

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}

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Abstract The impact of directional selection on specific trait types in plant species, and how a species' life history mediates this response to selection remains understudied. Discovering such interactions is however crucial for understanding the interplay between ecological and genetic processes underlying local adaptation in plants, and to evaluate a species' evolutionary potential with respect to changing environments. Furthermore, it remains unclear whether the degree of adaptive differentiation generally increases with the geographical distance between plant populations. Here, we present a weighted mixed model based meta-analysis aimed at unraveling the potential interactions between plant trait types, life history characteristics and Q_{ST} – F_{ST} comparisons, and assessing the effect of geographical scale on population differentiation. Based on 51 studies we found that Q_{ST} values exceeded their corresponding F_{ST} values in 71.74 % out of 401 cases. Furthermore, different trait types were found to be differently susceptible to natural selection and the magnitude of Q_{ST} – F_{ST} comparisons was mediated by a plant species' life span. These findings may be closely related to the genetic architectures of trait types and life histories, with the proportion of large-effect genes likely shaping the response to natural selection. Q_{ST} – F_{ST} values also increased with increasing distance between populations, pinpointing the combined effects of environmental differentiation and isolation by distance on the magnitude of population divergence. Finally, our model showed an inverse relationship between F_{ST} and Q_{ST} – F_{ST} values, presumably resulting from isolation by distance, the exchange of advantageous alleles, or genetic correlations among traits.

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Introduction

Elucidating the impact of local adaptation on population differentiation has always been a key issue in evolutionary biology and has even gained importance in light of adaptation to global change (O'Brien et al. 2007; Aitken et al. 2008; Hoffmann and Sgrò 2011; Colautti et al. 2012), certainly in sessile species such as plants which are considered to be more susceptible to spatially divergent selection (Ehrlich and Raven 1969; Levin 1979). One way to infer the impact of divergent selection on plant population differentiation is through the comparison of quantitative genetic differentiation (Q_{ST} ; Spitze 1993) versus neutral marker differentiation (F_{ST} ; Wright 1951). Q_{ST} – F_{ST} comparisons measure the relative contribution of Q_{ST} , which reflects population differentiation through both neutral processes and natural selection caused by environmental differences, and F_{ST} , which only measures neutral forces including genetic drift and gene flow. Although not free from criticism (e.g., Goudet and Martin 2007; Whitlock 2008; Edelaar et al. 2011), as we discuss below, Q_{ST} – F_{ST} comparison based studies have already yielded valuable insights into plant trait responses to spatial and temporal environmental heterogeneity (McKay and Latta 2002; Volis et al. 2005; Leinonen et al. 2008), and their number is steadily growing (Leinonen et al. 2008; Fig. 1). The outcome of Q_{ST} – F_{ST} is commonly interpreted as follows (Merilä and Crnokrak 2001; Leinonen et al. 2008). First, if Q_{ST} – $F_{ST} > 0$, the observed phenotypic differentiation is higher than expected by genetic drift alone. Consequently, the fraction not explained by genetic drift could be assigned to divergent selection, and the difference between Q_{ST} and F_{ST} reflects adaptive differentiation among populations. Second, if $Q_{ST} \approx F_{ST}$, genetic drift alone can be sufficient to explain patterns of differentiation, although the relative contribution of selection and drift are indistinguishable. Finally, if Q_{ST} – $F_{ST} < 0$, spatially uniform selection is assumed to favor the same phenotype in different environments. Q_{ST} – F_{ST} comparisons are widely employed to reveal general trends in intraspecific adaptive differentiation and still gain in popularity (Fig. 1). There is, however, little consistency in the literature whether some plant trait types are more susceptible to selection than other trait types, and whether their response to selection is mediated by the life history of the plant species (Leinonen et al. 2008; Lopez et al. 2008; Smith and Beaulieu 2009; Kingsolver and Diamond 2011; Kremer et al. 2012).

The response to selection of phenotypic traits results from fitness effects of genotype-by-environment interactions (Kawecki and Ebert 2004). The outcome of this process is in turn affected by the genetic architecture of the traits involved (Merilä and Sheldon 1999). A phenotypic trait that is regulated by numerous small-effect genes and involved in (pleiotropic) gene interactions, is expected to respond slowly to natural selection (Orr 2000; Wagner and Zhang 2011; Pavlicev and Wagner 2012). Because fitness traits, i.e. traits that are directly related to fitness such as growth, reproductive output and survival, are thought to have a more complex genetic architecture than non-fitness traits (Price and Schluter 1991; Merilä and Sheldon 1999; Chun et al. 2011), their response to selection is expected to be weaker. Traits that are only remotely related to fitness, on the contrary, are expected to show higher levels of divergence, associated with a less complex genetic background. Although Leinonen et al. (2008) did not find a significant difference in Q_{ST} – F_{ST} values between fitness and non-fitness traits in their review, meta-analyses of selection

