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Research article

Patterns of genetic variation within and among populations in *Arbutus unedo* and its relation with selection and evolvability

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ABSTRACT

The study of plant adaptation is especially relevant in the context of expected global change, which will modify key environmental factors, such as temperature and precipitation. Here, we study the strawberry tree (*Arbutus unedo* L.) throughout its climatically variable range: predominantly circum-Mediterranean, but also along the Atlantic coasts from Morocco to Ireland. In a common garden experiment, we studied 12 plant traits to assess the hypothetical effects of natural selection on the population genetic structure. These traits were selected because it is well known that they are highly affected by climatic factors such as temperature and precipitation. To this aim, we used the Q_{ST}–F_{ST} approach. Firstly we calculated the additive genetic variance (V_A), heritability (h^2) and evolvability. Then, we obtain Q_{ST}, which is a standardized measure of genetic differentiation among populations displayed by quantitative traits, and compare it with F_{ST}, a measure of the genetic differentiation of putatively neutral loci. Our results showed that Q_{ST} was significantly lower than F_{ST} in 6 of the 12 traits, and 11 of the traits had demonstrable V_A and evolvability. Low Q_{ST} values are typically explained by stabilizing selection. We propose that stabilizing selection may select for a norm of reaction that produces a similar phenotype even from diverse genotypes from different localities. Further, the evolvability that we found in key morpho-structural traits predicts that *Arbutus unedo* retains genetic variation that will allow it to continue to adapt to the diverse environments throughout its species range.

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Introduction

One of the main goals in evolutionary biology is the study of variation, as well as to find the reason for its origin and preservation. Heritable phenotypic variation is the raw material for evolutionary change, and its maintenance is crucial for the adaptability and evolutionary potential of a population or species (Frankham, 2005). Related to that, the study of plant adaptation has recently gained importance in the context of on-going global change (Aitken et al., 2008). It is known that the Earth's climate has warmed by approximately 0.6 °C over the past century, a rate of warming greater than at any other time during the past 1000 years (IPCC, 2013). The new environmental conditions arising as result of climate warming are leading to changes in plant species, such as climate-induced movement towards higher latitudes and/or altitudes (Parmesan and Yohe, 2003), shifts that may have consequences for the structure and dynamics of the ecosystems (Aerts et al., 2006). In this context, the study of widespread species, living under a wide range of climatic conditions is relevant to understand environmental effects on their genetic population structure. This is because populations existing under different environmental conditions are especially likely to experience different processes of local selection.

Arbutus unedo L. (strawberry tree) is a diploid species ($2n = 26$), belonging to the *Ericaceae* family, *Arbutoideae* subfamily (Torres et al., 2002). Its main distribution is around the Mediterranean Sea, but, interestingly, it has populations along the Atlantic coast of the Iberian Peninsula, France, and south western Ireland (Fig. 1), where its distribution limit coincides with the 4 °C isotherm for the January mean temperature (Sealey, 1949). *A. unedo* is one of the species belonging to the "Lusitanian group of flora". These are

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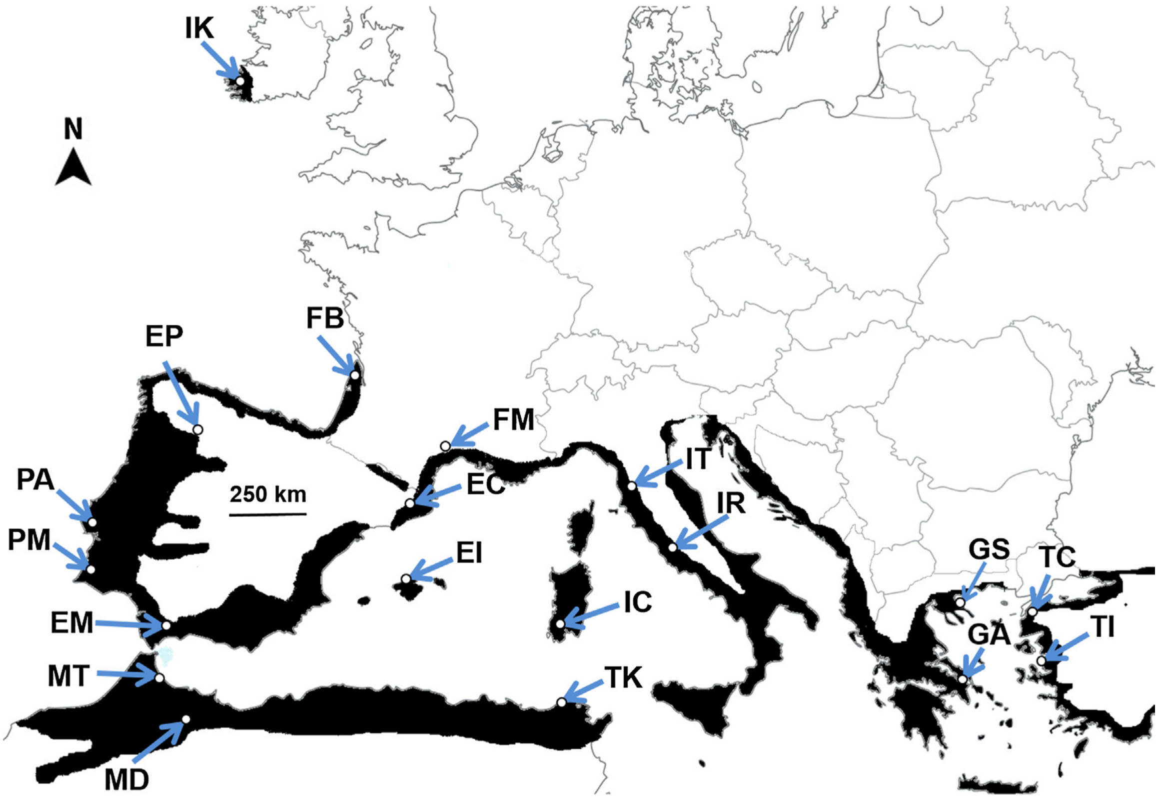

