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1 **Using long-term data to reveal the geographical variation in timing and quantity of pollen and**
 2 **seed production in silver and pubescent birch in Finland: implications for gene flow,**
 3 **hybridization and responses to climate warming**

4

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13

14 **Abstract**

15 Silver (*Betula pendula*) and pubescent birch (*B. pubescens*) are the two main broad-leaved tree
 16 species in boreal forests and Subarctic areas, with great significance for both northern societies and
 17 ecosystems. Silver birch has more economical importance as it grows taller, but pubescent birch
 18 reaches much further North. The adaptability and genetic diversity of Subarctic birch populations
 19 are assumed to derive from inter- and intraspecific hybridization. Southern pollen clouds could in
 20 turn increase the adaptability of northern populations to warming climate. In the boreal forest zone
 21 of warmer climate, incompatibility reactions may prevent interspecific hybridization and much
 22 depends on the synchrony of flowering. Direct in situ observations are, however, mostly lacking

and earlier results concerning the spatial and temporal match of flowering phenology between the species are contradictory. Conclusions based on pollen catches may also be biased as the pollen of silver and pubescent birch are notoriously difficult to sort out and the geographical origin of pollen is virtually impossible to determine. Here we employ direct flowering observations and reanalyze old pollen and seed production data, collected along a South-North gradient in Finland, to shed more light on these issues. Our results suggest that interspecific hybridization is an unlikely mechanism of adaptation in silver and pubescent birch as there is no significant overlap in flowering either near Subarctic or in more southern boreal areas (covering latitudes 60– 68° N). Long-distance southern gene flow also unlikely has importance in the adaptation of northern populations to a warming climate as heat sum requirements for flowering in northern and southern populations are equal and northern birches are therefore not receptive at the time of southern flowering. Long-term data of pollen and seed production in turn suggest that pubescent birch is more effective in seed production through the whole South-North gradient, but increasingly so towards the North. However, it appears that this difference is not due to silver birch flowering and regeneration being more sensitive to interannual variation as earlier suggested. Although there are more factors than reproduction alone that can affect species distributions, these two findings indicate that climate warming may not significantly alter the relative abundances of silver and pubescent birch in Subarctic Fennoscandia.

keywords: *Betula pendula*, *Betula pubescens*, adaptability, global warming, gene flow, hybridization, pollen

44 **Introduction**

45 Gene flow is one of the key processes that shape the genetic composition of tree populations.
 46 Addition of alien genes to populations of trees can lead to unfavorable, neutral or favorable changes
 47 depending on the source population (Lenormad 2002, North et al. 2010). Under climate warming,
 48 intraspecific gene flow from South to North can be important in adaptation to warming
 49 temperatures in the North, as suggested by the modeling work with Scots pine (*Pinus sylvestris*;
 50 Savolainen et al. 2007). Also, it has been suggested that interspecific gene flow between sister
 51 species and introgression support adaptation to extreme environments in many taxa (Lewontin &
 52 Birch 1966, Baskett & Gomulkiewicz 2011), including birches at their northern limits (Kallio et al.
 53 1983, Salojärvi et al. 2017).

54 Silver birch (*Betula pendula*) and pubescent birch (*Betula pubescens*), hereafter referred to as white
 55 birches, are the main broad-leaved tree species in European and Asian boreal forests, where their
 56 responses to environmental changes seem to closely accompany general ecosystem level responses.
 57 Their geographical distributions are mostly overlapping and both species occur at lower altitudes in
 58 most parts of boreal Eurasia (Atkinson 1992). Pubescent birch extends to more northern and higher
 59 sites (Hultén 1971), while silver birch is only sporadically found in Fennoscandia and Russia north
 60 of 67–68° N. Both species thrive on moraine and sandy soils, but silver birch often dominates dryer
 61 soils while pubescent birch is more common in organic soils and moist habitats. White birches are
 62 monoecious, with male and female flowers in different catkins. Silver birch is diploid ($2n=28$) and
 63 pubescent birch tetraploid ($2n=56$). The origin of pubescent birch is still open; it may be an
 64 autotetraploid of silver birch, or an allotetraploid with silver birch as one and possibly, *B. humilis* as
 65 another parent (Howland et al. 1995).

