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RESEARCH PAPER

Genetic diversity and genotypic stability in *Prunus avium* L. at the northern parts of species distribution range

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Abstract

• ***Key message*** **Large genetic variation was found in *Prunus avium* L. populations from the northern parts of the species distribution range. The ranking of genotypes in terms of growth was stable when tested at three trial sites within the northern parts of the species distribution range.**

• ***Context*** Peripheral populations especially those in the leading edge are isolated from rest of the areas in the species distribution range. This can make them less genetically diverse yet genetically distinct from the rest of the populations in the species distribution range. Evaluation of their genetic diversity is thus crucial in understanding the local adaptation potential of a species.

• ***Aims*** We investigated the genetic diversity and genotype by environment interaction at the northern parts of the distribution range of *P. avium*.

• ***Methods*** Quantitative genetic variation of growth, stem form, and spring phenology were assessed in progenies from 93 plus trees of *P. avium* selected from 43 locations at the north of the species distribution range in Sweden and tested at two Swedish sites and one Danish site.

• ***Results*** We find large quantitative genetic variation in growth and phenology at the northern part of the distribution range of *P. avium*. Only a limited genotype by environment interaction was observed with no clear indication of local adaptation at the northern parts of the species distribution.

• ***Conclusion*** We conclude that *P. avium* harbors a high level of genetic diversity at the north of its distribution range. Present patterns therefore reflect more likely the recent introduction of the species and dispersal dynamics rather than a long-term loss of diversity along South-North ecological clines during the Holocene. With no indications of genetic depletion in growth or phenology, the gene pool in the breeding program is considered suitable for the future propagation of the species in the tested area.

Keywords Marginal populations · Forest genetics · Climate change · Local adaptation · Wild cherry

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1 Introduction

Peripheral populations of a species are usually isolated and hence genetically divergent from the central populations (Gibson et al. 2009). Genetic variation within these populations is therefore lower compared to that in central populations in many conifers and deciduous tree species (Lesica and Allendorf 1995). However, this may not always be the case (Channell and Lomolino 2000; Lira-Noriega and Manthey 2014), and the genetically most distinct populations will not always be in the peripheral parts of the species distribution range. Divergence is caused by the interacting processes of selection, drift, and gene flow (Nadeau et al. 2016; Vucetich and Waite 2003) which in turn is affected by various factors such as isolation, mating systems, and life history traits that can vary over time and space (Loveless and Hamrick 1984). Also, the levels of genetic variation may reflect proximity to glacial refugia (Petit et al. 2003) that more often than not have been located in the southern parts of the present distribution of European tree species.

The leading edge of the species distribution range is often characterized by higher demographic stochasticity that can lead to low within population diversity due to founder effects, drift, or selection (Savolainen et al. 2011). At the southern edge, ongoing directional selection for especially drought resistance might lead to lower genetic diversity within populations for traits related to water use efficiency (Lamy et al. 2011) while directional selection may reduce genetic variation in traits related to winter hardiness at the northern limit (Kreyling et al. 2014). The partly geographic isolation combined with past and present selection for extreme environments makes the peripheral populations important from a genetic conservation and management point of view (Hampe and Petit 2005) as they may serve as source for migrants enabling species expansion under future climate change scenario (Fady et al. 2016). Increased availability of suitable habitats in the northern latitudes will trigger range expansion of pioneer tree species (Kremer et al. 2014), but the future climate may include increased risk of spring frost damage (Augspurger 2013), and the presence of genetic variation in spring phenology in northern populations (Kreyling et al. 2014) can therefore prove beneficial for survival.

Prunus avium L. (wild cherry) is such a pioneer species with the current northern distribution range extending up to southern Scandinavia although the present distribution may reflect human introduction for its wild cherries (Russell 2003; Welk et al. 2016). Wild cherry is insect pollinated with seeds dispersed by birds and other animals. It typically occurs scattered in forests dominated by other species, often with apparent small isolated population size (Ducci et al. 2013; Mohanty et al. 2001), where it is protected against inbreeding by a self-incompatibility system (Mohanty et al. 2001). In the present study, we investigate the genetic variation within and among populations of *P. avium* at the northern parts of the species distribution in Sweden. Specifically, we study (1) if the quantitative genetic variation within populations at the northern parts of the distribution range of *P. avium* in Sweden is low; (2) if population differences in phenology can be explained as adaptation to local climatic conditions; (3) if substantial levels of genotype by environment interaction is present suggesting ongoing divergent selection, and (4) if offspring from northern parts of the distribution range grow relatively better at northern test site (latitudinal patterns) suggesting local adaptation.

