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Insights into historic and genetic relationships of diverse common lilac (*Syringa vulgaris*) genotypes based on whole-genome profiling

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Abstract

Common lilac (*Syringa vulgaris* L.) is a popular landscaping plant. Our aim was to obtain a large set of SNP markers, to reveal the precise identities of the investigated *S. vulgaris* accessions, and to discover genetic relationships among them. The studied plant material included local Finnish, previously unidentified accessions, known reference cultivars, and so-called historical accessions i.e., old shrubs growing in historic cultural landscapes. We intended to verify cultivar names for some valuable local common lilac accessions and to provide insights into the history of common lilac cultivation in Finland. In the analyses, we used a set of 15,007 SNP markers. First, polymorphic information contents (PIC) were calculated (mean 0.190, range 0.012-0.500 per marker). Then, to investigate genetic relationships among genotypes, a phylogenetic tree was constructed, and a principal coordinate analysis (PCoA) was conducted. A Bayesian analysis of population structure was performed to determine the number and distribution of genetic clusters among samples. Genetic marker data combined with existing historical and phenotypic knowledge revealed novel information on the unidentified cultivars and on the genetic relationships among studied accessions and solved the arrival and early history of common lilac in Finland. Overall, such comprehensive genomic characterization and deep understanding of genetic relationships of *S. vulgaris* can be used when utilizing present cultivars and developing new ones in future breeding programs.

Key words:

cultivar identification**,** garden history**,** genetic relationships**,** phenotypic data, SNP markers**,** whole-genome profiling

Introduction

Common lilac (*Syringa vulgaris* L.) is a popular ornamental shrub in the family Oleaceae. The species is native only to the Balkan Peninsula, from Central Albania to Romania (Govaerts, 2020), where it grows in mountain crevices and on rocky hills. Despite its European origin, common lilac was first introduced into cultivation in the geographical area of modern Turkey, from where it was brought to European gardens around mid-sixteenth century (Lack, 2000). The lilac was cherished for its lovely, sweet-scented flowers, and since the shrub is easy to propagate by root suckers, common lilac was soon spread into Central Europe. In one hundred years, it had reached Denmark (Lange, 1999) and Sweden (Martinsson and Ryman, 2008). The first introduction of common lilac into Finland is known in detail from an academic thesis published in 1756 by D. E. Högman. The thesis refers to Jonas Synnerberg, a pharmacist, who brought the first lilac shrubs from Sweden to Finland in 1728, and "from his beautiful garden they have then been spread everywhere hereabouts [Turku, Finland]" (Högman, 1756, cited in Fiala and Vrugtman, 2008).

Turku was the largest and the most important Finnish city in the 18th century. While lilacs may have spread quickly among educated people and burghers in Turku, it took quite a long time before common people living in the countryside got to know the plant. In the end of the 19th century, when the first investigation on cultivated plants in Finland was published, common lilac was recorded as the most frequent of the overall still quite rare ornamental shrubs grown in the country (Elfving, 1897). In those days, lilac was spread in vernacular yards "here and there in the western part of the country", whereas in the east it was grown only by the sparse upper class (Elfving, 1897). Some 50 years later a domestic gardening book related common lilac as fully established in Finland, growing round nearly every cottage up to as far north as the species could survive (Schalin, 1953).

When common lilac became popular in vernacular gardens, the academic notice on its arrival in Finland (Högman, 1756) was long ago forgotten. Instead, it was generally believed that the place of lilac's arrival and dissemination was the fortress of Sveaborg in Helsinki (Tandefelt, 1924). Common lilac has flourished in Sveaborg since the 1760's at the latest (Helander *et al*., 1987), and lush, old lilac hedges are still today characteristic of the fortress islands. According to tradition, common lilac was spread by officers and tenure soldiers who took root suckers with them when returning home from fortification works at Sveaborg (Selander, 1939).

Two flower color variants of common lilac, the white (*S. vulgaris* var. *alba)* and the purple (*S. vulgaris* var. *purpurea)* ones, were recorded from cultivation during the 17th century (McKelvey, 1928). The diversity of flower color and form increased little by little when the early lilac growers conducted selection among seedlings or started propagating spontaneous sports. The earliest known double-flowered variety (*S. vulgaris* 'Azurea Plena') was produced in 1843 from seed by a Belgian horticulturist (McKelvey, 1928). While being a tiny-flowered curiosity with no ornamental value in itself, 'Azurea Plena' became the starting point in breeding the fine double "French hybrid" lilac cultivars introduced to the market during the late 19th century (Havemeyer, 1917).

Around the mid-19th century, when the deliberate breeding of common lilac started, there were ca. 25 garden varieties available (Meyer, 1952). The number of selections exceeded one hundred in late 1870's, and by World War I, more than 300 common lilac cultivars were already known (Meyer, 1952). The Lemoine Family of Nancy, France, is the most famous one among the early lilac breeders. Up to the 1920's, the Lemoines, together with other continental nurseries, had raised many outstanding cultivars widely grown still today and frequently utilized in further crosses. In 1928, Susan Delano McKelvey published a standard work on the genus *Syringa*, "The Lilac", a horticultural classic that treats garden forms and cultivars as well as the

species. Breeding of *S. vulgaris* has continued throughout the 20th century until now, especially in North America and in the former Soviet Union. Most cultivars result from crosses between various forms of *S. vulgaris*. The closely allied Chinese *S. oblata* Lindl. was first hybridized with *S. vulgaris* by the Lemoines (Bean, 1980). Several breeders later repeated the cross, and the resulting cultivars are usually designated as *S.* × *hyacinthiflora* Rehder.