66 White birches are known for their capacity to produce enormous amounts of light pollen, which in
 67 turn is one of the furthest transported pollen grains (Hjelmroos 1991, Sofiev et al. 2006). Long

distance transport covering several hundred kilometers is common. For instance, in northern Finland catches of birch pollen before local flowering can exceed local pollen production (Hicks et al. 1994, Oikonen et al. 2005). However, maximum distances of effective gene flow are difficult to verify for tree species with such dense populations and wide distribution as white birches. While some studies suggest that gene flow can effectively reduce variation among birch populations (Rusanen et al. 2003; Järvinen 2004), others conclude that efficient movement of pollen clouds can range some tens or hundreds of meters only (Sarvas 1952, 1956, Whitehead 1969, Andersen 1970, Koenig & Ashley 2003, for review see Ashley 2010). The gradual decrease of silver birch abundance towards the North could be expected to lead to pollen limitation, but it appears that pollen limitation is actually more common in mountainous populations of pubescent birch (Holm 1994). Northern seed production, on the other hand, appears to be more limited by resources in silver compared to pubescent birch (Holm 1994).

Apparently, gene flow largely depends on the flowering phenology of populations. In white birches, spring heat accumulation (temperature sum) determines the phenology of bud burst and flowering in spring, which in white birches occurs almost simultaneously (Rousi & Heinonen 2007, Rousi et al. 2011). However, many tree species also show fine-scale adaptation to the length of the frost free growing season (Frewen et al. 2000); southern populations of *Betula alleghaniensis*, *B. lenta* and *B. pendula* in common garden experiments tend to flush later compared to northern populations (Pauley and Perry 1954, Sharik & Barnes 1976, Junttila et al. 2003, Li et al. 2002). Smaller heat sum requirement of flowering in northern birches could enlarge the phenological window for southern pollen and thus enhance their adaptability to a warming climate. To confirm this, however, more research is needed concerning the match of flowering phenology in southern and northern areas.

Interspecific hybridization of birches was thought to be rare and to take place at the northern limits of their distribution only, since studies suggested synchronous flowering only above the Arctic

93 Circle (Kallio et al. 1983). However, more recent results have contradicted the idea of a
94 phenological barrier and the timing of pollen anthesis in white birches has been suggested to be
95 largely synchronous also in southern latitudes of 60–67 °N (Luomajoki 1999, Linkosalo et al.
96 2010). Supporting these results, studies of birch chloroplast DNA suggest that large-scale
97 interspecific hybridization of birches took place during postglacial colonization (Palmé et al. 2004).
98 And while some results suggest that interspecific hybridization is prevented by incompatibility
99 reactions (Hagman 1971), cold subarctic weather has been suggested to suppress such reactions
100 (Kallio et al. 1983)

101 Studies of duration and intensity of flowering in white birch populations have commonly been
102 based on data from pollen samplers (Sarvas 1952, Luomajoki 1999, Linkosalo et al. 2010). Early
103 studies by Sarvas (1952) suggest that pubescent birch flowers on average one week later compared
104 to silver birch, whereas more recent work by Luomajoki (1999) and Linkosalo et al. (2010) suggest
105 longer duration and a near complete overlap of the pollen season for the two species. These later
106 studies also, rather unexpectedly, show a tendency of increasing heat sum requirement for spring
107 phenology in silver birch when moving towards the North.

108 A difficulty and a potential source of error in studies with white birch pollen is that pollen cannot be
109 identified to species-level, let alone to origin (Clausen 1960, Prentice 1981, Birks 1986, Mäkelä
110 1996); apparently a serious obstacle with species, which have easily transported pollen. Here, we
111 suggest that this dilemma could be resolved by defining a window for ex situ pollen from sampler
112 data using temperature data (i.e. heat sum accumulation or temperature sum), as the timing of silver
113 birch pollen anthesis can be reliably predicted using spring heat sum accumulation (Rousi et al.
114 2011). Using this approach, we take another look at the data presented by Luomajoki (1999) and
115 Linkosalo et al. (2010).

116 We hypothesize that this re-analysis will show that (1) birches growing in southern Finland always
 117 flower earlier than those growing in the North. Nonetheless, because northern populations require a
 118 smaller heat sum and there is large interannual variation in temperatures, gene flow from southern
 119 to northern locations, or vice versa, might be possible in some years. Following the early results,
 120 which showed virtually no interspecific overlap in local flowering schedules (Sarvas 1952), we
 121 further hypothesize that (2) silver and pubescent birch have different flowering schedules, largely
 122 preventing local interspecific hybridization. As a potential explanation for the gradual increase of
 123 pubescent birch dominated stands towards the North, we also predict that (3) there is no difference
 124 in reproductive investment (amount of pollen and seeds produced) between the two species in
 125 southern Finland, whereas in northern Finland, pubescent birch is more efficient. Finally, we utilize
 126 the data to test the hypothesis that (4) the proportion of silver birch is lower in the North because
 127 reproduction of silver birch is more sensitive to environmental variation (Holm 1994). If supported,
 128 the latter two hypotheses would suggest that a warming climate could increase the relative
 129 proportion of silver birch in the North.

