Palacký University Olomouc

Faculty of Science

Department of Botany

Populations of service tree (*Sorbus domestica L.*) in Central Europe and their characteristics

PhD. Thesis

Mgr. Zdeněk ŠPÍŠEK

Supervisor: doc. RNDr. Vladan Ondřej, PhD.

Consultant: RNDr. Radim J. Vašut, PhD.

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Abstrakt:

Jeřáb oskeruše (*Sorbus domestica* L.) je neobvyklý a vzácný druh ovocné dřeviny, který má vzácně roztoušený výskyt v jižní a střední Evropě, nikde ve svém areálu oskeruše nevytváří souvislé porosty. Právě Českou republikou prochází severní hranice areálu rozšíření tohoto druhu. Člověk ovlivnil rozšíření druhu jakožto ovocného stromu, plody byly využívány v jižní Evropě již antickém Římu. Na území střední Evropy je konzumace a pěstování známo/známé až od vrcholného středověku. Jak je druh v ČR rozšířen a do jaké míry lze v charakteru rozšíření vysledovat vliv člověka je hlavním cílem předložené dizertační práce. Detailně se zabývala následujícími tématy: 1) Rozšíření druhu v Bílých Karpatech včetně variability plodů, dendrologickým parametrům a klimatickými podmínkami stanoviště. 2) Detailnímu výskytu druhu v České republice včetně srovnání historických údajů z herbářových položek a určení původu jedince 3) Genetickou variabilitou druhu ve svém areálu s důrazem na Českou republiku.

Práce ukazuje, že výskyt tohoto druhu v České republice je převážně v teplých a mírně teplých klimatických regionech (České středohoří a Jihovýchodní Morava). V oblasti Bílých Karpat je nejpravděpodobněji lidského původu většina stromů zde roste v nadmořské výšce 200 – 600 m n.m.. Velká většina stromů roste v sadech, vinicích nebo v otevřené krajině. Kromě řady vysazených stromů dochází i k spontánnímu šíření druhu. Srovnání tvarové variability plodů neprokázalo žádnou korelaci, ovšem mnohé ovocné tvary byly selektovány pěstiteli. Genetická diferenciace mezi populacemi není nikterak vysoká. Zvláště Panonské populace střední Evropy vykazují geneticky podobné pozadí. Tyto populace vykazují genetické vazby s Panonskými populacemi. Zajímavé je, že populace Českého středohoří vytváří skupinu (cluster), která se mírně liší od genetického pozadí panonských populací a je více propojena s německými (nebo francouzskými) populacemi. Vysoká alelická diverzita i v malých subpopulacích naznačuje příchod nových genotypů z jiných populací, což může být vysvětleno schopností přenosu pylu (opylovači) i na velké vzdálenosti a/nebo dávným obohacením populací člověkem, které se v současnosti samy spontánně šíří krajinou. Ačkoli většina zdokumentovaných stromů pravděpodobně má antropogenní původ, představují důležitý prvek v krajině střední Evropy, který vyžaduje ochranu.

Kličova slova: jeřáb oskeruše, *Sorbus domestica*, chorologie, archeofyt, tvar plodu, dendrometrická data, populace, genetická variabilita

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Abstract:

Service tree (*Sorbus domestica* L.) is a unique fruit species of rare occurrence in Central and Southern Europe. The Czech Republic represents the northern limit of natural distribution area. In the area, service tree grows in fragmented populations with scattered distribution. Human is responsible for the use of the as a fruit tree. Service tree fruit has been consumed in Southern Europe since the ancient times and it was known to be consumed in Central Europe since the Middle Ages. The main topic of the thesis is related to understanding the patterns of distribution of the species and to what extent is the distribution impacted by human activities. I the theseis, I particularly covered following topics: 1. species prevalence in the White Carpathians including fruit variability, dendrometric parameters and climatic conditions of the site. 2) Detailed species distribution in the Czech Republic including the excerption of historical data from herbarium specimens. 3) Genetic variability of the species in area of its natural occurrence with focus on the Czech Republic.

The study shows that the species distribution in the Czech Republic is predominantly in warm or mild climate regions (central Bohemia and Southeastern Moravia). Our data suggest that occurrence of the species in the White Carpathians is most likely strongly influenced by human activities and we havenot traced any signs of natural occurrence. The majority of the service trees grow at the altitude of 200 – 600 meters above sea level, mostly in orchards, vineyards or on open landscape. The comparison of the fruit types has not revealed any strong pattern, although the fruit types have been selected by the growers supposedly. Genetic differentiation among populations was not high, especially Pannonian populations of Central Europe shows similar genetic admixed background. Interestingly, population from the České

Středohoří Mts. forms distinct cluster slightly differing by the admixed genetic background from Pannonian population and more linked to German (or further French) populations. Although most of the documented trees probably have an anthropogenic origin, they represent an important part of the flora in Central Europe and require the protection.

Keywords: Service tree, *Sorbus domestica*, chorology, archaeophyte, fruit shape, dendrometric data, population, genetic variability

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Contens

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Declaration

I hereby declare that this thesis has been worked out by myself together with listed coauthors. All literary sources cited in this thesis are listed in the References section.

Author's Contributions

CHAPTER 1: Introduction *Sorbus domestica*: taxonomic position, biological and ecological characteritics and its historical and current use.