The present number of common lilac cultivars is nearly 2 000 (Fiala and Vrugtman, 2008). Many cultivars differ only slightly from each other in the form and color of their inflorescences and flowers. The great number of cultivars, together with inadequate or missing cultivar descriptions, makes positive identification of nameless common lilac plants extremely difficult. The breeders will benefit greatly from genetic studies that utilize effective molecular tools for precise identification and characterization of cultivars, and for securing plant breeder's rights.

Previous DNA-based studies on *Syringa* have involved the use of RAPD markers to investigate hybrid origins (Marsolais *et al*., 1993), phylogenetic relationships (Kochieva *et al.*, 2004) and cultivar identities (Xinlu *et al*., 1999; Kochieva *et al*., 2004; Melnikova *et al*., 2009), ISSR markers to investigate interspecific relationships (Rzepka-Plevneš *et al*., 2006), AFLP markers to study natural populations of *S. oblata* (Jun and Wanchun, 2006), EST-SSR markers for genetic diversity studies and association mapping with floral traits in cultivated *S. oblata* (Yang *et al*., 2020), and SNP markers for association mapping for remontancy in *S. meyeri* C.K.Schneid. × *S. pubescens* Turcz. (Chen *et al*., 2020). In addition, sequencing of nuclear and chloroplast regions (Lendvay *et al*., 2016; Smolik *et al*., 2010) and complete chloroplast genomes (e.g., Zhang *et al*., 2019; Zhao *et al*., 2020; Cheng *et al*., 2021; Wang *et al*., 2021) has been conducted in several *Syringa* taxa. Reliable microsatellite markers have been developed for several species in the Oleaceae family (de la Rosa *et al*., 2002; Harbourne *et al*., 2005, Kodama *et al*., 2008), and de la Rosa *et al*. (2002) reported that some markers developed for olive (*Olea*

europaea L.) amplified also in the genus *Syringa*. Later, microsatellite markers have been developed specifically for *S. vulgaris* (Juntheikki-Palovaara *et al*., 2013) and *S. josikaea* J.Jacq. ex Rchb. (five markers, Lendvay *et al*., 2013). In the study by Juntheikki-Palovaara *et al*. (2013), nine novel microsatellite markers were developed and tested in 75 common lilac samples, including 17 accessions that represented named cultivars. Although these markers appeared valuable for detecting differentiation among common lilac cultivars, their resolving power was insufficient for high-precision cultivar identification.

Single nucleotide polymorphism (SNP) markers have become popular for molecular characterization and genetic variation analyses after the development of high-throughput genotyping methods (e.g., Bastien *et al*., 2018; Ho *et al*., 2020). In this study, we performed simultaneously SNP discovery and genotyping that allows comprehensive genome-wide analysis of genetic diversity. Our aim was to obtain a large set of SNP markers and, by using them, to reveal the precise identities of the investigated *S. vulgaris* accessions and to discover genetic relationships among them. The studied plant material included local Finnish, previously unidentified accessions, known reference cultivars, and so-called historical accessions i.e., old shrubs growing in historic cultural landscapes. Specifically, we intended (1) to verify cultivar names for some valuable local common lilac accessions, and (2) to provide insights into the history of common lilac cultivation in Finland.

Materials and methods

Sampling

Originally, a total of 94 samples of *S. vulgaris* were included in this study. However, nine samples failed due to poor DNA quality and are not shown in Tables 1-3, which give basic information for the 85 samples successfully investigated. The sampled shrubs comprised 28 unidentified local accessions (Table 1), 28 reference cultivars (Table 2) and 29 historical accessions (Table 3). Most of the unidentified local accessions were old specimen shrubs recorded during a common lilac survey conducted in the city of Helsinki, Finland, in 2005 (Lindén *et al*., 2010). A few additional shrubs from Helsinki and Porvoo, Finland, were included on grounds of their interesting phenotype. The choice of the reference cultivars was based on the presumed identity of the 28 unidentified local accessions and on the cultivar assortment that has been on sale in Finland. The historical accessions included 24 samples from such parks and gardens that were settled in the 18th or early 19th century in Southern Finland (Fig. 1). In addition, three historical samples were obtained from Carl Linnaeus' summer residence Hammarby near Uppsala, Sweden, and two samples were acquired from the gardens of Versailles, located ca. 20 km to the southwest of Paris, France. From a systematic point of view, we treat these genotypes as unidentified. The historical accessions group was assembled to investigate the early history of the common lilac in Finland.

Table 1

Table 2

Table 3

Fig. 1

Leaf samples from unidentified and historical accessions were collected in 2006, 2009, 2013 and 2016 while the shrubs were in blossom. Morphological descriptors of single florets and inflorescences were registered for most of the chosen plants in connection with sample collection. Flower color notation was based on the Royal Horticultural Society's Color Chart (2001). Reference samples were acquired from botanical collections in 2009, 2012, 2013 and 2016. All samples, packaged in plastic bags, were shipped to the Department of Agricultural Sciences, University of Helsinki, and stored in open Eppendorf tubes at -80 °C until use.