130 **Material and methods**

131 The pollen anthesis, flowering and seed production data sets used here were collected by late
 132 professor Risto Sarvas, whose untimely death did not allow him to publish the data. The long-term
 133 measurements of the quantity of flowering and seed crop were available in Koski and Tallqvist
 134 (1978), while the calculations of pollen anthesis are based on the original data. Since spring
 135 phenology of trees, silver birch in particular (Rousi and Heinonen 2007, Rousi et al. 2011, Basler &
 136 Körner 2012), is driven by temperature (e.g. Hänninen & Tanino 2011), we calculated heat sum as
 137 growing degree days (dd) using a 5 °C threshold. This value is commonly used to evaluate
 138 phenology, also in silver birch (e.g. Hunter et al. 1992, Rousi et al. 2011). Temperature sum is the
 139 daily mean temperature above a threshold value (here +5°C), summed over a year, expressed in

140 degree days (dd)). In Finland, heat sum accumulation may in a warm spring day be more than 15
 141 dd, but cold periods of 1–2 weeks without heat sum development are also possible.

142 *Silver birch pollen data*

143 For silver birch, the pollen was collected in 1964–1973 in nine tree stands using one to three
 144 rotating, tree-top level pollen samplers (Sarvas–Vilksa) at each stand (Sarvas data). The two
 145 southernmost stands were by the Gulf of Finland in Hammarland and Bromarv (60°02'–60°14' N),
 146 four stands in southern Finland in Hartola, Punkaharju, Kerimäki and Vilppula (61°45'–62°04' N),
 147 two northern stands at the Arctic Circle in Rovaniemi (XXI and XXVIII; 66°21' N) and the
 148 northernmost stand in Kittilä in the world's northernmost natural silver birch stand (67°44' N). In
 149 Punkaharju, pollen was collected every year, while at other stands the time series cover 5–9 years.
 150 One data point in Hammarland and three in Rovaniemi were excluded from the analyses because of
 151 minimal pollen production. Unlike Luomajoki (1999), we also excluded the 10-year time series
 152 available for a curly birch (*B. pendula* var. *carelica*) stand in Punkaharju (stand LXIII). Also, the
 153 original data indicate large and seemingly random, interannual variation in the onset and
 154 termination of pollen collection both in terms of days and temperature sums. For instance, in the
 155 southern locations recordings of anthesis started at 1–30 dd and terminated at 68–163 dd. In the
 156 North, observation periods had less interannual variation and recordings terminated mostly at 90–
 157 100 dd.

158 Pollen sampler data can include both in situ and ex situ conspecific and heterospecific pollen.
 159 Conspecific ex-situ pollen is generally impossible to distinguish and in the case of silver birch and
 160 pubescent birch even heterospecific pollen cannot be reliably sorted out in large pollen samples. To
 161 our best knowledge, so far no effort has been made to sort out species in the present material. In a
 162 recent long-term data set of daily phenology observations for 30 silver birches, the lowest heat sum
 163 for the onset of anthesis (for any tree) was 32 dd and the highest heat sum for the termination of
 164 anthesis 82 dd (Rousi et al. 2011). To exclude heterospecific local pollen and long distance

165 conspecific pollen from the silver birch pollen data, we therefore delimited the 1964–73 pollen
 166 catches to a heat sum area of 30–90 dd and additionally shortened the tails of the 30–90 dd heat sum
 167 area by omitting dates when <5% and >95% of pollen were obtained (for shortening the tails see
 168 Dahl & Strandhede 1996, Ranta et al. 2006, Ranta & Satri 2007).

169 *Timing of anthesis and pollen catch for both species*

170 For pubescent birch, the timing of anthesis was visually observed for two phenotypes growing in
 171 the same stand, for the same years (1998–2004), using the same methodology (our own direct daily
 172 observations of the canopy) as in Rousi et al. (2011). This allows direct comparisons with
 173 concurrent silver birch phenology. A 10-year data set (1964–73) of daily pollen catch was also
 174 available for both species from two stands growing on mineral soils in Punkaharju less than 2 km
 175 apart.

176 *Quantity of pollen and seed production for both species*

177 Quantity of flowering and seed crop was measured in 1955–1973 using metal funnels (opening 0.05
 178 m²) set up in pure, mature birch stands (6–10 funnels in each stand) in different parts of Finland
 179 (61–68° N). Cloth bags, attached to the base of each funnel, were emptied once a month and the
 180 remains of male flowers were sorted out of the accumulated litter, dried at 105 °C and weighed. The
 181 quantity of shed pollen was then estimated for both species by multiplying the mass of male flower
 182 residue by 0.27 (Sarvas 1962).