The chapter is based on the published book "Oskeruše – strom pro novou Evropu". For the purpose of the Ph.D. thesis, the text represents an excerption from the book in which only appropriate topics were used. The original text was written by Z. Špíšek (ZŠ) and V. Hrdoušek as a contribution to the book by B Krška, L. Bakay and J. Šedivá. The chapter in the thesis have been written by ZŠ.

CHAPTER 2: *Sorbus domestica* L. at its northern Pannonian distribution limits: distribution of individuals, fruit shapes and dendrometric characteristics

ZŠ, R. J. Vašut (RJV), A. Uherková (AU) and M. Svitok (MS) have contributed to the experimental design and/or the analytical tools. ZŠ and AU did the data sampling in the field. ZŠ has performed the maps analyses. All of the authors have contributed to the final version of the manuscript.

CHAPTER 3: Distribution maps and comments on *Sorbus domestica,* et The distribution of vascular plants in the Czech Republic. Part 3

M. Lepší, P. Lepší, ZŠ and K. Kubát have contributed to the mapping. ZŠ provided data on 452 localities from whole country. All of the authors have contributed to the final version of the manuscript.

CHAPTER 4 Genotypic variability of *Sorbus domestica* in Central Europe suggests its anthropogenic origin.

ZŠ and RJV have conceived the study. ZŠ has conducted the plant sampling and the laboratory analyses. ZŠ and RJV have prepared the analyses and have written the manuscript. Both of the authors have contributed to the final version of the manuscript.

CHAPTER 5 Summary and conclusion

ZŠ has written the text.

CHAPTER 1:
Introduction *Sorbus domestica*: taxonomic position, biological and ecological characteritics and its historical and current use.

Zdeněk Špíšek

Vít Hrdoušek

Boris Krška

Laco Bakay

Jana Šedivá

Chapter is reduced compilation based on monography: Oskeruše strom pro novou Evropu (Hrdoušek et al. 2014)

Taxonomic characteristics of the species *Sorbus domestica*

The genus *Sorbus* includes about 250 species widespread in the northern hemisphere (Aldasoro et al., 2004). At the moment, we are not sure how the individual species are related to one another, but studies point to a significant amount of hybridization (interbreeding between different species) and complex and reticulate evolutionary relationships within the whole *Malinae* subtribe, which includes the *Sorbus* genus (Campbell et al., 2007; Potter et al., 2007; Robertson et al., 2010). In addition, recontructions of phylogenetic relationships of *Sorbus* s.l. taxa based on different genes (cp DNA vs. ITS in nuclear DNA) revealed different phylogenetic trees for the taxa. According to phylogenetic tree based on cpDNA loci, *Sorbus domestica* (as genus *Cormus*) is sister taxon to genera *Pyrus* and *Sorbus* s.str. (represented by *S. aucuparia*), whereas acording to ITS phylogeny the sister taxon of *Cormus* are *Cotoneaster*, *Photinia* and *Pyrus* (Campbell et al. 2007). The putative hybridogeneous origin of *Malinea* genera is expected since early beginnings of plant systematics; even Carl Linnaeus noticed the reticulate relationship of morphologic characteristics among *Malinae* genera. Therefore, he classified major members of the *Sorbus* s. l. genus (whitebeam, checker tree, dwarf whitebeam) in genera of *Crataegus* (*S. aria*, *S. torminalis*) or *Mespilus* (*S. chamaemespilus*) genera. Recent biosystematics approaches favour splitting the polyphyletic genus *Sorbus* s.l. into separated genera, *Sorbus domestica* is then accepted as *Cormus domestica* (L.) Spach (see e.g. Sennikov & Kurtto, 2017). In the Czech Republic, the *Sorbus* genus is represented by 5 primary species and further 19 hybridogenous species (Danihelka et al., 2012; Lepší et al., 2013). The primary species are: the service trees (*S. domestica*), whitebeam (*S. aria*), wild service tree (*S. torminalis*), dwarf whitebeam/false medlar (*S. chamaemespilus*), and the rowan/mountain-ash (*S. aucuparia*). All these 5 species have a diploid number of chromosomes (2n = 2x = 34) and that they all reproduce only sexually (Kovanda, 2003). Service trees, however, are notably different in one respect – unlike all the other species; they are never involved in interspecific hybridization. Therefore, it never forms neither F_1 diploid hybrids, nor polyploid hybridogeneous apomictic microspecies (Nelson-Jones et al., 2002). This can be related to the fact the species is isolated within the *Sorbus* s. l. genus (Potter et al., 2007); it might also have to do with the hypothetical evolutionary age of the species (Kárpáti, 1960).

The service tree (*Sorbus domestica*) is a robust and landscape-wise decorative tree. Free-growing trees have spherical or broadly oval treetops with massive fanned-out branches, and their height reaches 15–20 m. Trees in the forest canopy can grow up to 35 m (Paganová & Bakay, 2010), their treetops tend to be vertically oval, skeletal branches are horizontal, upward-arching, and densely branched (Kausch-Blecken von Schmeling, 2000). By the shape of its treetop and bark it resembles the wild service (*Sorbus torminalis*). However, it can also occur in the form of a shrub about 3–5 m tall, especially on rocky sites, dry Mediterranean area, and in biotopes exposed to grazing, harsh weather conditions, and salinization of the seaside. Solitary trees have spherical or broadly oval treetops with massive fanned-out branches, and their height reaches 15–20 m. Trees in the forest canopy can grow up to 35 m (Paganová et Bakay, 2010), their treetops tend to be vertically oval, skeletal branches are horizontal, upward-arching, and densely branched (Kausch-Blecken von Schmeling, 2000). Tap roots are strong, significantly deep and branched, and adapted to be able to intergrow into watery bottom layers of dry locations in which the tree grows.