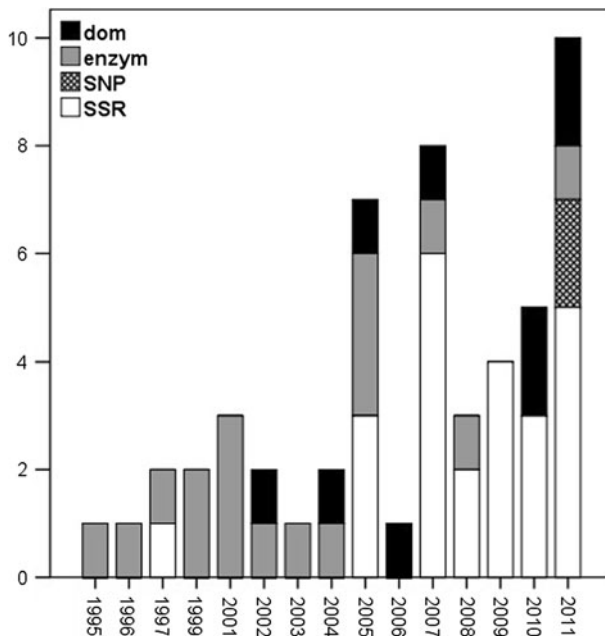


Fig. 1 Number of Q_{ST} – F_{ST} comparison studies ($n = 51$) as a function of publication year. Only studies using plant common gardens based on representative natural populations are included. Also the genetic marker type of each study is indicated

gradients and differentials showed that morphological traits (non-fitness traits) were subject to stronger selection than life history traits (fitness traits) on a contemporary scale (Kingsolver et al. 2001; Kingsolver and Diamond 2011). However, on a macro-evolutionary timescale, and using the direction of effects of quantitative trait loci, more consistent directional selection was found for life history traits than for morphological traits (Rieseberg et al. 2002), emphasizing the fundamental importance of fitness traits during speciation and suggesting a ‘fine-tuning’ role for non-fitness traits between contemporary populations. In addition to this frequently used but rather arbitrary typology based on a trait’s relatedness to fitness, a more functional categorization of phenotypic traits may lend more insight into their ecological relevance in adaptive processes. Functional traits directly relate to the function of a species in an ecosystem, and to its relation with the environment (Violle et al. 2007; Suding and Goldstein 2008). A typology of traits according to their role in fundamental processes, i.e. traits related to physiology, phenology, reproduction or biomass-accumulation, can therefore be expected to reflect the ecological performance of populations along an environmental gradient, and hence is more directly related to local adaptation (McGill et al. 2006; Violle et al. 2007). Likewise, the meta-analytical studies performed by Kingsolver et al. (2001) and Rieseberg et al. (2002) indicated relatively weak selection on phenological traits compared to reproductive and morphological traits, probably due to increased environmental variance (Rieseberg et al. 2002). However, these conclusions contradict many studies showing strong adaptation in phenological traits (e.g. Jaramillo-Correa et al. 2001; Haggerty and Galloway 2010; Keller et al. 2011).

How functional plant traits affect performance, and are subjected to natural selection, may not only depend on the local environmental conditions, but also on the life history of the plant

species, since plant trait*life history interactions are key aspects of functional plant strategies and niche differentiation (Grime 1977; Poorter et al. 2006; Baraloto et al. 2010; Zanne and Falster 2010). The extent to which leaf phenology is subject to selection, for example, may depend on the lifespan of a plant species, since long living species invest more in biomass, whereas annuals invest more in reproduction (Grime 1977; Roumet et al. 2006).

Furthermore, life history characteristics such as mating system and pollination mode can also be expected to mediate a species' overall response to selection. Theory predicts that adaptive differentiation between populations mostly reflects a balance between the diversifying effect of positive selection, and the homogenizing effect of gene flow (Slatkin 1987; Lenormand 2002). Life history characteristics related to gene dispersal, such as mating system and pollen or seed dispersal capacity, may therefore influence the magnitude of adaptive differentiation. In addition to gene dispersal, also plant longevity may have a profound impact. It has for example been demonstrated that rates of molecular evolution are linked to an organisms' lifespan (Andreasen and Baldwin 2001; Smith and Donoghue 2008; Thomas et al. 2010). Therefore, it can be expected that annuals have the ability to respond faster to selection than perennials.

A generalization of the susceptibility of phenotypic traits and of plant species in their response to selection can therefore yield important insights into (i) the interaction between selection and the genetic architecture of phenotypic traits (Aitken et al. 2008; Colautti et al. 2012), (ii) the influence of trait variation on ecosystem functioning (Díaz et al. 2007; Albert et al. 2010, 2011; Suding and Goldstein 2008; Bolnick et al. 2011; Lavorel and Grigulis 2012), and (iii) the responses of functional groups of plant species to environmental change (Lavergne et al. 2010; Bellard et al. 2012).

Our objective was to test (i) whether some plant trait types are more subjected to natural selection than other trait types compared to neutral expectations, and (ii) how life history characteristics such as mating system and pollination mode mediate the response of trait types to selection. Therefore, we conducted a meta-analysis on 51 plant common garden studies, reporting Q_{ST} – F_{ST} values. Our meta-analysis differs from previous meta-analyses (Merilä and Crnokrak 2001; Leinonen et al. 2008; Leimu and Fischer 2008; Hereford 2009) in at least two aspects. First, we only included studies of plants to be able to fully evaluate the effects of the life history of plants on Q_{ST} – F_{ST} comparisons. Second, we integrated the geographical distance between studied populations as an additional explanatory variable to account for the relation between geographical scale and adaptive differentiation (Galloway and Fenster 2000; Joshi et al. 2001; Bisschoff et al. 2006; Setoguchi et al. 2011). The recent increase of plant common garden studies (Fig. 1) also allowed us to improve the accuracy of the analysis.