2 Materials and methods

2.1 Sampling and field tests

A total of 100 plus trees were phenotypically selected (based on vitality, growth, and stem form) from 43 population sites (one to five trees per site) at the northern range of species distribution in southern Sweden (Fig. 1) during the period 1991 to 1992. The sites were ranging from small pure stands of wild cherry to single trees along agricultural fields. However, most trees were selected in mixed broad-leaved/conifer forests. All trees were grafted and planted in 1993 in one clonal seed orchard (CSO) in southern Sweden (55° 53′ N, 13° 53′ E, 50 m) for mass propagation of seed for commercial use. Open-pollinated (OP) seeds were harvested from 93 of the clones in the CSO in 2002 and seedlings of the 93 families were produced at the Skogforsk research station at Ekebo (55° 57′ N, 13° 07′ E, 80 m). These seedlings were planted in three progeny field trials (Fig. 1), Himmelev (55° 66′ N, 12° 11′ E) in Denmark and Omberg (58° 20′ N, 14° 40′ E) and Björnstorp (55° 37′ N, 13° 25′ E) in Sweden, in 2004 with 1-year-old seedlings. The three test sites are hereafter denoted by sites 1, 2, and 3, respectively. Progenies from all 93 OP families were planted at site 3, but only 86 and 64 families were included at sites 1 and 2, respectively. The families were randomized in the blocks per sites with a total of ten plants per family per trial. Details of the trial sites are provided in Table S1 (supplementary information); while the location of the 43 population sites of the plus trees origin and their respective climatic variables are provided in Table S2 (supplementary information).

2.2 Assessment of trials for growth, stem form, and phenology

The height of all the trees was measured using Vertex hypsometer in 2008 in trials 2 and 3. Diameter at breast height (DBH), height, and stem form was measured in all the three sites in 2013, and DBH was measured again in trial 1 in 2017. Stem form was assessed using a scale from 1 to 9, where "1" referred to a tree with extremely crooked main trunk with a

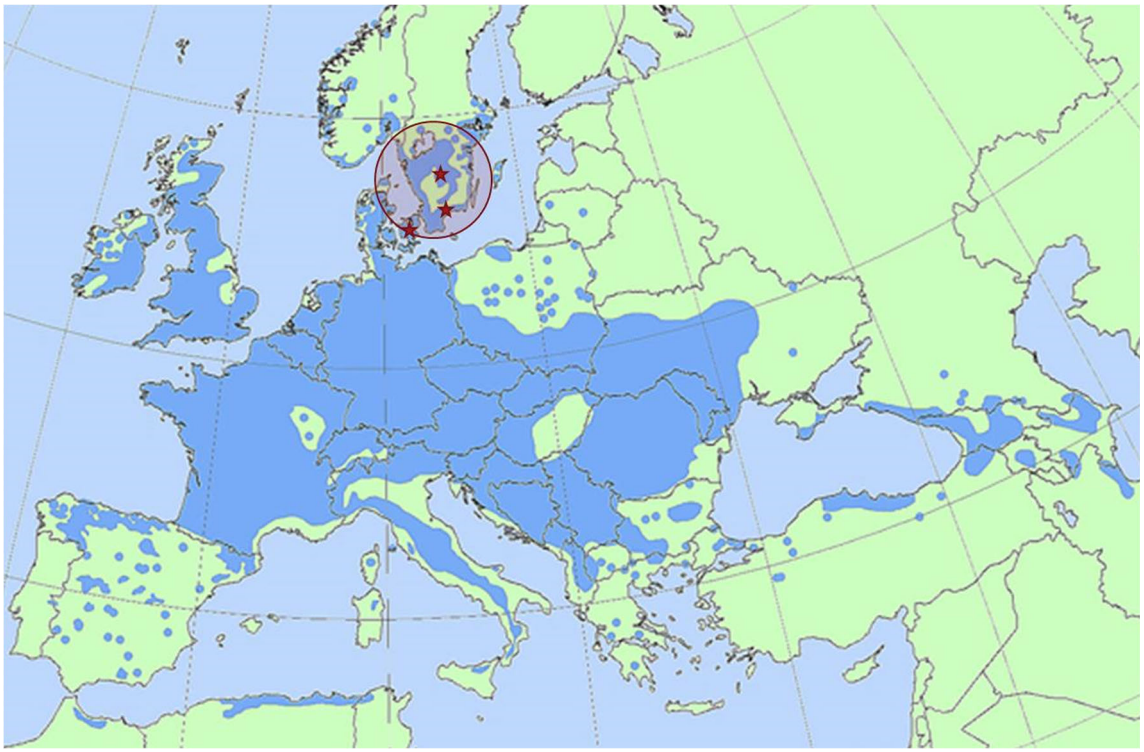

Fig. 1 Location of the trial sites (represented by stars) within the leading edge (shaded circle) of *Prunus avium* species distribution range (map source, EUFORGEN)