DNA extraction and genotyping

Genomic DNA was extracted from leaf tissue using the CTAB protocol of Doyle and Doyle (1990) or a commercial kit (E.Z.N.A.™ Plant DNA Mini Kit Spin Protocol, Omega Bio-Tek). The quality and quantity of extracted DNA were quantified with a spectrophotometer and further confirmed on 0.8% agarose gels. DNA concentrations were measured using NanoDrop Spectrophotometer (Thermo Scientific) and adjusted to 50 ng μl^{-1}. Genotyping of the *S. vulgaris* samples was conducted by Diversity Arrays Technology Pty Ltd. (Canberra, Australia, http://www.diversityarrays.com), following the DArT genotyping protocol of Kilian *et al*. (2012). In this method, DNA samples were first exposed to digestion-ligation reactions using two restriction enzymes, Pst1 in combination with Sphl, together with barcoded adaptors corresponding to the overhangs of the restriction enzymes. The resulting fragments were amplified by PCR, and the amplicons from each sample were pooled and used for cBot bridge PCR and then sequenced using Illumina. All SNP data were first analyzed using the DArTsoft software of the service provider. The SNP marker data were scored in a binary form using DArTsoft, which then computed several quality parameters for each SNP marker, such as the call rate, polymorphic information content (PIC) and reproducibility.

Analysis of genetic relationships

We assumed that the plant materials were diploid based on the information that the members of the genus *Syringa* are primarily diploids with basic chromosome numbers reported at x = 22, 23, or 24 (Darlington and Wylie, 1956). Pairwise genetic distances between *S. vulgaris* genotypes were calculated by GenAlEx 6.5 (Peakall and Smouse, 2012). Based on the distance values, a phylogenetic tree was constructed and visualized using the Neighbor-Joining method (Saitou and Nei, 1987) with Mega 6 (Tamura *et al*., 2013). In addition, GenAlEx was used to provide

descriptive statistics (BAFP), including the information index (I), expected heterozygosity (H_e), unbiased expected heterozygosity (uH_e) and the proportion of polymorphic loci (P).

A Bayesian analysis of population structure using software STRUCTURE 2.3.4. (Prichard *et al*., 2000) was carried out to determine the number and distribution of genetic clusters among samples. The correlated allele model was used, which assumes that at each locus allele frequencies are correlated. With this assumption, the model infers a population structure with K number of clusters. An admixture model was applied. The analysis was repeated with different values of K (range 1-10) to discover the value with the highest rate of log-likelihood probability (lnPr(X|K)) of the data. For each value of K, ten independent runs were conducted with burn-in length of 10^5 iterations, followed by data collection period of 10^6 iterations. Furthermore, to identify the correct number of clusters, the rate of change in the log probability of data between successive K values (ΔK) was calculated according to Evanno *et al*. (2005) using STRUCTURE HARVESTER v0.6.94 (Earl *et al.*, 2012). Visualization was aided by CLUMPAK (Kopelman *et al*., 2015), but the bar plot was edited and finalized manually. GenAlEx was used to conduct a principal coordinate analysis (PCoA) to investigate genetic relationships among genotypes and an analysis of molecular variance (AMOVA) to reveal contributions of among and within groups' variation to the total genetic variation. The significance of the variance components was evaluated using 999 permutations.

Results

A total of 15,007 SNP markers were generated to characterize the genetic diversity and relationships of 85 *Syringa vulgaris* genotypes including unidentified accessions from Finland,

international reference samples, and historical accessions from Finland, Sweden, and France. PIC values per SNP marker ranged from 0.012 to 0.500, with an average of 0.190. PIC values less than 0.1 were most frequent, while the frequency distribution was quite equal for PIC values between 0.1-0.5 (Fig. S1). The calculated descriptive statistics showed that the unidentified accessions possessed greater variability than the two other groups, and reference samples were more variable than the historical accessions. The values equaled 0.134, 0.130 and 0.124, respectively, for I; 0.082, 0.078 and 0.073, respectively, for H_e; 0.083, 0.079 and 0.074, respectively, for uH_e. All pairwise differences were significant ($P<0.05$, t-test), except for the I value between the unidentified and reference samples. The proportions of polymorphic loci (P) did not follow the same pattern, equaling, 39.9%, 48.8% and 57.3% for unidentified, reference and historical samples, respectively. Thus, the unidentified accessions from Finland had the lowest P value but highest I, H_e and uH_e values.

Based on pairwise genetic distances, a Neighbor-Joining tree was constructed to present the relationships among the genotypes (Fig. 2). It showed that the historical accessions grouped largely together, while the reference cultivars and unidentified accessions were highly mixed. An exception to the mixed positions of reference cultivars and unidentified accessions on the tree was formed by the accessions CSV1, CSV9, CSV21 and CSV27 that were clearly distinct from the rest. The reference sample from 'Maréchal Foch' (RSVI3) differed from the previous four accessions but still showed a relatively close relationship. Additionally, the unidentified accession CSIV20 formed an own cluster with the reference cultivars 'Indiya' (RSIV10) and 'Mme F. Morel' (RSVI28) (Fig. 2).

