsatellite diversity associated with ecological factors in natural populations of *Medicago laciniata* Mill. (Fabaceae). *Indian Academy of Sciences*, **87**, 241–255.
- Badri M, Zitoun A, Soula S, Houcine I, Huguet T, Aouani ME (2008b) Low levels of quantitative and molecular genetic differentiation among natural populations of *Medicago ciliaris* Kroch. (Fabaceae) of different Tunisian eco-geographical origin. *Conservation Genetics*, **9**, 1509–1520.
- Bergman A, Siegal ML (2003) Evolutionary capacitance as a general feature of complex gene networks. *Nature*, **424**, 549–552.
- Bradshaw AD (1991) The Croonian lecture, 1991: genostasis and the limits to evolution. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **333**, 289–305.
- Brent Burt D (2001) Evolutionary stasis, constraint and other terminology describing evolutionary patterns. *Biological Journal of the Linnean Society*, **72**, 509–517.
- Brodribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*, **149**, 575–584.
- Brodribb TJ, Bowman DJMS, Nichols S, Delzon S, Burrell R (2010) Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist*, **188**, 533–542.
- Brommer JE (2011) Whither PST? The approximation of QST by PST in evolutionary and conservation biology. *Journal of Evolutionary Biology*, **24**, 1160–1168.
- Cano JM, Laurila A, Palo J, Merilä J (2004) Population differentiation in G matrix structure due to natural selection in *Rana temporaria*. *Evolution*, **58**, 2013–2020.
- Carroll SB (2008) Evo-devo and an expanding evolutionary synthesis: a genetic theory of morphological evolution. *Cell*, **134**, 25–36.
- Carter AJR, Hermisson J, Hansen TF (2005) The role of epistatic gene interactions in the response to selection and the evolution of evolvability. *Theoretical Population Biology*, **68**, 179–196.
- Chapuis E, Martin G, Goudet J (2008) Effects of selection and drift on G matrix evolution in a heterogeneous environment: a multivariate Q_{ST} - F_{ST} test with the freshwater snail *Galba truncatula*. *Genetics*, **180**, 2151–2161.
- Chenoweth SF, Blows MW (2008) Q_{ST} meets the G matrix: the dimensionality of adaptive divergence in multiple correlated quantitative traits. *Evolution*, **62**, 1437–1449.
- Cheverud JM, Routman EJ (1995) Epistasis and its contribution to genetic variance-components. *Genetics*, **139**, 1455–1461.
- Cheverud JM, Ehrich TH, Vaughn TYT, Koreishi SF, Linsey RB, Pletscher LS (2004) Pleiotropic effects on mandibular morphology II: differential epistasis and genetic variation in morphological integration. *Journal of Experimental Zoology Part B-Molecular and Developmental Evolution*, **302B**, 424–435.
- Chun YJ, Le Corre V, Bretagnolle F (2009a) Adaptive divergence for a fitness-related trait among invasive *Ambrosia artemisiifolia* populations in France. *Molecular Ecology*, **20**, 1378–1388.
- Chun YJ, Nason JD, Moloney KA (2009b) Comparison of quantitative and molecular genetic variation of native vs. invasive populations of purple loosestrife (*Lythrum salicaria* L., Lythraceae). *Molecular Ecology*, **18**, 3020–3035.
- Debat V, David P (2001) Mapping phenotypes: canalization, plasticity and developmental stability. *Trends in Ecology & Evolution*, **16**, 555–561.
- Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment*, **33**, 2101–2111.
- Demont M, Blanckenhorn WU, Hosken DJ, Garner TWJ (2008) Molecular and quantitative genetic differentiation across Europe in yellow dung flies. *Journal of Evolutionary Biology*, **21**, 1492–1503.