lack of an axis while "9" referred to a tree with straight stem axis with few perpendicular branches. The rationale behind the stem form was to reflect the economic potential of the trees (9 being best), but a low score is also likely to reflect climatic damage to apical leader due to spring or autumn frost (1 reflecting most damage). Spring phenology was assessed on 2 May 2016 in trial 1 as budburst stages 1 to 9, where 1 was the score for trees with dormant buds and 9 denoted fully developed leaves at the time of assessment (Table S3 in supplementary information).

2.3 Estimation of genetic parameters

A linear model was applied to test differences among families:

$$Y_{ijk} = \mu + S_i + B_{j(i)} + f_k + \lambda_{ik} + \varepsilon_{ijk} \quad (1)$$

where Y_{ijk} is the value of the trait in question, μ is the grand mean, S_i is the fixed effect of site i, $B_{j(i)}$ is the fixed effect of block j within site i, f_k is the random effect of family k, λ_{ik} is the random interaction between site i and family k, and $_{ijk}$ is the residual. Normal plot histograms of residuals were made to examine for severe deviations from the assumption of normal distribution, and residuals were plotted as a function of predicted values to examine for lack of variance homogeneity. The family effect was tested using the Satterthwaite approximation (Satterthwaite 1946) in the procedure general linear model (GLM) in the statistical software program SAS (SAS Institute 2008). The effects of environmental heterogeneity within trial sites were reduced by adding a spatial model to the basic genetic model:

$$R = \sigma^2{}_{\varepsilon}[AR1(Pcol) \otimes AR1(Prow)] + \sigma^2{}_{\eta} I$$

where R is the variance-covariance matrix of the residuals, $\sigma^2{}_{\eta}$ is the spatial residual variance, σ^2 is the independent residual variance, AR1 is the auto regression of the first order for the columns and rows, P is the autocorrelation parameter, ⊗ is the Kronecker product, and I is the identity matrix (Dutkowski et al. 2002). The significance of the spatial structure was tested by comparing the log likelihood ratio (Kendall and Stuart 1979) with and without the spatial analysis in ASReml (Gilmour et al. 2009).

Within each trial site, the additive variance V_A was estimated as $4\sigma^2{}_f$ since the trees are assumed half sib progeny of the clones in the clonal seed orchard (Falconer and Mackay 1996). Subsequently, narrow sense heritability of traits was estimated according to Falconer and MacKay (1996) as

$$h^2 = V_A / V_p$$

where V_P is the total phenotypic variance, i.e., $\sigma^2{}_f + \sigma^2{}_{\eta} + \sigma^2$, where $\sigma^2{}_f$ is the variance among families, $\sigma^2{}_{\eta}$ is the spatial residual variance, and σ^2 is the independent residual variance.

For each trait, the expected genetic response corresponding to a phenotypic mass selection with the selection of 1%

superior individuals ($i = 2.665$) according to Falconer and MacKay (1996) was divided by the trial mean to obtain a measure of response potential.

The additive genetic correlations between two traits within sites or between the same traits at two sites were estimated as $r_A = \hat{cov}(fi,fj)/\sqrt{\sigma^2_{fi}\sigma^2_{ji}}$ where σ^2_{fi} and σ^2_{fj} are the estimated family variance for two traits within the site or same trait at different sites and $\hat{cov}(fi,fj)$ is the corresponding family covariance between traits within sites, or between the same trait or different traits across sites (Burdon 1977). The covariance matrix for calculating genetic correlation in a multi-site analysis was carried out in ASReml according to Ding et al. (2008), i.e., considering different block and error variance at different sites. The standard error of r_A was estimated using the post-analysis approach to calculate the functions of variance components in ASReml (Gilmore et al. 2009). A jackknife approach (Tukey 1958), where each family at a time was removed, was applied to identify the influence of each family on the additive genetic correlation across sites (as a measure of the genotype-environment interaction) as regards growth.

For each site, the population effect was tested by applying model 2. Furthermore, the model was used to obtain least square means for the populations.

$$Y_{ijk} = \mu + P_i + B_j + f_{k(i)} + \varepsilon_{ijk} \quad (2)$$

where Y_{ijk} is value of the trait in question, μ is the grand mean, P_i is the fixed effect of population i, B_j is the fixed effect of block j, f_k is the random effect of family k, and $_{ijk}$ is the residual.