183 To study the magnitude of interannual variation in anther and seed production in silver and
 184 pubescent birch populations at the same geographical locations, we utilized the long-term data sets
 185 available in Koski and Tallqvist (1978): i.e. a 13-year data set for southern Finland (Punkaharju), a
 186 17-year data set for northern Finland (Arctic Circle, Rovaniemi) and a 10-year data set for the
 187 location of northernmost silver birch stand (Kittilä).

188

189 **Results**

190 *Delimitation of 1964-1973 silver birch pollen records*

191 Delimiting silver birch pollen catches using the heat sum range 30–90 dd rejected part of catches in
 192 21% of the 120 observations. In Punkaharju, for example, the interannual variation of starting
 193 pollen collection was large (0 dd in 1967 and 1973, 27 dd in 1965), and the same is true for ending
 194 the recordings (73 dd in 1965, 138 dd in 1973). In coastal Bromarv, 55% and 16% of the total
 195 pollen catch was rejected in 1967 and 1971, respectively. Although the quantity of pollen rejected
 196 was generally very small, the impact of delimitation on the length of the pollen period was
 197 considerable. In Bromarv, for example, the time range of first and last pollen observation during the
 198 7-year observation period was reduced from 5 weeks (Luomajoki 1999) to two and half weeks by
 199 omitting those pollen catches, which based on current knowledge concerning the drivers of white
 200 birch phenology are unlikely to have originated from local silver birch stands. Shortening the tails,
 201 i.e. omitting periods of <5% and >95% of the cumulative pollen catch, had only a minimal impact
 202 on the duration of pollen period or the quantity of pollen collected. Also, shortening the tails had
 203 virtually no impact on the day when $\geq 50\%$ of the pollen was caught: in only 1.6% of cases the time
 204 was adjusted by one day.

205 *Phenological variation among and within silver birch populations across Finland*

206 Differences between coastal ($\sim 60^\circ$ N) and southern ($\sim 62^\circ$ N) silver birch populations in their
 207 interannual variation of onset and termination of pollen anthesis were small (Fig. 1). The range over
 208 years was April 30 –May 28 for coastal and May 10–28 for southern populations (Fig. 1). Peak
 209 pollen catch and the mean (50%) of anthesis took place May 17, on average (Fig.1, Table 1).
 210 Northern populations (67° N) had their anthesis about three weeks later, the range being May 29 –
 211 June 17 (Fig. 1). Both peak pollen catch and the mean of anthesis in these populations was June 4,
 212 on average (Fig. 1, Table 1). As a result, in every year the pollen was collected, the anthesis in the
 213 North started after pollen production in the South had terminated (Fig. 1). In the North, no pollen

214 was caught before 30 dd, thus only pollen caught after 90 dd was rejected. Dates of maximum
 215 pollen catch and 50% anthesis were the same in 64% of cases, the mean deviation between these
 216 two incidents being 0.7 d. The heat sum requirement for flowering was lower in the coastal stands
 217 (on average 50 dd) than in all other stands (on average 57 dd), but the southern inland and northern
 218 stands did not seem to differ (Table 1).

219

220 **Table 1.** Date and heat sum (dd) requirement of mean (50%) anthesis in nine silver birch stands
 221 ranging from Coastal (Bromarv and Hammarland), South (Hartola, Punkaharju, Kerimäki and
 222 Vilppula) to North (Rovaniemi and Kittilä) Finland.

223

224	Birch stand	Latitude	Date	dd	Observation years
225	Bromarv	60° 02'	May 16	49	7
226	Hammarland	60° 14'	May 18	50	4
227	Hartola	61° 45'	May 18	56	5
228	Punkaharju	61° 49'	May 17	57	10
229	Kerimäki	61° 50'	May 18	58	9
230	Vilppula	62° 04'	May 16	56	5
231	Rovaniemi XXI	66° 21'	June 3	58	7
232	Rovaniemi XXVIII	66° 21'	June 4	63	7
233	Kittilä	67° 44'	June 4	54	6

Figure 1. Duration of pollen period in coastal (C, 60°N), South (S, 61–62°N) and North Finland (N, 66–68°N) based on pollen catch data (the three dots denote the onset of pollen period, the day of peak pollen catch and the termination of pollen period).