Bark of young service trees is smooth, grey-brown, and has round lenticels. Bark of older trees (i.e., 6–10 years) starts to grow coarse and cleaves from the bottom. The bark of mature trees is grey-brown or red-brown, with frequent clefts (Fig. 1. a). It can peel off spontaneously in longitudinal right-angled sheets. Service tree wood is compact, has rich texture (especially with older specimens) and dull ochre or reddish colour. Growth rings are dense and hardly distinguishable; distinguishing sapwood from heartwood is possible only with new wood. Because of its hardness it is quite difficult to hew.

Buds are ovate, green-brown, brown or brown-red, glabrous, and sticky when young. Leaves alternate, compound odd-pinnate, 13–25 cm long, usually with 6–10 pairs of leaflets; individual leaflet 3–6 cm long and 1.1–2.0 cm wide. The leaflet margin is serrate in upper two thirds (Fig. 1. b), below is entire; upper surface dark green and glabrous; the lower surface grey-green and wooly (especially when young). Unlike leaves of the mountain-ash, service tree leaves are not acuminate but acute and do not have reddish leaf venation (Čížková, 1997). During September, leaves become yellow, orange or red, turning brown and falling off in the middle of October. Young plants shed their leaves sooner than older ones. In seedlings, the first assimilatory leaves are partly connate and may not be hairy.

Flowers are usually white (just scarcely pink) and fragrant; mostly nectariferous. Flowers are small 0,5 cm wide with 5 petals, 5 styles and numerous stamens, inflorescence ~6–10 cm wide, arranged into corymbous panicles of about 60–90 flowers (Fig. 1. c). Blossoms are prone to drying; usually 4–10, rarely 15–20 of them remain and turn into fruits. The service tree is in bloom at the beginning of May, exceptionally in late April, and the blossoms last only 10 to 14 days. It is a monoecious woody plant.

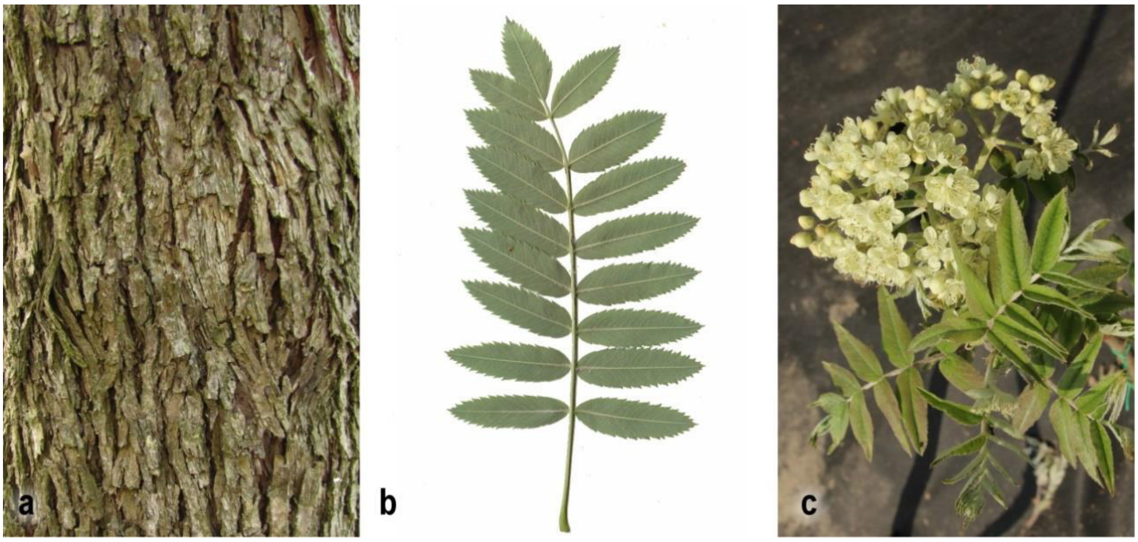

Fig.. 1. a) The bark of *Sorbus domestica* mature tree, b) The leaflet margin is serrate in upper two thirds c) white flowers are arranged into corymbous panicles