Fig. 2

Genetic relationships among the *S. vulgaris* genotypes were assessed also using the Bayesian Structure analysis, which revealed that the highest ΔK value was detected at K = 4, showing that the number of clusters was four for the studied data set. Again, the historical accessions were generally differentiated from the rest, while the reference cultivars and

Fig. 3

unidentified accessions showed a mixed clustering pattern (Fig. 3). The Structure results were consistent with the pattern visible in Fig. 2. For instance, the unidentified accessions CSV1, CSV9, CSV21 and CSV27 were distinct from the rest. Their genomes represented almost completely a cluster, which was otherwise found, to a considerable extent, only in the reference cultivar RSVI3, and to a small extent in reference cultivars RSIV10, RSIII16 and RSVI28, and in the unidentified local accession CSIV20.

Three local accessions (CSVII2, CSVII7 and CSVII19) clustered with the two reference samples from 'Andenken an Ludwig Späth' (RSVII17 and RSVII23; Fig. 2). The results of the Bayesian clustering analysis (Fig. 3) were consistent though a bit less clear. Yet, the whole group appears to represent 'Andenken an Ludwig Späth'. In addition, the SNP profiles revealed the cultivar identity of two local accessions (Figs. 2-3): the single, purple-flowering CSVII18 was 'Etna' (RSVII24), and the double CDIV12 with lilac-colored flowers proved to be 'Katherine Havemeyer' (RDV25), as was supposed even if the flower color did not fully match the cultivar description. The local accessions CSIII24 and CSIII28 were identical with each other but diverged from all reference cultivars (Figs 2-3).

Among the 29 historical accessions included in the analyses we discovered six different genotypes. Two of the Swedish samples from Linnaeus' Hammarby at Uppsala, HSIV23 and HSIV24, were most distant from other historical shrubs, and different from each other (Fig. 2). At the same time, the third Hammarby sample, HSIV25, was found in the quite homogeneous group of otherwise Finnish historical accessions including a total of 20 accessions (Figs. 2-3). The two samples from Versailles, France, H26 and H27, were identical, but clearly different from the Finnish and Swedish historical accessions (Figs. 2-3).

The altogether 23 Finnish historical accessions represented three genotypes. The SNP profile of HSIV3 was unique, and least distant from the local CSI14 and the two samples from Versailles (Figs. 2-3). Four historical accessions from Helsinki, HSIV1, HSIV10, HSIV13

and HSIV21, clustered closely together with the local, unidentified CSIII15, also from Helsinki (Figs. 2-3). This cluster was somewhat different from the main group of historical accessions.

AMOVA showed that most genetic variation (89%) was present within the three groups, while a significant proportion of the variation occurred among them (11%, P0.001). When the four distinct unidentified accessions CSV1, CSV9, CSV21 and CSV27 were separated into a fourth group, the AMOVA results were slightly different: 84% of the genetic variation was present within the groups, while 16% (P<0.001) of the variation occurred among them. The principal coordinate analysis revealed that the first two coordinates explained 28% of the total variation based on the original three-group approach (Fig. S2a), and when using the four-group approach, the first two coordinates explained the same proportion, i.e., 28%, of the total variation (Fig. S2b).

Discussion

Using the novel SNP markers, we verified cultivar names for five local *S. vulgaris* accessions: CSVII2, CSVII7 and CSVII19 represented 'Andenken an Ludwig Späth', CSVII18 was 'Etna', and CDIV12 was 'Katherine Havemeyer'. The phenotype of the local accessions matched their respective cultivars quite well apart from flower color in the local accession CDIV12. 'Katherine Havemeyer' should have mixed pink flowers (Fiala and Vrugtman, 2008), but we defined CDIV12 as lilac. The discrepancy may have resulted from environmental factors or flowering stage, as weather and edaphic conditions can affect color hues in lilac, and the color may also change during flower development (Meyer, 1952; Fiala and Vrugtman, 2008).

The rest of the local accessions remained unidentified. However, the SNP results clarified their potential cultivar identity. For example, accessions CSIII10 and CDI8 were placed

297 in the Neighbor-Joining tree among four blue- or white-flowering cultivars bred by the Lemoine
298 nursery, so they could probably be determined by studying such phenotypically similar Lemoine
299 cultivars that were not included in the present analysis. The local CDIV4 with unique flower
300 characteristics was supposed to represent 'Lemoinei', one of the first double *S. vulgaris* cultivars
301 (Havemeyer, 1917; Taylor, 1990). We could not trace 'Lemoinei' in any plant collection, but
302 instead received a sample of 'Guizot' (RDIV7), a 20 years later Lemoine cultivar with several
303 flower characteristics parallel to 'Lemoinei' (McKelvey, 1928). The SNP profiles of CDIV4 and
304 RDIV7 revealed that the local shrub was not 'Guizot', so our original hypothesis on the rare
305 'Lemoinei' genotype was left open.

306 The divergent group of four local accessions from Helsinki (CSV1, CSV9, CSV21
307 and CSV27) may represent a *S.* × *hyacinthiflora* cultivar with *S. oblata* in the pedigree. The only
308 sample (RSVI3) related to these represented 'Maréchal Foch', which Bean (1980) quotes as an
309 example of such Lemoine's later productions that may have *S. oblata* in their parentage even
310 though they are classified as cultivars of *S. vulgaris*. Our genotyping results corroborate Bean's
311 assumption, which was probably based on morphological and phenological features. The
312 appearance of all four was very similar: the shrubs were tall, carrying showy, full panicles
313 composed of extra-large flowers, deep pink when in bud, with a paler, bright pink shade when
314 opened.