Q_{ST} values were estimated to find the degree of differentiation among populations using the formula by Spitze (1993), $Q_{ST} = V_{POP}/(V_{POP} + 2V_A)$, where V_{POP} is the variance between populations and V_A is the estimated additive genetic variance.

2.4 Tests of diminishing quantitative genetic variation

A jackknife approach (Tukey 1958) was additionally carried out by systematically removing families from groups of plus trees belonging to one degree of latitude at a time followed by an estimation of the overall additive genetic variance. This was done to investigate if the overall additive genetic variance is larger when families from the most northern latitude are removed.

2.5 Test for local adaptation

A regression analysis was carried out to test if the population least square mean (LSM) estimates of bud burst were explained by climate, latitude, or longitude of the populations. The climate variables assumed most important for spring phenology and therefore tested as explanatory variables were minimum temperatures in March, April, May, and June, continentality index (difference between mean warmest month temperature and mean coldest month temperature, see Hamann et al. 2013), and difference between maximum and minimum temperatures in March, April, May, and June. Furthermore, it was examined if the growth performance was explained by the difference in climate between the sites where the trees (clones) were originally selected and climate at each of the trial sites, i.e., transfer functions for growth rate (Wang et al. 2006). The climate variables examined as explanatory variables for growth were minimum temperatures in the spring and autumn months, continentality index (Hamann et al. 2013), and summer precipitation. Plots of smoothing splines were made to examine for any common non-linear transfer functions for the populations. The procedure REG in the statistical software program SAS (SAS Institute 2008) was used to test both linear and quadratic relationships between population LSM estimates for DBH and height with climate variables. Climatic variables were obtained from the ClimateEU v4.63 software package available at http://tinyurl.com/ClimateEU (following the methodology described by Hamann et al. 2013).

Data availability Data for this study is available at University of Copenhagen - Electronic Research Data Archive (UCPH ERDA): https://sid.erda.dk/wsgi-bin/ls.py?share_id=hvtlsuTmIE.

3 Results

3.1 Genetic variation within the test sites

Autoregressions of the first order for the columns and rows were significant for all the traits assessed. Families were significantly different for all traits except for stem form measured in 2013 at site 2 (Table 1), but the variation among the sampling sites/populations and the corresponding Q_{ST} values were not significant for any of the traits assessed (Table 1). Narrow sense heritability (h^2) was the highest for budburst assessed on site 1 and was generally higher than for the growth traits (Table 1). h^2 estimates for DBH and height were moderate to high among the sites and the predicted responses from phenotypic mass selections ranged from 4 to 9% for height and 7 to 19 % for DBH (Table 1) for a selection intensity of $i = 2.665$ (corresponding to 1%) indicating a relatively high potential for a response in growth to moderate selection. The narrow sense heritability estimates for stem form were low to moderate and varied from 0.09 to 0.32 among the sites (Table 1). Within sites, growth (height and DBH) was negatively correlated to stem form (Table 2).

Table 1 Means, family variation, and genetic parameters of different traits analyzed

Trait	Mean	*P* value fam.	V_A	V_P	h^2	$SE\ (h^2)$	$R\ (\%)$	Q_{ST}
Site 1								
Height 2013 (dm)	51.34	0.0002	28.31	68.24	0.41	0.12	7	0.0002
DBH 2013 (mm)	55.95	< 0.0001	200.78	367.49	0.55	0.15	19	< 0.0001
Stem form 2013	4.20	0.001	1.59	5.31	0.30	0.12	16	< 0.0001
Budburst 2016	3.03	< 0.0001	0.52	0.61	0.85	0.16	22	< 0.0001
DBH 2017 (mm)	99.63	< 0.0001	321.46	514.46	0.62	0.15	14	< 0.0001
Stem form 2017	4.47	0.008	2.01	9.32	0.22	0.11	15	< 0.0001
Site 2								
Height 2008 (dm)	25.93	< 0.0001	12.68	32.64	0.39	0.10	9	< 0.0001
Height 2013 (dm)	64.47	0.0009	26.53	113.09	0.23	0.07	4	< 0.0001
DBH 2013 (mm)	74.12	< 0.0001	184.20	507.44	0.36	0.11	11	< 0.0001
Stem form 2013	5.10	0.06	0.39	4.25	0.09	0.08	4	0.04
Site 3								
Height 2008 (dm)	23.67	0.03	8.28	31.27	0.26	0.09	6	< 0.0001
DBH 2013 (mm)	83.89	0.01	121.36	429.06	0.28	0.15	7	< 0.0001
Stem form 2013	4.25	0.03	0.63	1.99	0.32	0.15	11	< 0.0001