Fruits—called sorb apples—in comparison with other *Sorbus* s.l. species are the largest fruit within the broadly accepted genus in the world (and in general, one of the largest among all wild taxa of the subtribe *Malinae*). The size of a sorb apple is about 2.5 cm on average, and its weight ranges approximately between 8 g–10 g. Sorb apples of some cultivars (e. g. from Germany, Southern Europe, and Crimea) are up to 5 cm in diameter and can weigh over 30 g (Kausch-Blecken von Schmeling, 2000). The fruit usually contains 1–2, scarcely up to 6 seeds (Paganová & Bakay, 2010). It is brown or brown-black, approximately 3 mm wide, about 1.5 mm thick, and around 5 mm long. Sorb apples are pomaceous, apple-shaped (pomifera) or pear-shaped (pyriformis), with a range of transition forms (Tamaro, 1915). The colour of fruits changes from basic green through green-yellow to yellow-orange with pink, red or red-purple cheeks depending on the position on trees or exposure to sun (Fig. 2. a). Lenticels on top of pomes are mostly russet red. Fruits are edible, however, due to high content of tannins and acids cannot be consumed directly from the tree but need to ripen first. They gradually fall and mature on the ground in most cases: they soften and change their colour from yellow-red to ochre-russet or cinnamon-brown, with pale lenticels. Ripe sorb apples are entirely soft and have light ochre pulp (Fig. 2. b). They ripen from the middle of August until the middle of November. Fruit of trees in one location can ripen at different times, and the interval between two maturation times can frequently reach up to several weeks. Fruit maturation on trees can last as long as a month. Sorb apples that fall off trees practically do not rot because of the high content of organic acids and tannin—they rather dry up. Mature trees of 50 years and above can produce 200–500 kg of fruits a year, sometimes as much as 1,000 kg of fruit in a seed year. Sorb apples are picked either by collecting them from the ground or by shaking them down. Shaken-down unripe green fruit withers and often does not ripen anymore. The service tree is a long-lived fruit tree, and therefore its full maturity, i.e. the seed year, in large trees above 100 years of age occurs once every 2–3 years. Fertility also decreases the infestation with pathogens, chiefly scab (*Venturia inaequalis*), which causes bad ripening and premature shedding of leaves and fruit (Kausch-Blecken von Schmeling, 2000).

Fig. 2. a) The different fruit colour from White Carpathian, b) Ripe sorb apples are entirely soft and have light ochre pulp.

Service tree habitat requirements

Service trees are heliophilous and thermophilic. They prefer soils that have a high nutrient content and are not overly moist. Májovský (1992) characterizes them as a European Sub-Mediterranean floral element. Borhidi (1993) describes the service tree as a sub-oceanic species of alkaline oligotrophic forest ecosystem; its seedlings can tolerate semi-shade, but they are unable to cope with salinated soils. Service trees prefer warm, temperate climates with a longer vegetation period. They require a small, but constant supply of water from the subsoil, especially when they bloom or when their fruit ripens (Májovský, 1992). The root system of a service tree can access even water that is several meters below the tree (Kausch-Blecken von Schmeling, 2000). Larrieu et al. (2013) compiled data from France and Spain and point out that service trees are resistant to wind and grow on loam and clay soils with varying amounts of water. When young, the service tree can grow rather quickly, but it often refuses to grow close to other trees; therefore, it can often be found in places with less than ideal growing conditions. The service tree limiting factors are: not enough light, not enough nutrients in the soil without loam, too much water in the subsoil, cold and damp microclimate.

In places where it occurs naturally, the service tree prefers soils rich in nutrient content, especially in calcium: rendzinas and cambisols on limestone or dolostone (in the Mediterranean region in particular), and also brown earth on loess or diluvial soils and cambisols on non-carbon soils or marl (in Central Europe) (Rotach, 2003; Kausch-Blecken von Schmeling, 2000; Benedíková, 2009; Paganová & Bakay, 2010). The service tree can tolerate both acid cambisols with pH values between 5.5 and 6.5 and limestone rendzinas with pH values between 7–8 (Šaly 1998 in Paganová & Bakay, 2010). To demonstrate the service tree habitat requirements better, we can use ecograms; the soil moisture and pH value seem to be the best indicators. Compared to the oak (*Quercus petraea, Quercus pubescens*), the service tree prefers a drier and more alkaline substrate (Kellenberger et al., 2003).

The service tree grows best on deep soil horizons, because it can access water quite effectively there. These trees generally prefer a more porous (more permeable) substrate, but they can tolerate a higher content of clay in the subsoil as well. They can also grow in soils with a high content of stones – in Switzerland and Austria, the service tree does quite well in beech forests on limestone detritus (Kausch-Blecken von

Schmeling, 2000). In Hungary, Slovakia, Croatia, and England, it sometimes grows in shallow soils (less than 0.3 meters deep) with a high content of stones on detritus slopes; it usually appears in a stunted form there. The service tree hates inverse damp regions, such as valleys with rivers and waterlogged lands with a high water table. Higher relative humidity (and related fungal diseases) is another negative factor. Another limiting factor is temperature—late frosts in May can seriously hamper the reproductive ability of blooming service trees (bare in mind that this species is not the most competitive even at the best of times).). As we can see, the species niche of the service tree is rather wide, at least in terms of soil pH values and habitat humidity (Kellenberger et al., 2003).

This broadleaved deciduous tree grows in Europe from Spain up to Turkey and Crimea, and reaches up to Leipzig in Germany and Cardiff in Britain. It does not create any continuous vegetation in the area of its distribution. It is dispersed in forests and open landscape, and often grows near human settlements. The density of service tree distribution in forests is mostly very low.