- DeWoody AJ, Bickham WJ, Nichols MK, Rhodes OEJ, Woeste EW (2010) *Molecular Approaches in Natural Resource Conservation and Management* (ed. Press CU), p. 374. Cambridge University Press, Cambridge.
- Edeelar P, Björklund M (2011) If F_{ST} does not measure neutral genetic differentiation, then comparing it with Q_{ST} is misleading. Or is it? *Molecular Ecology*, **20**, 1805–1812.
- Edmands S, Harrison JS (2003) Molecular and quantitative trait variation within and among populations of the intertidal copepod *Tigriopus californicus*. *Evolution*, **57**, 2277–2285.
- Eroukhanoff F, Hargeby A, Svensson EI (2009) Rapid adaptive divergence between ecotypes of an aquatic isopod inferred from F_{ST} - Q_{ST} analysis. *Molecular Ecology*, **18**, 4912–4923.
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Introduction to quantitative genetics., xv + 464 pp.
- Felix MA, Wagner A (2008) Robustness and evolution: concepts, insights and challenges from a developmental model system. *Heredity*, **100**, 132–140.
- Flatt T (2005) The evolutionary genetics of canalization. *Quarterly Review of Biology*, **80**, 287–316.
- Galpern P (2000) The use of common principal component analysis in studies of phenotypic evolution: An example from the Drosophilidae, PhD Thesis, University of Toronto, Canada.
- Gilchrist AS, Partridge L (2001) The contrasting genetic architecture of wing size and shape in *Drosophila melanogaster*. *Heredity*, **86**, 144–152.
- Goudet J, Buchi L (2006) The effects of dominance, regular inbreeding and sampling design on Q_{ST} , an estimator of population differentiation for quantitative traits. *Genetics*, **172**, 1337–1347.
- Goudet J, Martin G (2007) Under neutrality, $Q_{ST} \leq F_{ST}$ when there is dominance in an island model. *Genetics*, **176**, 1371–1374.
- Gould SJ, Lewontin R (1979) Spandrels of San-Marco and the Panglossian paradigm – A critique of the adaptationist program. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **205**, 581–598.
- Guillaume F (2011) Migration-induced phenotypic divergence: the migration-selection balance of correlated traits. *Evolution*, **65**, 1723–1738.
- Hansen TF (2006) The evolution of genetic architecture. *Annual Review of Ecology Evolution and Systematics*, **37**, 123–157.
- Hansen TF, Houle D (2004) Evolvability, stabilizing selection, and the problem of stasis. In: *Evolutionary Biology of Complex Phenotypes* (eds Pigliucci M, Preston K), pp. 130–150. Oxford University Press, Oxford.
- Hansen TF, Wagner GP (2001a) Epistasis and the mutation load: a measurement-theoretical approach. *Genetics*, **158**, 477–485.
- Hansen TF, Wagner GP (2001b) Modeling genetic architecture: a multilinear theory of gene interaction. *Theoretical Population Biology*, **59**, 61–86.
- Hermisson J, Hansen TF, Wagner GP (2003) Epistasis in polygenic traits and the evolution of genetic architecture under stabilizing selection. *American Naturalist*, **161**, 708–734.
- Hill WG, Goddard ME, Visscher PM (2008) Data and theory point to mainly additive genetic variance for complex traits. *PLoS Genetics*, **4**, e1000008.
- Kawecki TJ (2000) The evolution of genetic canalization under fluctuating selection. *Evolution*, **54**, 1–12.
- Kingsolver JG, Hoekstra HE, Hoekstra JM *et al.* (2001) The strength of phenotypic selection in natural populations. *The American Naturalist*, **157**, 245–261.