Site 1: Himmelev, Denmark; site 2: Omberg, Sweden; site 3: Björnstorp, Sweden

h^2 narrow sense heritability, V_A estimated additive genetic variance, V_P phenotypic variance, *DBH* diameter at breast height, *R* predicted response (in percentage of the mean) to a mass selection of 1% superior individuals ($i = 2.665$), Q_{ST} quantitative genetic differentiation among populations

3.2 Genotype-environment interaction and local adaptation

The additive genetic correlations (r_A) for DBH among the sites were moderate with the highest correlation between the two Swedish sites (Table 2). Between sites 1 and 2, r_A was deflated by three families, because removal of these families through a jackknife procedure increased the additive genetic correlation between sites 1 and 2 from 0.50 to 0.82. Among sites 1 and 3 and sites 2 and 3, the correlations between sites were deflated by a single family (Table 2) suggesting that the genotype by environment interaction is caused by a few random families irrespective of the latitude they come from (Table 2). Genetic correlation across sites for stem form was not significant.

Signs of local adaptation were absent. Budburst measured in the Danish site did not correlate significantly with growth or stem form at any sites. Populations from the northern latitudes did not show a tendency to grow better in the northern site or vice versa (Fig. 2). Regressions between population LSM estimates for budburst and climate, latitude, or longitude of the populations were not significant. The transfer functions (difference between climate at test site and climate at original population site) did not show any relationship to the growth of trees growing in any of the three test sites. The change in additive variance component (V_A) of DBH did not show any pattern when they were calculated by systematically eliminating families from each latitude group (Table 3).

4 Discussion

4.1 Genetic diversity of *Prunus avium* at its northern parts of species distribution

Denmark and Sweden are at the northern parts of the species distribution range of *P. avium* (Ducci et al. 2013; Russell 2003). Nevertheless, previous progeny testing of *P. avium* in Sweden has revealed high phenotypic variability within the species for growth and survival (Martinsson 2001). Our results show that the genetic variation was generally high among families of *P. avium* growing in the northern parts of its distribution area and there were no trends of declining genetic variation among trees from northern latitudes within the latitudinal range investigated (corresponding to a distance of ~ 450 km). Two factors could cause an overestimation of genetic variance for the different traits. One is polyploidy, which has been reported in *P. avium* (Cachi et al. 2017). The other is the fact that families could be made of not just half sibs, but also full sibs. We have no evidence of this being the case in our studied populations or in other populations to which we compare our results, thus making our comparative statements unbiased. Our results thus contrast the commonly proposed theory that the peripheral populations have less genetic diversity when compared to central populations (Rasmussen and Kollmann 2007; Arnaud-Haond et al. 2006; Yeh and Layton 1979). Similar trends have been previously reported in other woody species (Gapare et al. 2005; Muir et al. 2004; Jankowska-Wroblewska et al., 2016; Yakimowski and

Table 2 Significant genetic correlations (r_A) within and among the three trial sites for DBH, height, and stem form. Standard errors (SE) are in italics. Jackknife approach was used to systematically remove families to find its effect on correlations across site

Trait–trait	r_A	SE
Site 1		
Height 2013–DBH 2013	0.89	*0.05*
Height 2013–stem form 2013	− 0.67	*0.23*
DBH 2013–stem form 2013	− 0.61	*0.20*
DBH 2013–DBH 2017	0.99	*0.02*
Stem form 2013–stem form 2017	0.98	*0.06*
Site 2		
Height 2008–height 2013	0.94	*0.07*
Height 2013–DBH 2013	0.87	*0.07*
Site 3		
Height 2008–DBH 2013	0.94	*0.10*
Across sites		
DBH 2013 (site 1–site 2)	0.50	*0.19*
After removing three families	0.82	*0.16*
DBH 2013 (site 1–site 3)	0.59	*0.26*
After removing one family	0.82	*0.30*
DBH 2013 (site 2–site 3)	0.78	*0.27*
After removing one family	0.95	*0.33*

Site 1: Himmelev, Denmark; site 2: Omberg, Sweden; site 3: Björnstorp, Sweden

Table 3 Variation in additive genetic variance of DBH 2013 with systematic removal of families coming from each degree of latitude

Jackknife attribute	No. of families removed	V_A site 1	V_A site 2	V_A site 3
All latitudes	0	253.77	222.49	223.07
Minus 59–60	3	252.99	242.77	204.35
Minus 58–59	26	213.72	243.53	186.51
Minus 57–58	8	284.90	256.64	182.95
Minus 56–57	32	308.25	194.48	277.14
Minus 55–56	24	286.14	181.61	224.46

Eckert, 2008) where the genetic diversity was not different between the peripheral and core populations. In a review of population genetic studies, 64% of 81 studied plant species showed lower genetic diversity in the peripheral populations, and 33% of 37 studied plant species conformed to the hypothesis that the peripheral populations were genetically differentiated from their central counterparts. Most of these studies were based on molecular markers and the differences between the peripheral and central populations were generally not large (Eckert et al. 2008).