The service tree naturally occurs in thermophilic forest ecosystems, mainly with alkaline and neutral subsoils—these include, for instance, the Central European thermophilic oakwoods and oak and hornbeam woods, or the sub-Mediterranean thermophilic forests. It can be also found in calcareous beechwods, for instance in Switzerland or Hungary, although it is rare in those regions (Kamm et al., 2009). Within the Czech Republic, there are a few wild service trees in the Southern Moravia region in the Pannonian loess soil oakwood community (the *Quercetum pubescenti-roboris* association of the *Aceri tatarici-Quercion* union), where it is also stated as a diagnostic species (Chytrý et al. 2010). In Slovakia, it naturally occurs in thermophilic oakwoods and calcareous beechwods (Miko, 2004). Kevey (2008) points out several other vegetation types that include the service tree, especially thermophilic oakwoods and detritus forests with a higher concentration of sub-Mediterranean elements. In Serbia, the service tree is usually found in forest communities with dominant populations of pedunculated oaks (*Quercus robur*), Austrian oaks (*Quercus cerris*), and hornbeams (*Carpinus betulus*), but not in those with dominant populations of beaches (Fagus moesiaca) and black pines (*Pinus nigra*) (Miletić & Paunović, 2012). In Southern and Southeastern Europe, the service tree is also found in communities with *Quercus ilex* *and Q. frainetto* (ut *Q. conferta*) (Termentzi, 2006). When growing in extreme settings—on slopes, in detritus soils and on seashores—the service tree adopts a dwarfed, short, shrub-like form, which can only grow to be 5 meters tall with a trunk that has up to 30 cm in diameter (Croatia: Drvodelić, 2015; England: Hampton & Key, 1995; Italy: Bignami & Cammilli 1998). In open landscape—especially in Central Europe—service trees are notable for their large, centuries-old crowns that make them stand out in wineyards and gardens and in fields. In forests, core branches are subdued and crowns are higher, level with nearby trees. Similar to wild pear, apple, or cherry trees, the crowns have a lower volume.

In the original forest biotope, it always grows in small groups or completely isolated. In general, the harsher the climate, the drier and sunnier the place has to be for the service tree to grow there (Kellenberger et al., 2003). In forests, the service tree is more susceptible to competition pressure from other trees. Compared to other *Sorbus* species, it is more vulnerable to shading. Young trees have similar growth requirements as the bird berry (*Prunus padus*). Even though young trees have a relatively good growth ability, the species is competitively weak—this is the reason why these trees never form continuous groups. Coppicing occurs on forest borders, on sunny slopes and in extreme soil positions within forests (Rotach, 2003). Trees that successfully deal with competition grow to the main crown level and they sometimes have rather wide crowns (similar to the oak). It is clear that this species is heliophilous—these trees usually occur on forest slopes that face south-, southeast-, and southwestward (Paganová & Bakay, 2010). The trees that fail to grow to the main crown level of the forest suffer from shading, and they usually die. When growing in nutrient-rich soils, the service tree can grow to be taller than the oak; when service trees reach the harvesting age of 130 years, they can be up to 30 meters tall and their trunks can have up to 60 cm in diameter (Rotach, 2003).

Service tree in historical sources

The first direct written record concerning the Service tree fruit comes from ancient Greece: Theophrastos (371–287 B.C.) described the fruit in detail, also providing a precise description of the Service-tree leaves. The Greek term for the tree is "*Oia*" (οὔα, ὠϊά, ὠά, οὖα), and the fruit (ὄον). A translation (Kausch-Blecken von Schmeling, 2000) of Theophrastos would go something like this: “The Service trees are of two sexes: female, which bears fruit, and male, fruitless. We also discern them by fruit: they range from round to egg-shaped. The fruit can be further differentiated by taste: the round ones are quite fragrant and sweet, the pear-shaped ones are often not very fragrant and are sour”. There are many details in his description, for instance in the autumn the all leaves fall at the same time. Theophrastos describes the grafting of fruit trees.

Other ancient writers focused on the use of the fruits and other parts in medicine and gastronomy (Kausch-Blecken von Schmeling, 2000). In ancient Greece and Rome there are records of the production of cider and wine from Service tree fruit mixed with pears, quinces or medlars. The term “sorbum” can be found in the work “De Agri Cultura” (200 BC) by Roman censor Marcus Porcius Cato (234–149 BC), a form of which *sorbum* has been preserved as a name for the Service tree and even gave the name to a whole genus of rowans. In his book “Agricultural Topics in Three Books”, Marcus Terentius Varro (116–27 BC) categorises Service tree fruit, together with quinces and medlars, such as apples and describes their preservation by sun-drying of cut-up fruit, which is then kept in a cool, dry place. Virgil (Publius Vergilius Maro; 70–19 BC) mentions the production of sorb-apple wine by the Scythians in southeastern Europe (Kausch-Blecken von Schmeling, 2000).

In the Natural History (Naturalis historia, 77 CE) by Pliny the Elder (23–79 CE) describes three types of Service trees and discerns them from the wild Service (*Sorbus torminalis*). He mentions a way of "cutting" the real painting vermillion with goat blood or sorb-apple juice (Ajasson, 1833). Pliny the Younger (Gaius Plinius Secundus; 61–113 CE) describes the preservation of Service tree fruit in a large clay pot insulated by plaster and buried two feet under the ground in a sunny place (Kausch-Blecken von Schmeling, 2000). Described is also the drying of the fruit in a stream of fresh air.

Greeks and Romans disseminate pomology throughout Europe; they planted not only vine, but also Service trees (Rotach, 2003).