Materials and methods

Data extraction

In December 2011, we searched the Web of Science for plant common garden studies using the following search terms: “common garden AND plant AND neutral* OR marker”; “ Q_{ST} AND plant AND F_{ST} OR marker*”; “plant AND quantitative* AND neutral* OR marker”; “common garden AND plant AND F_{ST} AND Q_{ST} OR quantitative*”; “common garden AND plant AND genetic* AND Q_{ST} OR phenotypic*”. 15 773 papers resulted from these search terms and a first selection based on title and abstract relevance excluded most of these papers (Supporting information S1). Subsequently, we applied

several additional criteria to select a representative set of common garden studies. Only studies including more than 2 populations were selected, whereas studies including cultivated and invasive plant populations were excluded from the analyses, as well as studies where Q_{ST} and F_{ST} estimations were based on a different set of populations.

Modeling explanatory variables

The difference between Q_{ST} and F_{ST} for each reported trait ($Q_{ST}-F_{ST}$) was selected as the dependent variable in a range of mixed models, with plant traits, life history characteristics and geographic scale as independent variables. In line with Leinonen et al. (2008), preliminary ANOVAs showed no significant effect of marker type [3 classes: dominant markers (AFLPs and RAPDs), enzymes (allozymes and isozymes) and microsatellites] on F_{ST} ($F_2 = 0.802$; $p = 0.45$). Likewise, Q_{ST} -estimation methods (3 classes: ANOVA, Restricted Maximum Likelihood, Bayesian approach) did not significantly affect Q_{ST} -values ($F_2 = 0.096$; $p = 0.91$). Therefore, we did not correct F_{ST} and Q_{ST} for marker type and estimation method, respectively.

During model building, the following specific explanatory variables were used: (i) the F_{ST} value of a given study (covariate); (ii) LogScale, i.e. the logarithm of the average between the largest and the smallest pairwise inter-population distance (covariate); (iii) one out of three different a priori trait type classifications (3 categorical variables; Supporting information S2); and (iv) a set of individual life history characteristics (4 categorical variables). Figure 2 provides a scheme showing the explanatory variables and the order in which they were included during model building. Trait type classification I distinguished between fitness traits (F), traits that are directly related to survival and reproduction versus non-fitness traits (NF), which are only remotely related to fitness (Supporting information S2). Trait type classification II reflected a functional division of traits into four classes: biomass accumulation (Bio) versus reproductive (Rep) versus phenological (Phe) versus physiological (Phy) traits. Trait type classification III considered maternal influences and was categorized in early life (EL) versus adult traits (A). The latter classification was included to account for the effects of the maternal environment on $Q_{ST}-F_{ST}$ comparisons, because most studies used field-collected seeds or cuttings. The four species' life history characteristics investigated were: (i) *Mating system*: predominantly outcrossing versus selfing (clearly mixed mating systems were treated as missing values); (ii) *Pollinator vector*: insect pollination versus wind pollination; (iii) *Dispersal type*: good dispersers (through wind or animals) versus bad dispersers (ballistic, gravitational, and when no special seed dispersal mechanisms were present); (iv) *Life span*: perennial versus annual.

A stepwise procedure was used to build mixed models. A priori information was used as a valid means for ranking the relative importance of the predictor variables during the steps involved. First, F_{ST} is known to correlate with $Q_{ST}-F_{ST}$ comparisons (Leinonen et al. 2008), and was therefore added to the intercept model with Study as a random factor. To evaluate the role of geographic distance between populations (Galloway and Fenster 2000; Joshi et al. 2001; Bisschoff et al. 2006; Pico et al. 2008; Setoguchi et al. 2011), also LogScale was included in a second step. Three model sets were generated in the third step, each model set containing one of the three trait type classifications. Finally, all combinations of moderator variables (i.e. life history characteristics) and their interactions with Trait type classification were included in each model set (Supporting information S3 & S4). In each model set, a model was selected based on the statistical significance of its moderator variables ($p < 0.10$). Because we compare all possible models in each model set, unlike a standard forward selection procedure, the probability of erroneously rejecting

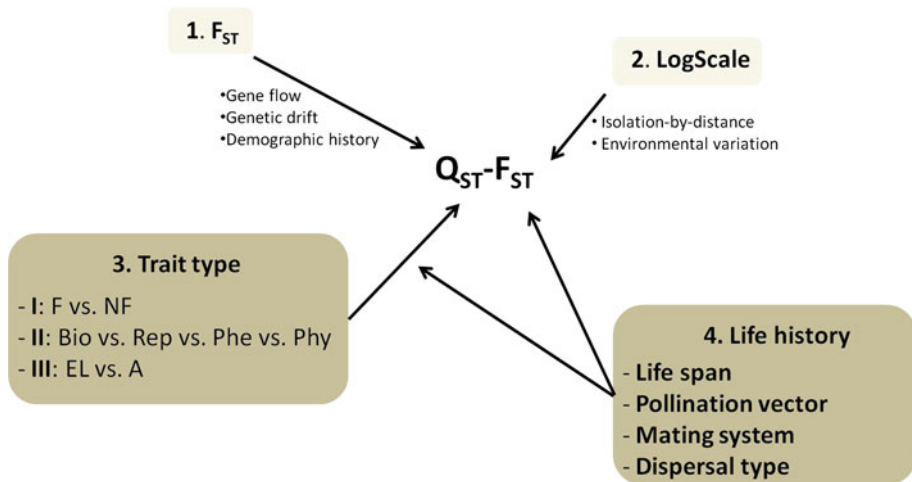


Fig. 2 Scheme representing the variables included during model building and how they may affect Q_{ST} - F_{ST} . The trait variables distinguish between fitness (F), non-fitness (NF), biomass accumulation (Bio), reproductive (Rep), phenological (Phe), physiological (Phy), early life (EL), and adult (A) traits

the true null hypothesis is not increased. AIC values were added (Supporting information S4) to justify the selected models in terms of model parsimony (Elith and Leathrick 2009).