Phenological differences between silver birch and pubescent birch in southern Finland

Based on the visual 6-year in situ observations in Punkaharju (southern Finland), silver birch was on average 5 d earlier in the onset and termination of anthesis compared to pubescent birch, with a heat sum difference of 25–30 dd (Table 2). In 2003, there was no overlap in pollen production between the species, while in other years, some of the latest flowering silver birches had a 1-d overlap with earliest pubescent birches.

Table 2. Interannual variation of date and heat sum (dd) for the onset and termination of pollen anthesis in silver birch and pubescent birch growing in the same forest stand in Punkaharju, South Finland (data for silver birch from Rousi et al. 2011; n.m. = not measured).

		Onset				Termination			
		Silver birch		Pubescent birch		Silver birch		Pubescent birch	
		Date	dd	Date	dd	Date	dd	Date	dd
1998		May 11	48	May 18	89	n.m.		n.m.	
2000		May 1	42	May 10	69	May 5	49	May 12	72
2002		May 2	48	May 4	67	May 3	58	May 5	69
2003		May 12	41	May 15	69	May 14	61	May 23	125
2004		May 5	41	May 8	71	May 7	60	May 10	84
2005		May 21	47	May 23	69	May 24	82	May 25	94
Mean		May 8	45	May 13	72	May 10	62	May 15	88

According to pollen captured in 1964-1973, the heat sum requirement for mean (50%) anthesis was on average 57 dd for silver birch and 75 dd for pubescent birch, which corresponds to an average of a 6-d difference (Table 3). The length of overlap of pollen periods between the two species had, however, large interannual variation (Table 3). For instance, a rapid accumulation of heat sum apparently led to a small difference in days, but not in heat sum requirement (e.g. years 1966, 1972 in Table 3), and in the year of exceptionally late flowering for silver birch (1971), a cool spell before main flowering evidently delayed silver birch, but not pubescent birch, leading to simultaneous flowering of the two species. In contrast, there was no overlap in flowering in 1965 and the difference between the species in mean anthesis was almost three weeks (Table 3). The day of mean anthesis seemed to reliably reflect the timing of in situ flowering: in most years, the days of

peak pollen catch and the days of mean anthesis coincided and the mean difference of these two observations was 0.5 and 0.7 d for silver birch and pubescent birch, respectively.

Table 3. Heat sum (dd) needed for mean anthesis (50% pollen production) for silver birch and pubescent birch in Punkaharju, South Finland in 1964-73, difference of mean anthesis between the species in terms of heat sum (dd) and days, and the proportion of pubescent birch pollen produced by mean silver birch anthesis.

Year	Mean anthesis (dd)		Difference		Pubescent birch pollen produced	
	Silver birch	Pubescent birch	dd	days	by mean silver birch anthesis (%)	
1964	55	67	12	3	18	
1965	56	82	26	19	0	
1966	61	74	13	1	23	
1967	48	63	15	3	12	
1968	52	77	25	11	13	
1969	57	83	26	13	10	
1970	55	74	19	5	22	
1971	75	76	1	2	34	
1972	65	73	8	1	41	
1973	50	81	31	4	11	
Mean	57	75	20	6.2	18	

294 The quantity of silver birch pollen that we rejected based on the 30-90 dd heat sum range was very
 295 small, on average 3% of total pollen (Table 4). This was mostly because small amounts of pollen
 296 were detected after 90 dd, and only in one year (1967) a larger amount of pollen (11%) was
 297 observed earlier than 30 dd (Table 4). On average 89% of pubescent birch pollen was produced
 298 before 90 dd, but in 1964 and 1971 almost one third of pollen was caught after 90 dd (Table 4).

299

300 **Table 4.** Interannual variation in the proportion of silver birch pollen caught within the heat sum
 301 range 30–90 dd, and the proportion of pubescent birch pollen caught after 90 dd and after silver
 302 birch pollination in forest stands growing in Punkaharju, South Finland.

303

304	% of silver birch pollen caught		% of pubescent birch pollen caught	
	305 Year	within 30–90 dd	after 90 dd	after silver birch pollination
306	1964	100	27	27
307	1965	100	11	60
308	1966	98	4	4
309	1967	88	2	2
310	1968	98	14	14
311	1969	100	14	35
312	1970	100	8	15
313	1971	93	27	2
314	1972	98	12	7
315	1973	96	18	18
316	Mean	97	11	18