Dante Alighieri (1265 - 1321) cites the service tree as a bitter fruit as compared to the fig tree that has a sweet fruit: *«..ed è ragion, ché tra li lazzi sorbi si disconvien fruttare al dolce fico. »* (Dante, Inferno, XV, 65-66) Translation: "..with reason, for among the bitter sorbs it is not natural the sweet fig should come to fruit"(Alighieri, 1989). In literature of 15th and 16th century, we can learn about the use and cultivation (grafting) of the Service tree, but primarily there are the—often verbatim—quotations of ancient such as Dioscorides and Theophrastos, without any new contribution (Moinet, 2009). An Italian painter Giovanni Cadamostra depicted selling the fruit in mediaeval Italy (Verona or Venice) in last quarter of 15th century (Fig. 3 a). The illustration probably captures the selling of the large pear-shaped Service-tree fruits. The accompanying text says that the fruit was supposed to have the ability to protect from cholera and heal the stomach. The manuscript is kept in the Austrian National Library in Vienna (Kausch-Blecken von Schmeling, 2000).

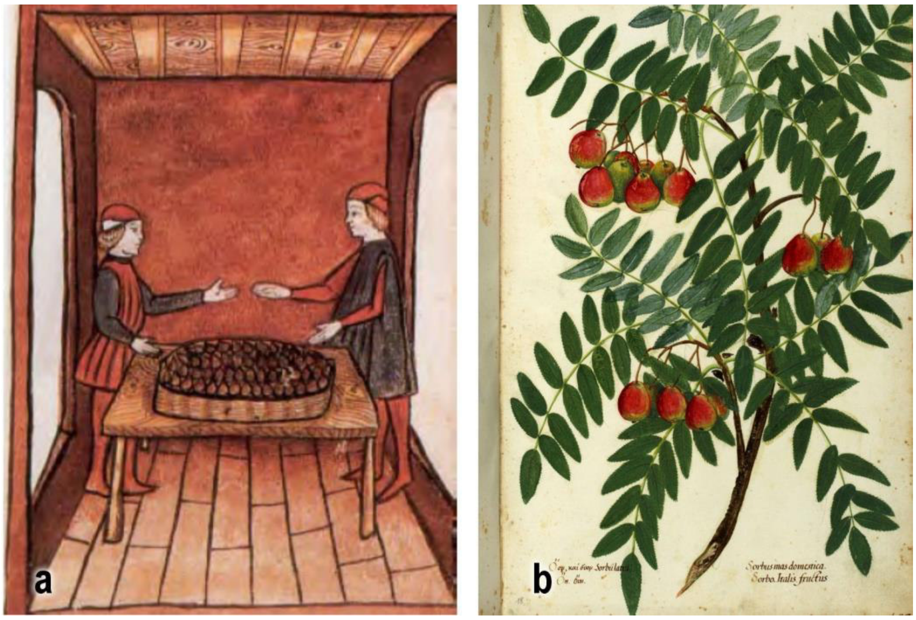

Fig. 3. a) Giovanni Cadamostra depicted selling the fruit in mediaeval Italy, b) Ulisse Aldrovandi (1522–1605) watercolour painting of the Service tree

The oldest mention of the service tree in Czech dates back to 1517. **J. Černý** (1456 - 1530) in his book „Medicinal book, which is called herbarium" writes the following: „The service tree fruit, forest fruit, round, yellowish. The earth element reigns over it, hence its bitterness. It is a good dish for a wet stomach and intestines, it puts an end to fat disorders and stops fever from entering the head. It is a remedy for blood and food vomiting when having chill. Before eating it makes the food more consistent, after eating it makes it soften as bitterness causes contraction of the stomach." (Černý, 1517). The text is accompanied by an illustration of the service tree in blossom (Fig. 4. a) the figure). Italian doctor, naturalist, botanist and entomologist Ulisse Aldrovandi (1522–1605) founded one of the first museums of natural sciences in the world—in his native Bologna. His rich collections of products of nature are exhibited in the Poggi Palace at the University of Bologna. Parts of this collection are the first herbarium specimens and sketches of the products of nature. This is where the very first herbarium specimen and a beautiful watercolour painting of the Service tree were preserved (Fig. 3. b). A caption under a drawing for a book he did not manage to publish is the first occurrence of the modern botanical name—*Sorbus domestica*—that was applied by Carl Linnaeus 200 years later. Linnaeus and Buffon considered Aldrovandi the founder of modern natural sciences.

In 1554 Pietro Andrea Mattioli (1501-1577) comes to Prague as the personal physician of the Archduke Ferdinand of Tyrol who significantly supported also the publication of the herbarium. For this reason the first print of Mattioli's herbal (Fig. 4. c) outside Italy was published in 1562 in the Czech translation by Tadeáš Hájek z Hájku (1525 - 1600) who completed it with his knowledge from Bohemia. In the description he clearly distinguishes botanical species: oskeruše – woskeruše (*Sorbus domestica*), jeřabina- ržeřabina (*Sorbus aucuparia*), břek – břekyně (*Sorbus torminalis*). The scientific name *Sorbus domestica* is spread by print for the first time by means of this work. The herbarium was originally a commentary to Dioscorides' work "*De materia medica*". Mattioli continued to expand the knowledge and thus each new published edition was extended. In 1563 a German translation was published, in 1564 an Italian one and in 1574 a Latin translation was printed in Venice. The interest in this publication was growing, so Daniel Adam z Veleslavína decided to publish new edition of the herbarium. Its translation was made by the professor of the Prague Medical Faculty, Adam Huber z Risenpachu. The woodcut illustrations had to be made new (Fig. 4. b) as Mattioli on his departure from Bohemia took the wooden blocks with him. In another Czech translation of the herbarium from 1596 by Adam Huaer from Riesenpach it is literally stated the following: „The service tree is of two sexes, the male has round apples, the female oval ones.... Domestic or garden service tree is in Italy known tree, in Boemia it is rare and not known to all. In the garden of his Majesty Emporor in Prague several young trees can be found. The fruit is collected in spring, it is tied and hang out or laid down on straw or hay until it become bletted“.