Study identity was included as a random factor in all models to account for non independence of data within studies. Preliminary analyses of possible phylogenetic constraints showed that neither a ‘species (within family)’ nor a ‘plant family’ term in the random part of the model explained additional residual variation. These random terms explained only 2.29 % ($p = 0.58$) and 0 % ($p = 0.11$) of the residual variation, respectively. To provide more strength to the results of larger experiments in terms of accuracy (O’Hara and Merilä 2005; Whitlock 2008), the residuals between the predicted Q_{ST} - F_{ST} (based on the model specifications) and the actual, observed values were weighted based on their sample sizes. Large studies are therefore more influential regarding the estimation of regression coefficients. Study weights were calculated according to Reed and Frankham (2003): $[(A - 2)N]^{0.5}$, with A the number of studied populations and N the number of individuals per population. When studies used different sample sizes to measure Q_{ST} or F_{ST} , we took the average of their weights. Models were fitted using the REML estimation. The Kenward–Rogers approximation was applied to determine appropriate denominator degrees of freedom (Kenward and Roger 1997; Littell et al. 2002). All statistical analyses were conducted in SPSS 17 (SPSS Inc., Chicago IL).

Publication bias

Publication bias refers to the publication of a non-random sample of research findings, resulting in poorly representative results. Although Leinonen et al. (2008) did not test for Q_{ST} - F_{ST} publication bias, they expected that publication bias could favor studies reporting high phenotypic divergence in the face of significant gene flow. We visualized possible publication bias by means of a funnel plot, which shows a measure of sample size (study weight) on the vertical axis as a function of effect size (Q_{ST} - F_{ST}) on the horizontal axis (Egger et al. 1997; Møller and Jennions 2001). In the absence of publication bias, the

studies should be distributed symmetrically around the average effect size. The funnel plot regression method and Egger's regression method were applied to identify possible publication bias statistically (Egger et al. 1997; Macaskill et al. 2001; Kromrey and Rendina-Gobioff 2006). In an attempt to identify the causes and consequences of a possible bias, the dataset was partitioned into life history characteristics and trait types, and each of these groups was subjected to the Egger test and funnel plot analysis.

Results

Review statistics

51 studies met the inclusion criteria, reporting 401 Q_{ST} – F_{ST} comparisons (Fig. 1, Supporting Information S5). The studies included 44 plant species from 18 plant families. The Brassicaceae and Asteraceae were most common, with 7 and 6 plant species, respectively. The number of populations per study varied from 4 to 20, and the distance among populations ranged from 1.3 to 2,700 km. Most studied species were perennial (69 %), and the majority of the species was good dispersing (64 %), insect pollinated (55 %), outcrossing (76 %) and not clonal (86 %).

The number of traits used for Q_{ST} estimation varied between 1 (one study) and 18 (three studies), with an average of 8 traits per study. 49 % of the traits were non-fitness traits, most of them biomass-related (57 % of the data), whereas 51 % represented fitness traits. Furthermore, 12 % of the traits were phenological, 25 % reproductive, 10 % of the traits represented early life traits, and 7 % were physiological traits.

Meta-analysis

Q_{ST} values exceeded their corresponding F_{ST} values in 71.74 % out of the 401 cases. The mean difference between Q_{ST} values and their F_{ST} equivalents was 0.173 (95 % CI: 0.153–0.193). Additionally, a paired t test revealed that Q_{ST} values were significantly larger than their corresponding F_{ST} values (0.345 vs. 0.172; $t_{50} = 4.020$; $p < 0.01$).

A total of 47 models were built, and within each model set, all models were compared based on p values and AIC values (Supporting information S3 and S4). The model with only F_{ST} as covariate and Study as random effect, showed that F_{ST} covaried significantly with Q_{ST} – F_{ST} ($F_{49,28} = 12.05$; $p < 0.01$), with Q_{ST} – F_{ST} decreasing with increasing F_{ST} (Fig. 3). This trend remained significant during further model building (Supporting information S4). The next step indicated a significant effect of LogScale on Q_{ST} – F_{ST} , with Q_{ST} – F_{ST} increasing with increasing geographical scale ($F_{49,2}$ and $p < 0.05$, Fig. 4). Also the effect of LogScale on Q_{ST} – F_{ST} remained significant during further model building (Table 1; Supporting information S4). Until the final step of model building, AIC values decreased, except for model set III (Supporting information S4).