Fig. 1. European map showing the distribution range of *Arbutus unedo* and the location of the 19 sampled populations.

species present in the Iberian Peninsula and in Western Ireland, but absent in Britain (Sealey, 1949). A suggested explanation for this presence in Ireland is arrival via a postglacial migration (Sealey, 1949; Webb, 1983). It is intriguing how the Irish populations can survive in climate conditions so different to those of the Mediterranean populations. Therefore, the study of this disjunct and wide range distribution pattern (more than 2000 km latitude) may be of special interest (Cox and Moore, 2005). Specifically, the study of their genetic differentiation is relevant to understand the effect of the Atlanto-Mediterranean contrast. Likewise, the knowledge of its genetic diversity is crucial to predict the evolvability and, therefore, the hypothetical survival of the species. This knowledge is especially relevant for traits with proven responses to changes in light, temperature and precipitation, which have been predicted to vary as a result of the ongoing climate change (IPCC, 2013).

Frequently, the influence of selection on population divergence has been estimated by comparing the genetic differentiation in quantitative traits, Q_{ST} (Spitze, 1993), with neutral marker differentiation, F_{ST} (Wright, 1951). Populations can diverge genetically without selection due to migration and drift, and this variation is estimated using F_{ST} from neutral markers. Therefore, if $Q_{ST} = F_{ST}$, genetic drift is enough to explain the genetic structure in the population. However, if $Q_{ST} > F_{ST}$, the differences in quantitative traits are higher than expected due only to drift, which is interpreted as evidence of spatially divergent selection on the trait. In the opposite situation, $Q_{ST} < F_{ST}$, the existence of convergent (stabilizing) selection is inferred, because the differences in quantitative traits are lower than expected (Whitlock, 2008). However, some criticisms about the use of Q_{ST} must be taken into account. First, the use of quantitative trait measures taken from individuals grown in diverse localities is not appropriate, because differences in environmental effects on development could mask (or exaggerate) the real genotypic differentiation among populations (Pujol et al., 2008). Second, the use of highly variable neutral markers such as microsatellites to calculate F_{ST} produces biases and must be avoided (Edelaar and Björklund 2011; Edelaar et al., 2011). Third, the use of >10 populations is highly advisable to increase the reliability of the Q_{ST} F_{ST} comparison (Whitlock and Guillaume, 2009). Consequently, we decided to use a common garden design and the application of AFLP neutral markers (not highly variable), and we obtain samples from 19 populations (further details follow) to mitigate these difficulties.

Q_{ST} has been frequently used to test for the effects of spatially divergent selection, as has been shown in several reviews (Merilä and Crnokrak, 2001; Leinonen et al., 2008; Kort et al., 2012). These reviews found positive correlations between Q_{ST} and F_{ST}. They found that, on average, Q_{ST} was higher than F_{ST}, revealing the main role of divergent selection for quantitative traits. Therefore, natural selection, including indirect selection through correlated characters, is a powerful force in the evolution of plant phenotypes for adaptations to local environments and the evolution of functional traits (Linhart and Grant, 1996; Geber and Griffen, 2003). However, reports of $Q_{ST} > F_{ST}$ potentially contain several biases: trait selection bias, due to the deliberate selection of populations from contrasting environments, and publication bias, favouring studies reporting the outcome $Q_{ST} > F_{ST}$ (Leinonen et al., 2008). Likewise, there is a bias in the calculation of F_{ST} due to the use of highly variable neutral markers, such as microsatellites, whose mutation rate is higher than the genome on average (thus higher than in quantitative traits). This kind of marker leads to a higher within-population heterozygosity (H_e) that produces an F_{ST} value lower than for low-mutation loci or traits, causing a bias in Q_{ST}–F_{ST} comparisons (Edelaar and Björklund, 2011). Because our study includes a wide range of climatic conditions, we could expect *a priori* a result of $Q_{ST} > F_{ST}$. However, if $Q_{ST} < F_{ST}$, an alternative and reasonable explanation for plant adaptation, especially for plants living under such contrasted climatic

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