Similar results, as regards high genetic diversity as suggested by this study based on quantitative genetics, were reported for the *P. avium* from its central regions of distribution range in Europe (Curnel et al. 2003). At its southern margin of distribution range, the genetic diversity of *P. avium* populations was even larger compared to that of central populations (Ganopoulos et al. 2011). The ability to retain genetic diversity of *P. avium* populations at the southern edge compared to that of central populations might be attributed to self-incompatibility and/or the occurrence of polyploid individuals within this species as observed by Cachi et al. (2017). Furthermore, the ability of making root suckers (Ducci et al. 2013) could potentially also help to retain rare alleles within populations. High genetic diversity within populations and low differentiation among populations, as seen in our results and other studies from the southern margins of species distribution range (Ganopoulos et al. 2011), can be retained in a system where gene flow is ensured by insect pollination and seed dispersal by birds (Ducci et al. 2013).

A high gene flow in *P. avium* is possibly beneficial for the populations in the northern parts of species distribution area studied here, as it will enrich the gene pool with potential valuable alleles for adaptation from the core populations. Long-distance insect pollination (Jolivet et al. 2012) as well as bird-mediated seed dispersal to long distances (Breitbach et al. 2010) has been reported in *P. avium*. This may bring in adaptive alleles to the peripheral populations resulting in increased fitness of the species and increase the reproductive success and colonization of suitable habitats at its leading edge of distribution range (Aitken and Whitlock 2013). Long-distance gene flow in species with long generation time like trees has a beneficial effect of introducing rare alleles thereby enhancing the genetic diversity (Kremer et al. 2012). This in turn can enhance the potential for local adaptation by introducing new genes available for selection (Sexton et al. 2014). But, high gene flow from the range core to the peripheries can

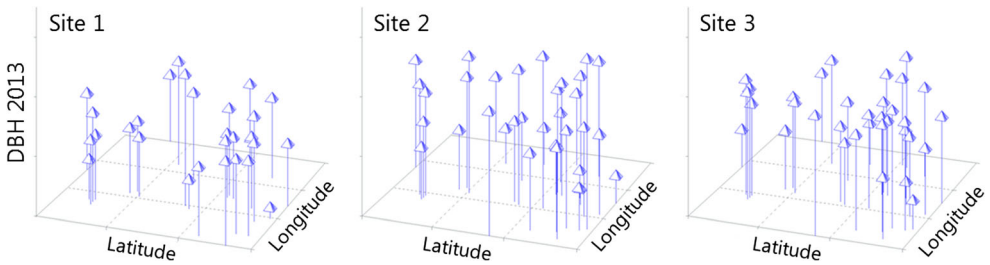

Fig. 2 Growth (population least square mean DBH in 2013) plotted as a function of latitude and longitude of population origin shows no pattern in the three trial sites

also counteract adaptive selection at the peripheral populations thereby reducing the speed of local adaptation (Savolainen et al. 2007; Lenormand 2002; Ramos and Kirkpatrick 1997).

4.2 Lack of signs of local adaptation

The present study has not been able to prove any occurrence of natural selection towards a better adaptation to local climatic conditions, because we found no indications of high genotype-environment interaction in growth and no clear differentiation among populations regarding budburst. No clear pattern of families coming from the northern latitudes growing better in the northernmost trial site and families from southern latitudes growing better in the southernmost field trials was observed either. Also, the growth and survival of the trees at the trial sites did not correlate with the climate of the original populations from where the families were selected. The lack of provenance specific climate response together with high genetic correlation across sites in growth, points towards that *P. avium* at its northern distribution range in Sweden occurs as one large breeding zone or has at least not yet reached an equilibrium based on a balance between divergent selection versus gene flow. Given the importance of the cherry fruits for humans, it is likely that *P. avium* has been introduced not just once but several times, which can also explain/support the finding of high levels of diversity in the northern part of the distribution range. The high genetic diversity and the selection response supports that continued tree improvement of this species in the region can be based on the identified and tested native genotypes.

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Author contribution Albin Lobo is responsible for data collection in Danish field trial, data analysis, and writing of manuscript.

Erik Dahl Kjær is the responsible for supervising the project and writing of manuscript.

Ditte Christina Olrik is responsible for the field trial in Denmark, data collection, and writing of the manuscript.