Q_{ST} – F_{ST} comparisons did not differ between early life versus adult stage traits (Table 1), and the model set with trait type classification III is not further discussed. The two remaining linear mixed model sets, including Trait type classification I and II, showed significant differences in Q_{ST} – F_{ST} values between trait types. In model set I, larger Q_{ST} – F_{ST} values were found for non-fitness traits than for fitness traits (model I-10, Supporting information S3 & S4; Table 1; Fig. 5). Q_{ST} – F_{ST} differences between non-fitness and fitness traits were not significantly affected by life history characteristics (Supporting information S4). In model set II, Q_{ST} – F_{ST} values were lower for physiological traits

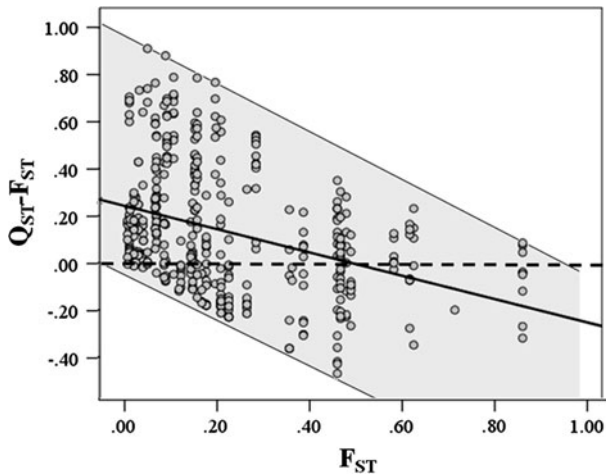


Fig. 3 The relation between $Q_{ST}-F_{ST}$ and F_{ST} . The regression parameters of the *solid line* result from a linear mixed model with F_{ST} as covariate, and Study as random factor ($y = -0.484x + 0.242$). The colored area reflects the zone where natural selection is possible and visualizes the arithmetic limits of $Q_{ST}-F_{ST}$ comparisons along an F_{ST} gradient. The *horizontal dashed line* corresponds to neutrality ($Q_{ST} = F_{ST}$)

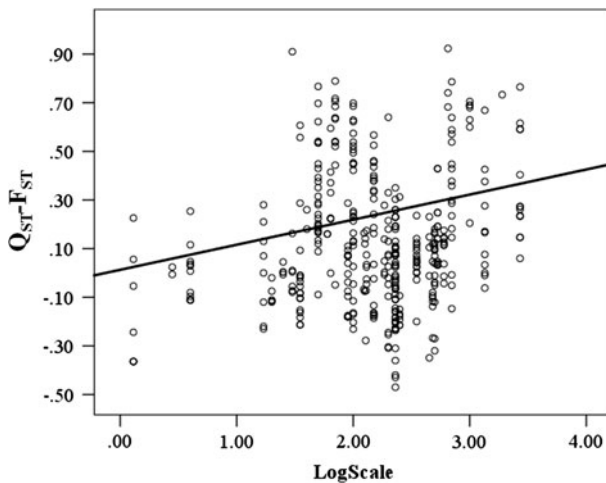


Fig. 4 The relation between $Q_{ST}-F_{ST}$ and LogScale. The regression parameters result from the linear mixed model with F_{ST} and LogScale as covariates, and Study as random factor

compared to reproductive, biomass-related and phenological traits ($p < 0.01$). Moreover, the differences in $Q_{ST}-F_{ST}$ values between trait types varied with Life span (significant interaction term in all models; Table 1), with $Q_{ST}-F_{ST}$ for reproductive traits being higher in annuals than in perennials (Fig. 6). Life span also showed significant $Q_{ST}-F_{ST}$ differences, with annuals having higher $Q_{ST}-F_{ST}$ values than perennials (Fig. 6). Other moderator variables rendered overall higher AIC values ($\Delta AIC > 2$), and revealed no significant main effects (Supporting information S4). On average, 11.27 and 10.35 % of the variation not explained by model sets I and II respectively, could be attributed to the Study effect ($p < 0.01$).

Table 1 Test statistics of the fixed variables included in the selected model of each model set

	Model I (Trait type: F vs. NF)		Model II (Trait type: rep vs. bio vs. phy vs. phe)		Model III (Trait type: EL vs. A)	
	df	F-stats	df	F-stats	df	F-stats
Intercept	51.11	0.01	55.60	0.00	53.18	0.01
F _{ST}	52.64	14.25***	52.40	15.06***	50.00	14.31***
LogScale	50.28	8.87***	50.30	7.91***	50.00	7.53***
Trait type	351.63	4.26**	369.60	2.92**	381.36	0.01
Life span			69.30	3.70*		
Trait type * Life span			369.50	5.00***		

Model selection was based on p values ($p < 0.01$) and AIC values ($\Delta\text{AIC} < 2$) of stepwise included variables. In each model set, none, or only one moderator variable (i.e. life history characteristic) significantly influenced $Q_{\text{ST}}\text{--}F_{\text{ST}}$ values, resulting in maximum one selected model per model set. The models accounted for sample size and a random Study effect

F Fitness traits, NF non-fitness traits, rep reproductive traits, bio biomass traits, phy physiological traits, phe phenological traits, EL early life traits, A adult traits

* $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$

Publication bias

The funnel plot regression method yielded a significant intercept ($p < 0.01$) and the Egger's regression method revealed a significant slope ($p < 0.01$), indicating a relationship between the effects size and the precision of its estimates. According to the funnel plot, the bias is situated at low precision and high $Q_{\text{ST}}\text{--}F_{\text{ST}}$, suggesting a small study effect (Fig. 7). Partitioning of the data into trait types and life history groups revealed no distinct patterns (p value < 0.01). Nevertheless, the upper right outliers (high sample size and high effect size) belong to the tree species *Pinus pinaster*, *Quercus petraea* and *Populus balsamifera*. A subsequent partitioning of the dataset into woody versus non-woody species revealed a significant correlation between sample size and effect size for woody species (Egger's test: $p < 0.01$), but not for non-woody species ($p = 0.097$) (Fig. 7).