317

318

319 *Pollen and seed production of silver and pubescent birch across Finland*

320 Interannual variation ($n = 10$ years) of pollen production correlated strongly and positively with
 321 interannual variation of anther residual production in silver birch populations in Punkaharju ($r =$
 322 0.87) and Rovaniemi ($r = 0.91$) and in a pubescent birch population in Punkaharju ($r = 0.95$).
 323 Variation of anther residual production was further positively correlated, not only among stands of
 324 the same species, but among stands of different species, both in the North ($r = 0.87$ – 0.94 , $n = 17$ for
 325 two pubescent birch stands and one silver birch stand in Rovaniemi; $r = 0.73$, $n = 10$ for one stand
 326 of both species in Kittilä) and in the South ($r = 0.87$ – 0.95 , $n = 13$ for two pubescent birch stands and
 327 one silver birch stand in Punkaharju). The corresponding correlations for seed production were even
 328 stronger ($r = 0.96$ – 0.97). Finally, the interannual variation of anther residual production was
 329 strongly correlated with the variation of seed production for both species both in the South and the
 330 North (Fig. 2). In the South, the anomaly of relatively low seed production following the highest
 331 production of anther residuals is explained by June and July precipitation, which in Punkaharju in
 332 1964 covered one third of the 1961–1991 climate normal only (i.e. drought). In the North, the silver
 333 birch stand in Kittilä showed poorer anther residual–seed correlation than the stands in general (Fig.
 334 2).

335

336 **Figure 2.** Correlation of anther residual and seed production across years in silver birch (black dots)
 337 and pubescent birch (white dots) stands (identified by roman numerals when applicable) in South
 338 (Punkaharju, $n = 13$ years) and North Finland (Rovaniemi, $n = 17$; Kittilä, $n = 10$). Data is from
 339 Koski and Tallqvist (1978).

340

341 For both species, the pollen (estimated using the mass of collected anther residuals) and seed
 342 production were 6-10 times higher in southern Finland than near the Arctic Circle (Table 5, Fig. 3).

343 However, interannual variation (measured as coefficient of variation among the years) was large in
 344 all stands and for both anther residual and seed production (Table 5, Fig. 3). The variation was
 345 generally larger in northern compared to southern stands except for the production of anther
 346 residuals, which did not vary more in Kittilä than in Punkaharju (Table 5). Intraspecific differences
 347 among stands were also significant; e.g. production of anther residuals was 98% and production of
 348 seeds 45% higher in pubescent birch stand XVII than in stand XX, although both are situated in
 349 Rovaniemi (Table 5). It appears that the two species did not generally differ in pollen production,
 350 but pubescent birch produced more seeds than silver birch across Finland and was therefore always
 351 more effective in seed production (i.e. in the number of seeds produced per unit of pollen) (Table 5,
 352 Fig. 3).

353

354 **Table 5.** Mean production (with the coefficient of variation, CV of yearly records in brackets) of
 355 anther residuals (g m^{-2}) and seeds (number m^{-2}) and the mean reproduction efficiency (number of
 356 seeds produced per g anther residuals) in pubescent and silver birch forest stands in Punkaharju,
 357 South Finland (a record of 13 years), and Rovaniemi (17 years) and Kittilä (10 years), North Fin-
 358 land.

		Pubescent birch			Silver birch		
		Anther	Seeds	Eff	Anther	Seeds	Eff
361	Punkaharju XIV	14.1 (79)	106000 (83)	7500	13.8 (85)	48000 (83)	3500
362	Punkaharju LXII	10.8 (76)	66000 (101)	6100			
363	Rovaniemi XX	1.37 (95)	10400 (117)	7600	2.45 (106)	4800 (128)	1900
364	Rovaniemi XVII	2.71 (84)	15000 (116)	5500			
365	Kittilä	1.37 (77)	6200 (116)	4500	1.26 (77)	4000 (116)	3200

Figure 3. Interannual variation of anther residual and seed production for silver birch (dashed line) and pubescent birch (continuous line) stands (identified by roman numerals when applicable) in South (Punkaharju) and North Finland (Rovaniemi and Kittilä). Data is from Koski and Tallqvist (1978); note the different scales in South and North Finland graphs.

Discussion

As a drastic environmental change, the ongoing climate warming requires high adaptability of the boreal and Arctic tree species. In this study, we examined if the adaptation of white birches – i.e. silver birch and pubescent birch – in the North could be enhanced by gene flow from the South or interspecific hybridization, and if the current dominance of pubescent birch in the North is due to the reproduction of silver birch being more adversely affected by northern conditions. Our data

378 suggest that white birches growing in southern Finland always flower earlier than those growing in
 379 the North. Also there appears to be no significant overlap in local flowering schedules among the
 380 boreal populations of the two species. These results suggest that gene flow from the South and
 381 interspecific hybridization likely play a minor role in the adaptation of white birches to the present
 382 climate warming. Contrary to our expectations, we found that pubescent birch produces
 383 significantly more seeds and has a higher reproduction efficiency than silver birch, not only in the
 384 North, but also in southern Finland. Also, based on the interannual variation in pollen and seed
 385 production among years, the susceptibility of the two species to interannual weather variation does
 386 not significantly differ. Together, this suggests that the current dominance of pubescent birch in the
 387 far North is not due to the reproduction of silver birch being more adversely affected by the
 388 northern climate. This in turn indicates that climate warming may not significantly alter the relative
 389 abundances of silver and pubescent birch in Subarctic Fennoscandia.