Lars-Göran Stener is responsible for the field trials in Sweden, data collection, and writing of manuscript.

Jon Kehlet Hansen is responsible for supervising the study, data analysis, and writing the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. Annu Rev Ecol Evol Syst 44:367–388

Arnaud-Haond S, Teixeira S, Massa SI, Billot C, Saenger P, Coupland G, Duarte CM, Serrão EA (2006) Genetic structure at range edge: low diversity and high inbreeding in southeast Asian mangrove (*Avicennia Marina*) populations. Mol Ecol 15:3515–3525

Augspurger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. Ecology 94:41–50

Breitbach N, Laube I, Steffan-Dewenter I, Böhning-Gaese K (2010) Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. Oecologia 162:965–976

Burdon RD (1977) Genetic correlation as a concept for studying genotype–environment interaction in forest tree breeding. Silvae Genet. 26:168–175

Cachi AM, Wünsch A, Vilanova A, Guárdia M, Ciordia M, Aletá N (2017) S-locus diversity and cross-compatibility of wild *Prunus avium* for timber breeding. Plant Breed 136:126–131

Channell R, Lomolino MV (2000) Dynamic biogeography and conservation of endangered species. Nature 403:84–86

Curnel Y, Jacques D, Nanson A (2003) First multisite clonal test of wild cherry (*Prunus avium* L.) in Belgium. Silvae Genet 52:45–51

Ding MM, Tier B, Dutkowski GW, Wu HX, McRae TA (2008) Multi-environment trial analysis on *Pinus radiata*: step by step to search "real" G×E interaction. N.Z. J For Sci 38:143–159

Ducci F, De Cuyper B, De Rogatis A, DufourJ SF (2013) Wild cherry breeding (*Prunus avium* L.). In: Pâques LE (ed) Forest tree breeding in Europe: current state-of-the-art and perspectives. Springer Netherlands, Dordrecht, pp 463–511

Dutkowski GW, Silva JC, Gilmour AR, Lopez AG (2002) Spatial analysis methods for forest genetic trials. Can J For Res 32(12):2201–2214

Eckert CG, Samis KE, Lougheed SC (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Mol Ecol 17:1170–1188

Fady B, Aravanopoulos FA, Alizoti P, Mátyás C, Wühlisch G, Westergren M, Belletti P, Cvjetkovic B, Ducci F, Huber G, Kelleher CT, Khaldi A, Kharrat MBD, Kraigher H, Kramer K, Mühlethaler U, Peric S, Perry A, Rousi M, Sbay H, Stojnic S, Tijardovic M, Tsvetkov I, Varela MC, Vendramin GG, Zlatanov T (2016) Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations. For Ecol Manag 375:66–75

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, Ed 4 edn. Longmans Green, Harlow

Ganopoulos I, Aravanopoulos FA, Argiriou A, Kalivas A, Tsaftaris A (2011) Is the genetic diversity of small scattered forest tree populations at the southern limits of their range more prone to stochastic events? A wild cherry case study by microsatellite-based markers. Tree Genet Genomes 7:1299–1313

Gapare W, Aitken S, Ritland C (2005) Genetic diversity of core and peripheral Sitka Spruce ((Bong.) Carr) populations: implications for conservation of widespread species. Biol Conserv 123(1):113–123

Gibson SY, Van Der Marel RC, Starzomski BM (2009) Climate change and conservation of leading-edge peripheral populations. Conserv Biol 23:1369–1373

Gilmour AR, Gogel BJ, Cullis BR, Thompson R (2009) ASReml user guide release 3.0 VSN International Ltd, Hemel Hempstead, HP1 1ES, UK. www.vsni.co.uk

Hamann A, Wang T, Spittlehouse DL, Murdock TQ (2013) A comprehensive, high-resolution database of historical and projected climate