Fig. 5 $Q_{\text{ST}}\text{--}F_{\text{ST}}$ differences between non-fitness and fitness traits. Bars reflect the means and 95 % CI estimated by mixed linear modeling with F_{ST} and LogScale as fixed covariates and Study as random factor

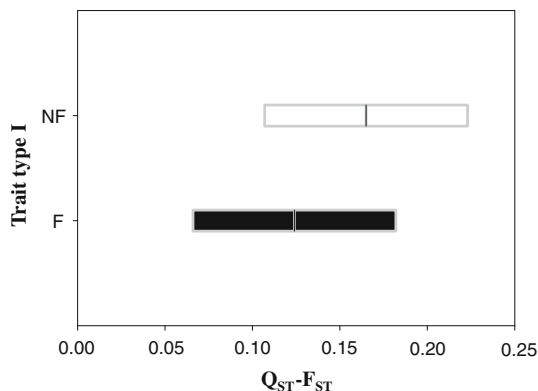


Fig. 6 The effect of Life Span on Q_{ST} – F_{ST} differences between Trait types. Bars reflect the means and 95 % CI estimated by mixed linear modeling with F_{ST} and LogScale as fixed covariates and Study as random factor

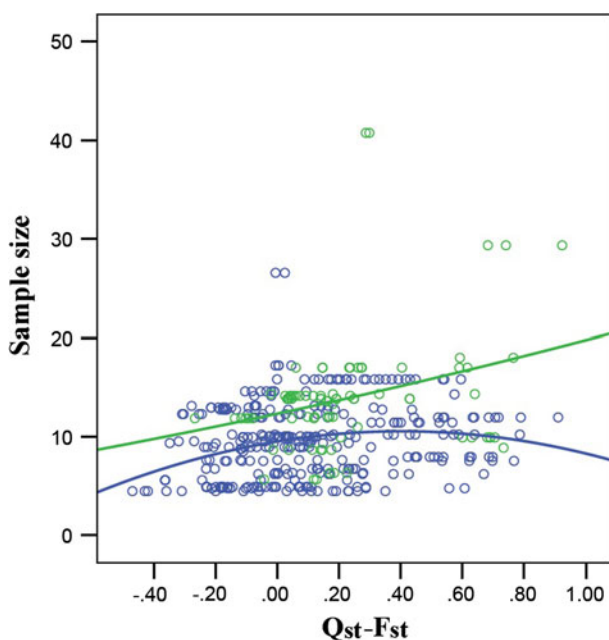
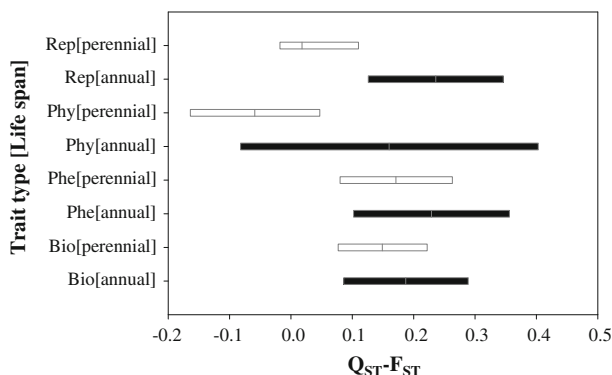


Fig. 7 Funnel plot of sample size (weight factor) versus effect size (Q_{ST} – F_{ST}), partitioned into woody (green) versus non-woody (blue) species

Discussion

Q_{ST} versus F_{ST} and potential biasing effects

Q_{ST} exceeded F_{ST} in 76 % of the cases, demonstrating that neutral processes (F_{ST}) alone are often insufficient to explain the observed phenotypic trait divergence. This finding indicates that environmental selection generally contributes to differentiation among plant populations. However, we cannot exclude that a portion of Q_{ST} not explained by F_{ST} partially results from a number of confounding factors. Therefore, we first discuss these factors before focusing on our own results. First, phenotypic plasticity possibly related to