315 One of the earliest named garden forms of *S. vulgaris* is 'Prince Notger', which
316 became commercially available round 1840 and was frequently cultivated around (McKelvey,
317 1928). Based on old nursery catalogues, 'Prince Notger' has been traded in Finland since 1877.
318 Our reference sample from 'Prince Notger' (RSIII14) came from the Arnold Arboretum, Boston,
319 MA. The sampled shrub was the same that McKelvey (1928) compared with a plant of the same
320 name in the Department of Parks, Rochester, NY, concluding that the two were dissimilar in
321 appearance, and that she felt "uncertain which, if either, is true to name". In the Neighbor-

Joining Tree those local accessions provisionally identified as ‘Prince Notger’ (CSIII24 and CSIII28) were near neighbours with RSIII14, but in a separate branch of the family tree. The flower features fit well with historical descriptions of ‘Prince Notger’ (McKelvey, 1928), yet the SNP profile did not match the reference sample.

We genotyped two reference accessions of the cultivars ‘Andenken an Ludwig Späth’ and ‘Belle de Nancy’. For both pairs, the SNP profiles were identical indicating that the plants were correctly named and quite likely originated from the same original plant as a vegetatively propagated line. The identical SNP profiles for RDI13 (‘Edith Cavell’) and RDI22 (‘Mme Casimir Périer’) proved that they belong the same cultivar and so one or the other of the reference samples came from a mislabeled plant. Mislabellings are rather common in germplasm collections (e.g., Nybom *et al.*, 2014; Venison *et al*., 2022).

The second aim of our study was to trace the history of common lilac in Finland. The SNP analyses revealed a group of 20 historical accessions, 17 of which were identical with each other. The minor differences shown by three accessions were probably due to somatic mutations accumulating in long-lived plant specimens (e.g., Tomimoto and Satake, 2023). In the main historical group, six specimens were collected from sites in or near Turku in the province of Varsinais-Suomi, thirteen samples originated from the province of Uusimaa, and one sample (HSIV25) came from Carl Linnaeus’ country estate Hammarby in Uppsala, Sweden. HSIV25 came from a shrub, which is assumed to belong to the very oldest of Hammarby’s common lilacs (Kårehed, e-mail July 5, 2013). The SNP profiles support the assumption considering that HSIV25 was identical with 16 Finnish accessions, which quite probably originate from the Linnean times. Furthermore, the present SNP analyses corroborate the old report on common lilac’s arrival in Finland from Sweden (Högman, 1756, cited in Fiala and Vrugtman, 2008).

In addition to the main historical group, the Finnish historical accessions involved one unique accession (HSIV3) and a group of five accessions (CSIII15, HSIV1, HSIV10,

HSIV13, HSIV21), which had strongly backwards curled, often twisted corolla-lobes, and a little larger flowers than shrubs in the main historical group. Based on their growing sites, the slightly different historical shrubs had been planted between the 1790's and the 1820's (Nikander, 1928). The results indicate that more than one common lilac form was introduced into Finland already towards the end of the 18th century.

Four of the altogether five non-Finnish historical accessions we analysed were clearly different from all Finnish historical samples. Two of them (HSIV23 and HSIV24) came from the small Baroque style Uppland Garden, established in Linnaeus' Hammarby in the late 19th century. Uppland Garden's two samples differed that much from each other that they were placed in separate branches in the Neighbor-Joining tree indicating that *S. vulgaris* was introduced to Hammarby more than once and probably from more than one source.

The two historical accessions (H26 and H27) from the gardens of Versailles, France, proved to be identical and dissimilar from other historical samples. We wanted to compare lilacs from Versailles to Finnish historical accessions, because oral tradition says that common lilac was brought to the Finnish Sveaborg fortress in mid-18th century from France (Suominen 1997), maybe directly from the gardens of Versailles (Pettersson, 1948; Enkainen, 1950). However, our SNP results did not lend any support to the story.

The informativeness of the novel SNP markers was estimated by the PIC index. The average PIC value equaled 0.190 (range 0.012-0.500), and the distribution was biased towards lower values. These values are in the same range of PIC values found in many other SNP-based investigations on mainly clonally propagated woody plants (e.g., Oh *et al*., 2019; Lyu *et al*., 2020). Based on the descriptive statistics, the unidentified accessions possessed greater variability than the two other groups, and reference samples were more variable than the historical accessions, although the proportion of polymorphic loci was lowest in the otherwise

more variable unidentified accessions. These results indicate differences in the amount and pattern of genetic variation among the studied groups.

To the best of our knowledge, the present genotyping by sequencing study is the first one that analyzes the genetic relationships of *S. vulgaris* L. genotypes in depth and provides detailed knowledge of the history, origin and identity of different accessions and cultivars of this popular ornamental shrub. The information can be used when utilizing present cultivars and developing new ones in future breeding programs.