- Kinnison MT, Unwin MJ, Quinn TP (2008) Eco-evolutionary vs. habitat contributions to invasion in salmon: experimental evaluation in the wild. *Molecular Ecology*, **17**, 405–414.
- Kohn HJ, Shapiro J, Wu C-I (2008) Decoupled differentiation of gene expression and coding sequence among *Drosophila* populations. *Genes, Genetics and Systematics*, **83**, 265–273.
- Kremer A, Le Corre V (2012) Decoupling of differentiation between traits and their underlying genes in response to divergent selection. *Heredity*, **108**, 375–385.
- Kremer A, Zanetto A, Ducouso A (1997) Multilocus and multitrait measures of differentiation for gene markers and phenotypic traits. *Genetics*, **145**, 1229–1241.
- Kronholm I, Loudet O, de Meaux J (2010) Influence of mutation rate on estimators of genetic differentiation - lessons from *Arabidopsis thaliana*. *BMC Genetics*, **11**, 18.
- Kruuk LEB, Slate J, Wilson AJ (2008) New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annual Review of Ecology Evolution and Systematics*, **39**, 525–548.
- Lamy J-B, Bouffier L, Burrett 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**, e23476.
- Lande R (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, **22**, 1435–1446.
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.
- Le Corre V, Kremer A (2003) Genetic variability at neutral markers, quantitative trait loci and trait in a subdivided population under selection. *Genetics*, **164**, 1205–1219.
- Le Corre V, Kremer A (2012) The genetic differentiation at quantitative trait loci under local adaptation. *Molecular Ecology*, **21**, 1548–1566.
- Lee CE, Frost BW (2002) Morphological stasis in the *Eurytemora affinis* species complex (Copepoda: Temoridae). *Hydrobiologia*, **480**, 111–128.
- Leinonen T, O'Hara RB, Cano JM, Merilä J (2008) Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology*, **21**, 1–17.
- Liang ZC, Huang P, Yang J, Rao GY (2009) Population divergence in the amphicarpic species *Amphicarpa edgeworthii* Benth. (Fabaceae): microsatellite markers and leaf morphology. *Biological Journal of the Linnean Society*, **96**, 505–516.
- Lind ML, Ingvarsson PK, Johansson H, Hall D, Johansson F (2010) Gene flow and selection on phenotypic plasticity in an island system of *Rana temporaria*. *Evolution*, **65**, 684–697.
- Lopez-Fanjul C, Fernandez A, Toro MA (2003) The effect of neutral nonadditive gene action on the quantitative index of population divergence. *Genetics*, **164**, 1627–1633.
- Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. In: *Genetics and analysis of quantitative traits.*, p. xvi + 980 pp. Sinauer Associates, Inc.
- Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.
- Manu, Surkova S, Spirov AV *et al.* (2009) Canalization of gene expression in the *Drosophila* blastoderm by gap gene cross regulation. *PLoS Biology*, **7**, 0591–0603.
- Martin G, Chapuis E, Goudet J (2008) Multivariate Q_{ST} - F_{ST} comparisons: a neutrality test for the evolution of the G matrix in structured populations. *Genetics*, **180**, 2135–2149.
- McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, **17**, 285–291.
- Meirmans PG, Philip WH (2011) Assessing population structure: F_{ST} and related measures. *Molecular Ecology*, **11**, 5–18.
- Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, **14**, 892–903.
- Meyer C-L, Kostecka A, Saumitou-Laprade P *et al.* (2009) Variability of zinc tolerance among and within populations of the pseudometallophyte *Arabidopsis halleri* and possible role of directional selection. *New Phytologist*, **185**, 130–142.
- Miller JR, Wood BP, Hamilton MB (2008) F_{ST} and Q_{ST} under Neutrality. *Genetics*, **180**, 1023–1037.
- Navarro C, Cavers S, Pappinen A *et al.* (2005) Contrasting quantitative traits and neutral genetic markers for genetic resource assessment of Mesoamerican *Cedrela odorata*. *Silvae Genetica*, **54**, 281–292.
- O'Hara RB, Merilä J (2005) Bias and precision in Q_{ST} estimates: problems and some solutions. *Genetics*, **171**, 1331–1339.
- Olivieri I, Singer CM, Magalhães S *et al.* (2008) Genetic, ecological, behavioral and geographic differentiation of populations in a thistle weevil: implications for speciation and biocontrol. *Evolutionary Applications*, **1**, 112–128.
- Ovaskainen O, Karhunen M, Zheng C, Cano Arias JM, Merilä J (2011) A new method to uncover signatures of divergent and stabilizing selection in quantitative traits. *Genetics*, **189**, 621–U729.
- Pujol B, Wilson AJ, Ross RIC, Pannell JR (2008) Are Q_{ST} - F_{ST} comparisons for natural populations meaningful? *Molecular Ecology*, **17**, 4782–4785.
- Ramírez-Valiente JA, Lorenzo Z, Soto A, Valladares F, Gil L, Aranda I (2009) Elucidating the role of genetic drift and natural selection in cork oak differentiation regarding drought tolerance. *Molecular Ecology*, **18**, 3803–3815.
- Santure AW, Ewen JG, Sicard D, Roff DA, Moller AP (2010) Population structure in the barn swallow, *Hirundo rustica*: a comparison between neutral DNA markers and quantitative traits. *Biological Journal of the Linnean Society*, **99**, 306–314.
- Scheepens JF, Stocklin J, Pluess AR (2010) Unifying selection acts on competitive ability and relative growth rate in *Scabiosa columbaria*. *Basic and Applied Ecology*, **11**, 612–618.
- Spitze K (1993) Population structure in *Daphnia obtusa*: quantitative genetic and allozymic variation. *Genetics*, **135**, 367–374.
- Stearns S (1994) The evolutionary links between fixed and variable traits. *Acta Palaentologica Polonica*, **38**, 215–232.
- Stearns SC, Kawecki TJ (1995) Fitness sensitivity and the canalization of life-history traits. *Evolution*, **48**, 1438–1450.
- Turelli M (1984) Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical and Population Biology*, **25**, 138–193.
- Visscher PM (2008) Sizing up human height variation. *Nature genetics*, **40**, 489–490.
- de Visser JAGM, Hermisson J, Wagner GP *et al.* (2003) Perspective: evolution and detection of genetic robustness. *Evolution*, **57**, 1959–1972.
- Vonlanthen P, Roy D, Hudson AG, Largiadèr CR, Bittner D, Seehausen O (2009) Divergence along a steep ecological gradient in lake whitefish (*Coregonus sp.*). *Journal of Evolutionary Biology*, **22**, 498–514.
- Waddington CH (1942) Canalization of development and the inheritance of acquired characters. *Nature*, **150**, 563–565.
- Waddington CH (1953) Epigenetics and evolution. *Journal of Experimental Zoology*, **7**, 187–199.
- Wagner GP, Zhang JZ (2011) The pleiotropic structure of the genotype-phenotype map: the evolvability of complex organisms. *Nature Reviews Genetics*, **12**, 204–213.