surfaces for western North America. Bull Am Meteorol Soc 94(9): 1307–1309
Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett 8(5):461–467
Jankowska-Wroblewska S, Meyza K, Sztupecka E, Kubera L, Burczyk J (2016) Clonal structure and high genetic diversity at peripheral populations of *Sorbus torminalis* (L.) Crantz. iForest 9:892–900
Jolivet C, Höltken AM, Liesebach H, Steiner W, Degen B (2012) Mating patterns and pollen dispersal in four contrasting wild cherry populations (*Prunus avium* L.). Eur J For Res 131:1055–1069
Kendall MG, Stuart A (1979) The advantage theory of statistics. Vol. 2. Inference and relationship. Griffin and Co. London
Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle JR, Gomulkiewicz R, Klein EK, Ritland K, Kuparinen A, Gerber S, Schueler S (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecol Lett 15: 378–392
Kremer A, Potts BM, Delzon S (2014) Genetic divergence in forest trees: understanding the consequences of climate change. Funct Ecol 28: 22–36
Kreyling J, Constanze B, Sabrina B, Martin H, Gerhard H, Lukas H, Anke J (2014) Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus Sylvatica* L. as affected by temperature and extreme drought in common garden experiments. Ecol Evol 4:594–605
Lamy JB, Bouffier L, Burlett R, Plomion C, Cochard H, Delzon S (2011) Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. PLoS One 6:e23476
Lenormand T (2002) Gene flow and the limits to natural selection. Trends Ecol. Evol 17:183–189
Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conserv Biol 9:753–760
Lira-Noriega A, Manthey JD (2014) Relationship of genetic diversity and niche centrality: a survey and analysis. Evolution 68:1082–1093
Loveless MD, Hamrick JL (1984) Ecological determinants of genetic structure in plant populations. Annu Rev Ecol Syst 15:65–95
Martinsson O (2001) Wild cherry (*Prunus avium* L.) for timber production: consequences for early growth from selection of open-pollinated single-tree progenies in Sweden. Scand J For Res 16: 117–126
Mohanty A, Martin JP, Aguinagalde I (2001) A population genetic analysis of chloroplast DNA in wild populations of *Prunus avium* L. in Europe. Heredity 87:421–427
Muir G, Lowe AJ, Colin CF, Claus V (2004) High nuclear genetic diversity, high levels of outcrossing and low differentiation among remnant populations of *Quercus Petraea* at the margin of its range in Ireland. Ann Bot 93:691–697
Nadeau S, Meirmans PG, Aitken SN, Ritland K, Isabel N (2016) The challenge of separating signatures of local adaptation from those of isolation by distance and colonization history: the case of two white pines. Ecol Evol. 00:1–16. https://doi.org/10.1002/ece3.2550 8664
Petit RJ, Aguinagalde I, de Beaulieu JL, Bittkau C, Brewer S, Cheddadi R, Ennos R, Fineschi S, Grivet D, Lascoux M, Mohanty A, Müller-Starck G, Demesure-Musch B, Palmé A, Martín JP, Rendell S, Vendramin GG (2003) Glacial refugia: hotspots but not melting pots of genetic diversity. Science 300:1563–1565
Ramos G, Kirkpatrick M (1997) Genetic models of adaptation and gene flow in peripheral populations. Evolution 51:21–28
Rasmussen KK, Kollmann J (2007) Low genetic diversity in small peripheral populations of a rare European tree (*Sorbus torminalis*) dominated by clonal reproduction. Conserv Genet 9:1533–1539
Russell K (2003) In: EUFORGEN (ed) Technical Guidelines for genetic conservation and use for wild cherry (*Prunus avium*). International Plant Genetic Resources Institute, Rome, Italy, p 6
SAS Institute (2008) SAS/STAT 9.2 user's guide: the GLM procedure (book excerpt). SAS Institute
Satterthwaite FE (1946) An approximate distribution of estimates of variance components. Biometrics 2(6):110–114
Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. Annu Rev Ecol Evol Syst 38:595–619
Savolainen O, Kujala ST, Soko C, Pyhäjärvi T, Komlan A, Knürr T, Kärkkäinen K, Hicks S (2011) Adaptive potential of northernmost tree populations to climate change, with emphasis on Scots pine (*Pinus sylvestris* L.). J Hered 102:526–536
Sexton JP, Hangartner SB, Hoffmann AA (2014) Genetic isolation by environment or distance: which pattern of gene flow is most common? Evolution 68:1–15
Spitze K (1993) Population structure in Daphnia obtusa: quantitative genetic and allozymic variation. Genetics 135:367–374
Tukey JW (1958) Bias and confidence in not-quite large samples. Ann Math Stat 29(2):614–614
Vucetich JA, Waite TA (2003) Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conserv Genet 4:639–645
Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) Use of response functions in selecting lodgepole pine populations for future climates. Glob Change Biol 12(12):2404–2416
Welk E, de Rigo D, Caudullo G (2016) *Prunus avium* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European atlas of forest tree species. Publ. Off. EU, Luxembourg, pp.e01491d
Yakimowski SB, Eckert CG (2008) Populations do not become less genetically diverse or more differentiated towards the northern limit of the geographical range in clonal *Vaccinium stamineum* (Ericaceae). New Phytol 180:534–544
Yeh FC, Layton C (1979) The organization of genetic variability in central and marginal populations of lodgepole pine *Pinus contorta spp.latifolia*. Canad J Genet Cytol. 21:487–503