390 *Timing of anthesis in southern and northern silver birch populations*

391 Long distance gene flow is often thought to increase the ability of anemophilous species, such as
 392 birches, to adapt to global change. Our data suggest that long distance (100–200 km) gene flow
 393 among silver birch populations is possible in southern Finland as not only the onset of pollen
 394 season, but also the timing of main pollen production of southern inland and coastal stands showed
 395 a good match. However, contrary to earlier results with birch (Sharik & Barnes 1976, Junttila et al.
 396 2003, Li et al. 2002) and other species (Beuker 1994), it appears that heat sums needed for silver
 397 birch flowering are equal all over Finland, which means that there is no phenological overlap
 398 between southern and northern birch populations. This suggests that, at least for birches, gene flow
 399 between the southern (60–62° N) and northern (66–67° N) populations is unlikely. On the other
 400 hand, the regional phenological patterns that occur in present climatic conditions may change under
 401 climate warming (Ruosteenoja et al. 2011) and subsequently, adjust the present interpopulation
 402 flowering synchrony.

403

404 Apart from the lack of phenological overlap in flowering between the southern and northern birch
 405 populations, other reasons also speak against effective south-north gene flow. First, movement of
 406 pollen clouds depends on complex dynamics of atmosphere (Solomon 2002) and pollen quantities
 407 usually fall exponentially with distance (Sarvas 1952, 1956). Second, the frequency of male and
 408 female catkins is -at least in silver birch- strongly and positively correlated (Rousi et al. 2011). As a
 409 result, in good flowering years, prolific local pollen production hinders the possibilities of ex situ
 410 pollen, whereas in years of low flowering, the success of ex situ pollen is reduced by pollen dilution
 411 and low frequency of female flowers. Third, very little is known of the tolerance of pollen to high
 412 altitude climatic conditions, but it appears that fertility of birch pollen deteriorates easily because of
 413 unfavorable abiotic conditions and even prolonged flowering can reduce germinability (Saarnijoki
 414 1941, Friedman & Barret 2009).

415 *Flowering phenology of co-occurring silver and pubescent birch populations*

416 The pollen catch data that we used suggest that the mean difference of flowering time between
 417 silver and pubescent birch in warm springs is only a few days and that in most years pubescent
 418 birch produces a substantial amount of pollen at the end of silver birch flowering. In situ
 419 observations of catkins, in contrast, show a minor overlap in flowering phenology even when the
 420 species grow at the same site and therefore, suggest low likelihood for silver and pubescent birch
 421 hybridization in present climatic conditions in Finland. When pondering the reliability of the pollen
 422 catch data, it is good to note that we used very conservative heat sum delimitation (i.e. the largest
 423 observed heat sum for silver birch anthesis with a safety margin). As a consequence almost all
 424 (90%) pollen collected in the southern pubescent birch stand remained in the data. Nevertheless,
 425 even if we had used the mean heat sum for the onset of pubescent birch flowering (72 dd, Table 2),
 426 still only 50% of pubescent birch pollen (yearly variation 28–79%) would have been omitted.

427 The discrepancy between the shorter duration of flowering in direct observations of silver birch
 428 catkins and the longer duration estimated from pollen catch data suggests that pollen catch data can
 429 have risks when concluding the duration of birch pollen period. The pollen recordings in southern
 430 Finland suggest occasional days of pollen sharing, which are mostly late pollen peaks in silver birch
 431 stands accompanied by simultaneous abundant pollen production in a nearby pubescent birch stand.
 432 Exceptionally late pollen recordings in southern stands may, however, be due to drifting pollen
 433 from the North in years of exceptionally prolific pollen production all over Finland (e.g. 1964 and
 434 1971). Earlier studies did not make an effort to distinguish heterospecific and conspecific ex-situ
 435 and in-situ pollen. This is a likely explanation for the longer estimate of 15 d for the duration of
 436 silver birch pollen period in Linkosalo et al. (2010) in comparison to the estimate of 7 d in the
 437 present study and 6 d in visual in-situ observations (Rousi et al. 2011). Drifting pollen (see Sarvas
 438 1952) may also be the main reason why silver birch and pubescent birch flowering periods were
 439 suggested to be almost identical by Luomajoki (1999) and Linkosalo et al. (2010). This suggestion
 440 is not supported by our findings, and while the explanation for this discrepancy may largely be
 441 pollen mixing, it could also partly originate from the different proportion of northern populations
 442 among the examined silver birch and pubescent birch populations (Linkosalo et al 2010). All in all,
 443 it appears that because pollen movements are unpredictable and no reliable methods, despite recent
 444 advances in pollen analyses (Heidmann et al. 2016), are available for separating the pollen of the
 445 two birch species on a practical scale (Jenyts-Szaferowa 1928, Mäkelä 1996 and references therein),
 446 pollen catch data should not be used to estimate silver birch and pubescent birch flowering
 447 phenology. Direct observations of flowering phenology are more reliable and not hindered by
 448 methodological issues.