Conclusions

Based on the data generated by genotyping in combination with existing historical and phenotypic knowledge, we discovered the identities, origin, and genetic relationships of diverse *S. vulgaris* accessions, including previously unidentified Finnish accessions, known reference cultivars, and historical accessions i.e., old shrubs growing in historic cultural landscapes. As far as we know, this is the first genetic analysis on *S. vulgaris* utilizing high-throughput genotyping that produces excessive amounts of genetic marker data, i.e., 15,007 SNP loci with an average PIC value of 0.190. We learned that when attempting to identify unknown accessions, it is a challenge to find correct reference cultivars for comparison, since plants representing different genetic backgrounds may show similar phenotypic traits. In the present study, the clearest results concerned those cultivars, which are likely to have *S. oblata* in their lineage. The local unidentified accessions from Helsinki (CSV1, CSV9, CSV21 and CSV27) were distinct from all other genotypes. In the Neighbor-Joining tree they clustered only with the phenotypically similar ‘Maréchal Foch’(RSVI3), which is supposed to be of hybrid origin. Our results also showed that most old common lilacs in Finland originate from one clone, which has been brought to the

country from Sweden in the early 18th century. More common lilac origins were introduced round the turn of the 18th century and thereafter, including garden forms related to 'Prince Notger', which is an old, blue-flowered cultivar. The novel information generated in this study can be used when utilizing present genetic resources of *Syringa* and when developing new cultivars in future breeding programs.

Data. Genotyping data are archived in Dryad https://doi.org/10.5061/dryad.x3ffbg7nh

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Conflict of interest. None

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561 **Figure legends**

562

563 **Fig. 1.** A map showing the collection sites for historical *Syringa vulgaris* L. accessions collected
564 in Finland (see Tables 1-3).

565

566 **Fig. 2.** Genetic relationships of 85 *Syringa vulgaris* L. genotypes inferred using the Neighbor-
567 Joining method. Green, blue and red sample codes represent unidentified accessions, reference
568 cultivars and historical accessions, respectively. Accession codes are explained in Tables 1-3.

569

570 **Fig. 3.** Assignment of *Syringa vulgaris* L. genotypes to four different gene pools (proportions
571 shown) based on SNP markers as inferred by Bayesian clustering analysis. Green, blue and red
572 sample codes represent unidentified accessions, reference cultivars and historical accessions,
573 respectively. Accession codes are explained in Tables 1-3.

574

575 **Fig. S1.** Frequency distribution of PIC values for SNP markers.

576

577 **Fig. S2.** Genetic relationships of 85 *Syringa vulgaris* L. genotypes representing unidentified
578 accessions, reference cultivars and historical accessions as determined by principal coordinate
579 analysis based on SNP markers. A) The original division to three groups was used. B) The four
580 distinct unidentified accessions CSV1, CSV9, CSV21 and CSV27 formed a fourth group.
581 Accession codes are explained in Tables 1-3.

Table 1. Unidentified local accessions of common lilac (*Syringa vulgaris* L.) analyzed in this study. The first letter in the code denotes the accession being unidentified accession (C), while the second letter stands for single (S) or double (D) flowers. The Roman numeral indicates flower color according to the Wister color classification (DeBard and ILS, 2019): I white, II violet, III blue and bluish, IV lilac, V pink and pinkish, VI magenta, VII purple. The Arabic numeral marks each accession's running number. Shrubs with a putative cultivar or code name were assumed to represent a cultivar, unidentified or known, based on morphological characters.

Accession code	Putative cultivar or code name	Site of origin	Type and color of flowers*
CSV1	K17	Mäkelänkatu, Helsinki	S, pinkish
CSVII2	M70	Matosaari, Helsinki	S, purple
CSIII3	R71	Keijukaistenpolku, Helsinki	S, bluish
CDIV4	Lemoinei	Annala, Helsinki	D, lilac
CSIII5	A19	Annala, Helsinki	S, bluish
CSI6	K4	The City Garden, Helsinki	S, white
CSVII7	Andenken an Ludwig Späth	Mäkelänkatu, Helsinki	S, purple
CDI8	M12	Hesperia Park, Helsinki	D, white
CSV9	K17	The City Garden, Helsinki	S, pinkish
CSIII10	M36	Hesperia Park, Helsinki	S, bluish
CSIII11	E42	Eira Park, Helsinki	S, bluish
CDIV12	Katherine Havemeyer	Hesperia Park, Helsinki	D, lilac
CSI13	K4	Hesperia Park, Helsinki	S, white
CSI14	-	Hannula, Kaarenkylä, Porvoo	S, white
CSIII15	-	Itäväylä, Helsinki	S, bluish
CSVII16	A20	Annala, Helsinki	S, purple
CSII17	K22	The City Garden, Helsinki	S, violet
CSVII18	K25	The City Garden, Helsinki	S, purple
CSVII19	Andenken an Ludwig Späth	The City Garden, Helsinki	S, purple
CSIV20	M30	Mäkelänkatu, Helsinki	S, lilac
CSV21	K17	Mäkelänkatu, Helsinki	S, pinkish
CSIV22	E38	Eira Park, Helsinki	S, lilac
CDV23	Belle de Nancy	Eira Park, Helsinki	D, pinkish
CSIII24	Prince Notger	Stansvik Manor, Helsinki	S, bluish
CSIV25	M56	Matosaari, Helsinki	S, lilac
CSVII26	M57	Matosaari, Helsinki	S, purple
CSV27	K17	Viikki Campus, Helsinki	S, pinkish
CSIII28	Prince Notger	Kulosaari Manor, Helsinki	S, bluish

*S, single flowers; D, double flowers

Table 2. Reference cultivars of common lilac (*Syringa vulgaris* L.) analyzed in this study. The first letter in the accession code denotes the cultivar being reference cultivar (R), while the second letter stands for single (S) or double (D) flowers. The Roman numeral indicates flower color according to the Wister color classification (DeBard and ILS, 2019): I white, II violet, III blue and bluish, IV lilac, V pink and pinkish, VI magenta, VII purple. The Arabic numeral marks each accession's running number.