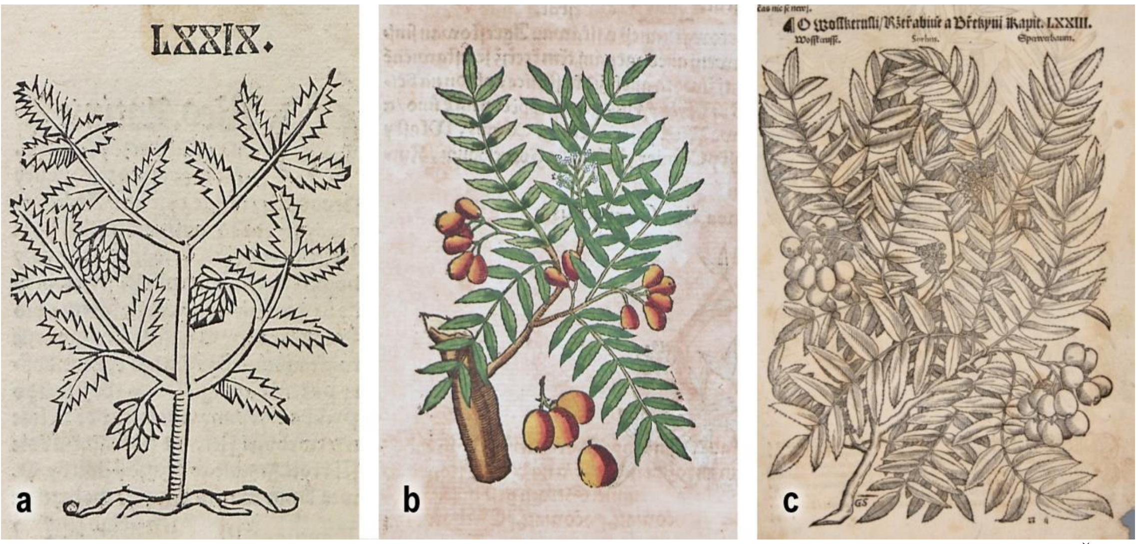

Fig. 4. a) The illustration of the service tree in blossom from book Medicinal book, which is called herbarium, Černy 1517, b) Coloured illustration from second Czech print of Mattioli’s herbal 1596, c) Illustration from first print of Mattioli’s herbal 1562

Botanist and mycologist Pier Antonio Micheli (1679–1737) described and depicted various sorts of service trees for the Grand Duke of Tuscany at the beginning of the 18th century. A multitude of different varieties was described by pomologist Domenico Tamaro (1859–1939) in his work “*Trattato di frutticoltura*” (Tamaro, 1915).

Service tree – utilization of wood

The service tree has one of the most remarkable types of wood. It is distinguished by its hardness and durability, it is resistant to friction, vibrations, and tear. Thanks to these features, it has been used for the production of stress-resistant wooden parts of machines and the production of tools. Like the yew (*Taxus*), laurel (*laurus*) bay tree, hawthorn (*Crataegus*), honeysuckle (*Lonicera*) or the box (*Buxus*), the service tree has one of the heaviest woods among European woody plants. Its specific weight is approximately 800 kg/m^3 (Čížková, 1997). Kausch-Blecken von Schmeling (2000) from Germany claims it to be 880 kg/m^3 and Mathieu from Italy (in Lieutaghi, 1975) states its specific weight to be 810–930 kg/m^3. Its wood is hard, compact but elastic and flexible at the same time. Wood fibres grow spirally with advancing age and the wood is therefore hard to cleave and process on a turning machine. However, it can be polished well; a clean cut can even be polished to achieve the smoothness associated with marble (Lieutaghi, 1975). Spiral growth creates a very decorative effect in the cross section. This forms a unique zigzag arrangement of wood in buttresses, places of forced branching, and often even in the trunk, and this appearance is greatly treasured by cutlers. Wood is bunchy and porous, its growth rings are only hardly distinguishable.. Fresh wood is pinkish, may have a tint of orange, and can turn brown if exposed to air. Dry wood can be brown or brown-red and comparatively dark (Fig. 5. b). Due to its interesting texture, it is often valued in the production of furniture.

Colour differentiation of heartwood from sapwood is possible only in fresh or steamed wood. Medullary rays are usually distichous, sometimes monostichous (Kausch-Blecken von Schmeling, 2000). It is very difficult to distinguish between the woods of individual *Sorbus* species (wild service, service tree, whitebeam, and mountain-ash) even using a microscope. Historical remnants of woods belonging to this group cannot therefore be analysed (Kausch-Blecken von Schmeling, 2000). According to their colour, structure, and texture, woods are well-distinguishable from other *Rosacae* species, e.g. apple and pear wood.