449 *Reproduction of silver and pubescent birch in the North*

450 We speculated that the dominance of pubescent birch over silver birch in the Subarctic
 451 Fennoscandian forests might be explained by its more effective reproduction in the far North.

452 However, it appears that pubescent birch produces more seeds and has a higher efficiency of
 453 reproduction (with respect to seeds produced per unit pollen) than silver birch already in southern
 454 boreal forests. Therefore, although there is a trend of difference in the efficiency of reproduction
 455 between the species growing towards the North, other factors are clearly needed to explain the
 456 northern dominance of pubescent birch. Long-term, over 40-year old tree line common gardens near
 457 the Kevo Subarctic field station of the University of Turku (70° N) show that transplanted silver
 458 birches of more southern origin can, not only acclimate, but also be superior in growth compared to
 459 other white birches (pers. obs.). During centuries, this may have led to selective cutting, thus
 460 diminishing silver birch occurrence. Silver birch regeneration is also effectively prevented by
 461 reindeer grazing in the North as illustrated by reindeer exclosures at sites suitable for silver birch
 462 (pers. obs.). Generally, the efficient reproduction may though explain why pubescent birch, and not
 463 silver birch, was the first to invade Northern Europe after the ice age.

464 Our data show how intrapopulation variations in reproduction can be large (compare the two
 465 pubescent birch populations in Punkaharju and Rovaniemi, Table 5) in spite of no apparent
 466 difference between the sites (same dominant tree height and age) and climatic conditions
 467 (measurements carried out in common years). This is clearly a caveat in species comparisons, which
 468 are based on a few tree stands, and cannot be compensated by temporally extensive data sets. For
 469 instance, the interspecific difference in reproduction efficiency (as measured by seed production) at
 470 the very northern site in Kittilä is surprisingly small when compared to the difference in Rovaniemi.
 471 This is likely to be explained by an unrepresentative Kittilä pubescent birch stand, which produced
 472 a significantly smaller seed set by using double amount of pollen than another, nearby stand (Koski
 473 and Tallqvist 1978). We did not measure the quality of seeds, but interspecific differences may not
 474 be large (Sarvas 1955, Holm 1994) although Sarvas (1952) suggested that seed germinability
 475 increases exponentially with pollen quantity. Relating to this observation, it could be that the

476 relatively larger pollen production of silver birch in the North is needed to maintain seed
 477 germinability in places, where birch stands are dominated by pubescent birch.

478 We expected the interannual variation in heat sum to have the strongest effect on reproduction at the
 479 tree limit of silver birch – the average heat sum in Kittilä is only half that in Punkaharju – but found
 480 the main leap in interannual variation in pollen and seed production between Punkaharju and
 481 Rovaniemi and no further increase between Rovaniemi and Kittilä. The reason could be that many
 482 environmental parameters, over and above heat sum, have significant effects in the marginal areas
 483 of species distributions as recently found for Scots pine survival and growth (Rousi et al. 2018).
 484 Based on the conclusions by Holm (1994), we further expected that in the far North, silver birch is
 485 more reliant on favorable circumstances for large seed production than pubescent birch. However,
 486 our material suggests that there is no difference between the species in this respect; i.e. there is no
 487 difference in coefficients of variation of yearly records in anther and seed production in Kittilä. If
 488 anything, it appears that the interannual variation of reproduction is higher for silver than pubescent
 489 birch at the Arctic Circle. While these results need to be treated with caution as the comparisons are
 490 based on one or two stands only, they seem to suggest that in the far North silver birch reproduction
 491 is not more vulnerable to the interannual weather variation than the reproduction of pubescent birch.
 492 As a result, the ongoing climate change may not significantly affect the relative abundance and
 493 distribution of silver and pubescent birch in the North through altering the differences in their
 494 reproductive output.

495

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