- Wagner GP, Booth G, Bagheri HC (1997) A population genetic theory of canalization. *Evolution*, **51**, 329–347.
- Wagner GP, Kenney-Hunt JP, Pavlicev M, Peck JR, Waxman D, Cheverud JM (2008) Pleiotropic scaling of gene effects and the “cost of complexity”. *Nature*, **452**, 470–479.
- Weedon MN, Frayling TM (2008) Reaching new heights: insights into the genetics of human stature. *Trends in genetics*, **24**, 595–603.
- Whitlock MC (1999) Neutral additive genetic variance in a meta-population. *Genetical Research*, **74**, 215–221.
- Whitlock MC (2008) Evolutionary inference from Q_{ST} . *Molecular Ecology*, **17**, 1885–1896.
- Whitlock MC (2011) G_{ST} and D do not replace F_{ST} . *Molecular Ecology*, **20**, 1083–1091.
- Whitlock MC, Guillaume F (2009) Testing for spatially divergent selection: comparing Q_{ST} to F_{ST} . *Genetics*, **183**, 1055–1063.
- Williams GC (1992) *Natural Selection: Domains, Levels and Challenges*. Oxford University Press, USA.
- Wortemann R, Herbette S, Barigah TS *et al.* (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree physiology*, **31**, 1175–1182.
- Yoshida Y, Honjo M, Kitamoto N, Ohsawa R (2008) Genetic variation and differentiation of floral morphology in wild *Primula sieboldii* evaluated by image analysis data and SSR markers. *Breeding Science*, **58**, 301–307.
- Yoshida Y, Honjo M, Kitamoto N, Ohsawa R (2009) Reconsideration for conservation units of wild *Primula sieboldii* in Japan based on adaptive diversity and molecular genetic diversity. *Genetics Research*, **91**, 225–235.
- Zhang X-S (2006) The phenotypic variance within plastic traits under migration-mutation-selection balance. *Evolution*, **60**, 1125–1136.

J.-B.L.’s interests are centered on the processes that drive or limit adaptation, population differentiation, in order to quantify adaptive capacities of tree species.

C.P.’s interests are centered on combining different approaches (genomics, quantitative and population genetics, ecology) for understanding the interplay between genetic adaptation, plasticity and their interaction in the response of forest trees to past, present and future edapho-climatic conditions.

A.K.’s interests are centered on the evolution of genetic diversity and differentiation between natural populations, at various hierarchical levels where diversity is expressed (from genes to phenotypic traits). The main emphasis of my research activities is the understanding of evolutionary forces that contribute to the distribution of diversity and differentiation.

S.D.’s interests are centered on the processes that drive the evolution of ecophysiological traits and the adaptation of populations, with a particular interest in drought resistance, tree hydraulic and leaf phenology.

doi: 10.1111/mec.12017

Data accessibility

All the data used in this study have been provided as supplementary material.

Supporting information

Additional Supporting Information may be found in the online version of this article.

Table S1 Synopsis of comparative studies of marker and quantitative genetic population structure (based on and updated from Leinonen *et al.* (2008).

Table S2 The full length dataset.