Accession code	Cultivar name	Originator and year	Origin of sample	Accession number	Type and color of flowers*
RDV1	Belle de Nancy	Lemoine 1891	Nancy Botanic Garden	19830008	D, white
RSIII2	Firmament	Lemoine 1932	Nancy Botanic Garden	19810720	S, bluish
RSVI3	Maréchal Foch	Lemoine 1924	Nancy Botanic Garden	19840383	S, magenta
RDVI4	Mrs Edward Harding	Lemoine 1922	Nancy Botanic Garden	19830013	D, magenta
RSVII5	Volcan	Lemoine 1899	Nancy Botanic Garden	19921683	S, purple
RSVII6	Negro	Lemoine 1899	Nancy Botanic Garden	19980446	S, purple
RDIV7	Guizot	Lemoine 1897	Nancy Botanic Garden	20050538	D, lilac
RSV8	Gloire de Moulins	origin unknown, pre 1867	Arnold Arboretum	2978-1*A	S, pinkish
RDV9	Belle de Nancy	Lemoine 1891	Arnold Arboretum	308-96*A	D, pinkish
RSIV10	Indiya	Kolesnikov 1955	Luke Natural Resources Institute Finland	TTA852 14636	S, lilac
RSV11	Altayskaya Rozovaya	Luchnik 1984	Luke Natural Resources Institute Finland	TTA854 14638	S, pinkish
RDI12	Miss Ellen Willmott	Lemoine 1903	Arnold Arboretum	615-56*A	D, white
RDI13	Edith Cavell	Lemoine 1916	Arnold Arboretum	300-95*B	D, white
RSIII14	Prince Notger	origin unknown, pre 1841	Arnold Arboretum	3001-1	S, bluish
RSIII15	Ambassadeur	Lemoine 1930	Nancy Botanic Garden	20010081	S, bluish
RSIII16	Maurice Barrès	Lemoine 1917	Nancy Botanic Garden	20010069	S, bluish
RSVII17	Andenken an Ludwig Späth	Späth 1883	Bergius Botanic Garden	48b	S, purple
RSV18	Dr von Regel	Späth 1883	Bergius Botanic Garden	59	S, pinkish
RSVI19	Louis van Houtte	origin unknown, pre 1877	Bergius Botanic Garden	60	S, magenta
RSVI20	Réaumur	Lemoine 1904	Bergius Botanic Garden	66	S, magenta
RSVI21	Ruhm von Horstenstein	Wilke 1928	Bergius Botanic Garden	75	S, magenta
RDI22	Mme Casimir Périer	Lemoine 1984	Bergius Botanic Garden	53	D, white
RSVII23	Andenken an Ludwig Späth	Späth 1883	Montréal Botanical Garden	9450-37-1949	S, purple
RSVII24	Etna	Lemoine 1927	Montréal Botanical Garden	4808-39-1949	S, purple
RDV25	Katherine Havemeyer	Lemoine 1922	Montréal Botanical Garden	5246-39-1944	D, pinkish
RSI26	Marie Legraye	Legraye, pre 1879	Montréal Botanical Garden	9443-37-1950	S, white
RSIV27	Marlyensis	origin unknown, pre 1733	Montréal Botanical Garden	1450-1957	S, lilac
RSVI28	Mme F. Morel	Morel, F. 1892	Montréal Botanical Garden	3514-39-1950	S, magenta

*S, single flowers; D, double flowers

Table 3. Historical common lilac (*Syringa vulgaris* L.) accessions analyzed in this study. The first letter in the accession code denotes the cultivar being historical cultivar (H), while the second letter stands for single (S) flowers. The Roman numeral indicates flower color according to the Wister color classification (DeBard and ILS, 2019): all IV lilac. The Arabic numeral marks each accession's running number.