common garden environments, and genetic correlations between phenotypic traits may explain part of Q_{ST} – F_{ST} (Kruuk et al. 2008; Guillaume 2011). In a common garden, a particular genotype may outperform other genotypes due to adaptation to the local garden environment, and adaptive phenotypic plasticity to the native conditions may remain hidden (Kawecki and Ebert 2004; Pujol et al. 2008; Moloney et al. 2009; Draghi and Whitlock 2012). Several common garden studies on plant Q_{ST} – F_{ST} comparisons along an environmental gradient have indeed reported indications of phenotypic plasticity, next to adaptive differentiation (e.g. Anderson and Geber 2009; Scheepens et al. 2010). Second, also environmental maternal effects may overestimate the degree of local adaptation in common garden studies, due to a higher performance of offspring growing under sympatric than under allopatric conditions (Kawecki and Ebert 2004). Yet, such maternal effects particularly target early life traits such as seed mass, germination rate and early growth (Castro et al. 2008; Donohue 2009), which represent less than 10 % of the traits in our dataset. Furthermore, our results revealed no significant Q_{ST} – F_{ST} differences for adult traits versus early life traits and therefore, environmental maternal effects are unlikely to bias our main Q_{ST} – F_{ST} result. Third, non-additive genetic interactions, including dominance and functional epistasis, may further affect Q_{ST} estimations (Lynch and Walsh 1998; Goudet and Martin 2007; Muir and Moyle 2009; Santure and Whang 2009). Multilocus models predict that dominance effects raise Q_{ST} values of adaptive traits, and that these effects increase with increasing genetic complexity and selection pressure (López-Fanjul et al. 2003, 2007; Santure and Whang 2009). For neutral traits, overestimation of Q_{ST} – F_{ST} by dominance is limited, making a false detection of selection unlikely (López-Fanjul et al. 2007; Santure and Whang 2009). Thus, although the magnitude of Q_{ST} – F_{ST} may be affected by dominance effects, it is unlikely that our general result of $Q_{ST} > F_{ST}$ is significantly biased by dominance effects. Unlike dominance effects, epistatic interactions generally appear to decrease those values because of antagonistic effects between loci (Whitlock 1999; López-Fanjul et al. 2003; Muir and Moyle 2009; Khan et al. 2011). Fourth, pleiotropic effects, involving loci that participate in multiple molecular pathways and therefore affect several phenotypic traits simultaneously, may further complicate the true relation between Q_{ST} – F_{ST} and natural selection (Kruuk and Garant 2007; Whitlock 2008; Guillaume 2011; McGuigan et al. 2011). Finally, the mutation rate of the traits underlying Q_{ST} should equal the mutation rate of the markers underlying F_{ST} to draw accurate conclusions (Hendry 2002; Goudet and Büchi 2006; Edelaar et al. 2011). When the mutation rate of neutral markers is higher than the mutation rate of quantitative traits (resulting in a F_{ST} that is biased upward), this may decrease Q_{ST} – F_{ST} estimates. Microsatellite markers in particular have high mutation rates, and are therefore not recommended to use in Q_{ST} – F_{ST} comparisons (Edelaar et al. 2011). F_{ST} values were, however, not affected by marker type in our study, indicating that bias caused by relatively high mutation rates is likely negligible.

Q_{ST} – F_{ST} differences between plant traits depend on a species' life history

We clearly demonstrated that different plant trait types have differentiated in a different way by natural selection compared to neutral expectations, as quantified by Q_{ST} – F_{ST} differences. These results confirm the expectation that fitness traits respond in general slower to directional selection than non-fitness traits (Merilä and Sheldon 1999; Kingsolver et al. 2001; Leinonen et al. 2008). The evolutionary change of fitness traits through directional selection may be restrained due to their more complex genetic background, with numerous small-effect loci and genetically-based correlations among traits (pleiotropy; Kruuk et al. 2008;

Morrissey et al. 2012; Sztepanacz and Rundle 2012). Our functional trait classification revealed that traits related to plant physiology and, to a lesser extent, to reproduction had overall lower Q_{ST} – F_{ST} values than biomass-related and phenological traits. This is likely associated with the general importance of reproduction and of physiological processes for general plant fitness, whereas the importance of biomass-related and phenological traits is expected to vary across spatial and temporal environmental gradients (Linhart and Grant 1996). The adaptive fine-tuning of biomass-related and phenological traits to new and changing environments is indeed essential for populations and species to survive and reproduce (Hoffmann and Sgrò 2011). Weak or stabilizing selection on plant reproduction and physiology may also be associated with a complex genetic background specific to these traits. The higher Q_{ST} – F_{ST} values for biomass-related and phenological traits on the other hand may be associated with a genetic architecture composed of few large-effect genes. Adaptive differentiation of timing of bud set in *Populus tremula* for example, seems to involve several moderate to large effect genes (Bradshaw and Stettler 1995; Frewen et al. 2000; Rohde et al. 2011). Similarly, few large effect genes have been found for biomass production in *Eucalyptus globulus* (Freeman et al. 2009) and *Arabidopsis thaliana* (Prinzberg et al. 2010).

We also found that in perennial species, traits related to biomass and phenology, were more strongly differentiated compared to neutral expectations than reproductive and physiological traits. In annuals on the other hand, all traits responded equally to natural selection when taking neutral forces into account. In general, perennial species maximize resource conservation to withstand competitors and harsh conditions during their relatively long lifetime (Grime 1977; Roumet et al. 2006), which may explain why biomass-related and phenological traits are more often the target of strong selection in perennials. Short-lived species on the other hand invest in rapid reproduction (Grime 1977; Roumet et al. 2006). Annuals are therefore more likely than perennials to have their reproductive and physiological traits adapted to local environmental conditions (Jia et al. 2011).

Irrespective of trait type, only life span showed an overall effect on Q_{ST} – F_{ST} comparisons, with annuals having higher Q_{ST} – F_{ST} values than perennials. As hypothesized, annuals may indeed respond faster to selection due to higher rates of molecular evolution (Smith and Donoghue 2008; Thomas et al. 2010).