Accession code	Site of origin of flowers*	Province and country	Type and color
HSIV1	Traverse Adlerfelt, Suomenlinna, Helsinki	Uusimaa, Fi	S, lilac
HSIV2	Saari Manor, Mynämäki	Varsinais-Suomi, Fi	S, lilac
HSIV3	Saari Manor, Mynämäki	Varsinais-Suomi, Fi	S, lilac
HSIV4	Perno New Manor, Turku	Varsinais-Suomi, Fi	S, lilac
HSIV5	Sipsalo Farm, Turku	Varsinais-Suomi, Fi	S, lilac
HSIV6	Sipsalo Farm, Turku	Varsinais-Suomi, Fi	S, lilac
HSIV7	Manor Espoonkartano, Espoo	Uusimaa, Fi	S, lilac
HSIV8	Träskända Manor, Espoo	Uusimaa, Fi	S, lilac
HSIV9	Alberga Manor, Espoo	Uusimaa, Fi	S, lilac
HSIV10	Tuomarinkylä Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV11	Boxbacka Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV12	Puotila Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV13	Herttoniemi Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV14	Saksa Residence, Tuusula	Uusimaa, Fi	S, lilac
HSIV15	Wäfvars Residence, Tuusula	Uusimaa, Fi	S, lilac
HSIV16	Jeppas Residence, Tuusula	Uusimaa, Fi	S, lilac
HSIV17	Klemetsskog croft, Tuusula	Uusimaa, Fi	S, lilac
HSIV18	Kankainen Manor, Masku	Varsinais-Suomi, Fi	S, lilac
HSIV19	Piper's Park, Suomenlinna, Helsinki	Uusimaa, Fi	S, lilac
HSIV20	J.L. Runeberg's Home, Porvoo	Uusimaa, Fi	S, lilac
HSIV21	Stansvik Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV22	Viikki Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV23	Uppland Garden, Hammarby, Uppsala	Uppsala County, Swe	S, lilac
HSIV24	Uppland Garden, Hammarby, Uppsala	Uppsala County, Swe	S, lilac
HSIV25	East Wing, Hammarby, Uppsala	Uppsala County, Swe	S, lilac
H26*	King's Garden, Gardens of Versailles	Île-de-France, Fr	unknown
H27*	King's Garden, Gardens of Versailles	Île-de-France, Fr	unknown
HSIV28	Stansvik Manor, Helsinki	Uusimaa, Fi	S, lilac
HSIV29	Perno Old Manor, Turku	Varsinais-Suomi, Fi	S, lilac

* The samples were taken from a clipped hedge with no inflorescences, so the type and color of flowers could not be ensured

Fig. 1

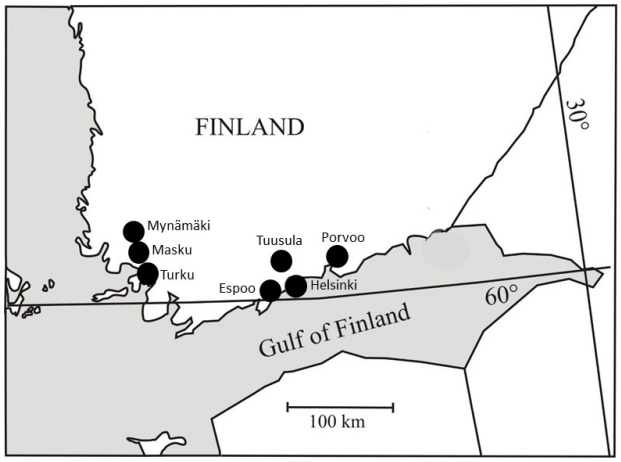

Fig. 1. A map showing the collection sites for historical Syringa vulgaris L. accessions collected in Finland (see Tables 1-3).

338x190mm (96 x 96 DPI)

Fig. 2

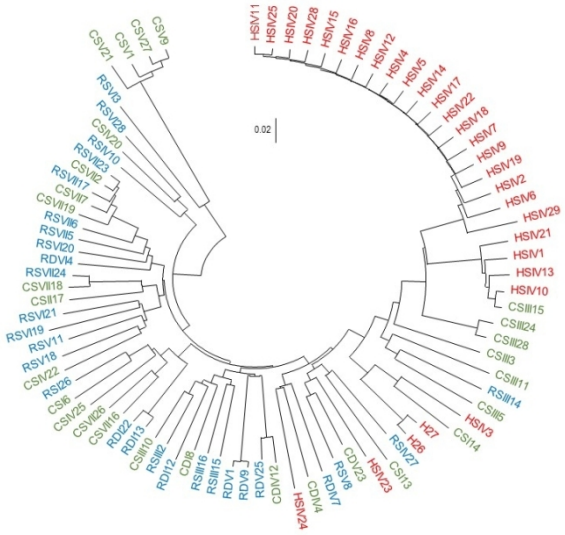

Fig. 2. Genetic relationships of 85 Syringa vulgaris L. genotypes inferred using the Neighbor-Joining method. Green, blue and red sample codes represent unidentified accessions, reference cultivars and historical accessions, respectively. Accession codes are explained in Tables 1-3.

338x190mm (96 x 96 DPI)

Fig. 3

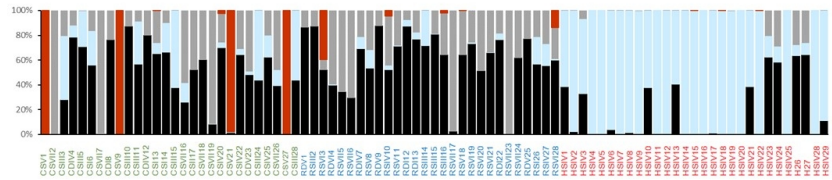

Fig. 3. Assignment of Syringa vulgaris L. genotypes to four different gene pools (proportions shown) based on SNP markers as inferred by Bayesian clustering analysis. Green, blue and red sample codes represent unidentified accessions, reference cultivars and historical accessions, respectively. Accession codes are explained in Tables 1-3.

338x190mm (96 x 96 DPI)