The effect of scale on local adaptation

Adaptation is generally thought to be stronger across larger scales, due to the combined actions of decreasing among population gene flow and increasing environmental heterogeneity (Galloway and Fenster 2000; Joshi et al. 2001; Bisschoff et al. 2006; Setoguchi et al. 2011). Many empirical studies have demonstrated that local adaptation was stronger among more distant populations (Sambatti and Rice 2006; Becker et al. 2006; Pico et al. 2008; Setoguchi et al. 2011), although substantial adaptive differentiation among neighboring populations in contrasting environments has also been reported (Kittelson and Maron 2001; Lenssen et al. 2004). Our results show that the impact of divergent selection on population differentiation generally increases with geographic distance. This finding may result from the joint actions of increased environmental differentiation across larger distances and isolation by distance (IBD). IBD results in a positive correlation between F_{ST} and the distance between populations, which may explain the positive relation between LogScale and Q_{ST} – F_{ST} if F_{ST} covaries positively with Q_{ST} – F_{ST} . However, after including F_{ST} as a covariate in our models, the effect of LogScale on Q_{ST} – F_{ST} remained highly significant and the inclusion of LogScale in the model improved model fit. Moreover, F_{ST}

covaried negatively with $Q_{ST}-F_{ST}$, suggesting that environmental differentiation rather than IBD plays a key role in shaping population differentiation through natural selection.

F_{ST} covaries with $Q_{ST}-F_{ST}$

Theory predicts a negative slope between F_{ST} and $Q_{ST}-F_{ST}$ (Hendry 2002). There is little room for Q_{ST} to exceed F_{ST} if both mutation and migration rates are low and divergence time is large (high F_{ST}), even under strong selection (Hendry 2002). This implies negative $Q_{ST}-F_{ST}$ values when F_{ST} reaches unity because $Q_{ST}-F_{ST}$ values are confined to the $[-1, 1]$ interval (see also Leinonen et al. 2008). Therefore, increasing F_{ST} values would be associated with decreasing $Q_{ST}-F_{ST}$ values. Our results confirm the expected negative correlation between $Q_{ST}-F_{ST}$ and F_{ST} (Hendry 2002; Leinonen et al. 2008; Guillaume 2011). Most species had relatively low F_{ST} values, accompanied with high Q_{ST} values, suggesting that selection pressures must be generally high to overcome the homogenizing effects of gene flow, and to promote local adaptation. The decrease of $Q_{ST}-F_{ST}$ with increasing F_{ST} could be attributed to a reduced exchange of potentially advantageous alleles, preserving less desirable traits in the populations. An increased rate of gene flow could overcome stochastic drift of potentially advantageous alleles and therefore promote them to become fixed in a population if selection pressure is strong enough, especially when mutation rates affecting fitness are relatively high (Alleaume-Benharira et al. 2006; Kremer et al. 2012). It should be kept in mind, however, that some of the very high F_{ST} values may partially result from non-neutrality among putative neutral markers, which could overestimate the slope of the regression of $Q_{ST}-F_{ST}$ against F_{ST} . By including F_{ST} as a covariate in our models, however, the results with respect to trait type and life history are not confounded with potential F_{ST} biases. Nevertheless, gene flow can potentially influence the response of plant traits to environmental variation and therefore increase Q_{ST} values erroneously. Although empirical studies are scarce (reviewed by Guillaume 2011), gene flow may induce phenotypic divergence in traits under balancing selection if they are genetically correlated with traits under directional selection (Guillaume 2011).

Publication bias

We found evidence of publication bias, with small studies with large effects being underrepresented compared to large studies. Identifying the funnel plot outliers (Fig. 7) revealed that the observed relation between sample size and effect size was largely caused by woody species. Indeed, it has been demonstrated that trees in particular show strong phenotypic clines along environmental gradients due to local adaptation and phenotypic plasticity (Savoleinen et al. 2007; Aitken et al. 2008; Vitasse et al. 2010). Therefore, the sampling of populations along large scales may cause stronger $Q_{ST}-F_{ST}$ effects in trees than in herbs, causing the funnel plot to be right skewed. This finding suggests that the bias induced by non-random publication of research findings has little influence on any of our findings. Nevertheless, deliberate choices made by researchers toward populations with a priori knowledge about phenotypic divergence should be kept in mind. For example, if a species showed positive signs of adaptation in a previous study, authors may decide to investigate a relatively small set of populations and still find significant results, potentially inducing publication bias.

Conclusion

Although the generality of local adaptation in plants has recently been questioned (Leimu and Fischer 2008; Hereford 2009), our meta-analysis suggests that plant species generally do respond to natural selection, but that different trait types respond differently. Moreover, the differences in Q_{ST} – F_{ST} comparisons between trait types also depend on the life history characteristics of the plant species under study. Here, we found longevity mediating the magnitude of Q_{ST} – F_{ST} differences between trait types. More specifically, our results highlight the susceptibility to selection of physiological and reproductive traits in short-lived plant species. These findings may be closely related to the genetic architectures of trait types and life histories, with the proportion of large-effect genes presumably shaping the response to natural selection. Further empirical research is needed to elucidate the relationship between genetic architecture and phenotypic differentiation and to evaluate the consequences of these findings with respect to adaptation to a changing environment. Moreover, there is still a lot of controversy with respect to the magnitude of pleiotropy (the number of traits involved in pleiotropic effects) and the effects of pleiotropy on evolution (Razeto-Barry et al. 2010; Stearns 2010; Wagner and Zhang 2011; Hill and Zhang 2012). This advocates the need for further research in order to understand the generality of pleiotropy among trait and species groups, and the effects of pleiotropy on adaptive differentiation (see also Bergelson and Roux 2010). Finally, the positive correlation between the average inter-population distance and their Q_{ST} – F_{ST} values suggests that isolation by distance plays an important role in adaptive evolution.

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