Fig. 5.. a) handle made from service tree wood, b) Dry wood can be brown or brown-red and comparatively dark

In the past, service tree wood was used for the production of wheel toothing in mills or wine press screws because, as one of few types of wood, it can resist high friction, pressure, and vibrations in constructions. Sporadic evidence of such historical tools are found in the whole Central and Southern Europe (Moinet, 2009; Drvodelić, 2015). The service tree was greatly important in the 16th–19th centuries when craftsmen's tools or tools in factories consisted of many wooden parts. Screws (especially the ones in presses), teeth in gearing, cams, and shuttles made of service tree wood were one of the most resistant and durable ones. Turned objects—from rifle stocks through knife handles to piano parts—were made of service tree wood (Fig. 5. a). Up to the present, the best jack planes have been made of service tree wood too. This wood, much sought-after by wood carvers and cabinet makers, is especially valuable for engravers who can hardly find better wood for their jobs (the boxwood quality can compare to it but not in its dimensions; moreover, it is much more expensive). It is therefore processed in the form of planks 23 mm wide, very meticulously smoothed and cleaned, usually composed of paired planks that provide balance in case of prospective deformations. Such wood enables extraordinarily fine engraving (Lieutaghi, 1975). A number of statues in Italian rural areas are also made of service tree wood (Bignami & Cammilli, 1998). In her publication, historical use of this wood in the 19th century in France is recorded by Evelyne Moinet (2009): mill wheel toothing, fruit press screws, cattle yokes, rests, holders, vices, and handles of tools for carpenters and cabinet makers, straw rakes, brake sliders (sliding shoes) for carts and carriages, carriage wheel hubs, shoe moulds and lasts, clock gearing, hay-rake toothing, butcher's blocks and boards, hunting rifle stocks, and occasionally furniture. She also claims that the first printing press letter blocks were made of service tree wood in the Middle Ages.

Service tree wood is currently used locally in Germany, Switzerland, northern Italy, and France for the production of sticks, musical instruments, such as harpsichords and bagpipes, in craft joinery and wood-carving, the production of casting moulds, stress-resistant tools, such as jack planes and chisels, and for various other uses (e.g. shafts, ninepins, billiards and bowling balls, rulers, screws, etc). The traditional production of wooden game balls and sharp knives (piquettes) made from service tree wood survives locally in France (Moinet, 2009). In the manufacture of guns and rifles in Germany, service tree wood is still in demand for the production of stocks; in butchery, it is used for the production of butcher's blocks and swinglebars for hanging the pigs in some regions (Kausch-Blecken von Schmeling, 2000).

The price of good-quality service tree wood is currently high as well: 1 m^3 cost 1,500 Euro in Germany in 2000 (Kausch-Blecken von Schmeling, 2000). The wild service and service tree are most often imported to Germany from France. Recently, France is the biggest European producer of wood from wild fruit trees (pear trees, *Sorbus* species, wild cherry trees). Foresters from France and other countries aim to incorporate service trees into forestry planting plans again. The re-discovered forestry species is valued for its diversification of stands within forest reproduction today.

It can be assumed that a growing lack of heavy tropical woods will increase the significance of service tree wood (Kausch-Blecken von Schmeling, 2000). The quality of the wood and its high price will gradually surely contribute to the productive cultivation of this woody plant in Czech forests too. The introduction of the service tree into forest stands of altitudinal zones 1 and 2 (categorisation for the Czech Republic) will not only increase their biodiversity but also their market value.

Service tree – use of fruits

Recently, the tradition of using service tree fruits for food production or direct consumption disappeared from the region of Central Europe. People are usually not aware of service trees growing nearby. However, the tradition is still kept by some people having the local knowledge of use of service tree—mainly by older people living in the countryside. Just occasionally, one might encounter service tree fruits in markets in European cities—in Italy, France, Luxembourg, Turkey as well as in the Czech Republic. In Southern European countries (Italy, France, Croatia, Greece), you might still find places with specialised shops and restaurants that offer service tree fruit marmalades, sauces, or liquors; occasionally, there are exhibitions featuring these products. In France, Germany, Switzerland, and Northern Spain, you can still get both an undiluted service tree wine and drinks that are mixtures of this wine and an apple wine or a grape wine. In Central Europe—i.e. in Czechia, Slovakia, Hungary, Austria, Germany, France, and Luxembourg—one can sometimes find and taste a unique service tree brandy (Kausch-Blecken von Schmeling, 2000).

Mature fresh fruits are sweet, juicy, and slightly aromatic, and their taste is reminiscent of pears. Fruits with grey-bronze skin taste like medlar fruits. Dried ground fruits taste like figs (Moinet, 2009). After mellowing, the fruits can be used to make a whole range of products: whole fruits can be used to make compotes, the pulp can be turned into purées, sauces, and marmalades, and its juice can be put into ciders, syrups, vinegars, and wines. These fruits are also used to provide new, interesting flavours – they can be served in fruit bowls, with pasta, and with various kinds of meat (including venison). We have many historical depictions that document these uses. For instance, we know that Romans ate large service tree fruits that had been cooked in wine (Moinet, 2009). The juice squeezed from mature fruits has been used as an additive for a few centuries now – it can be poured into ciders and syrups made from other kinds of fruits in order to clarify them faster, to improve their taste, and to prolong their shelf-life (all of these are consequences of bactericidal and fungicidal properties of the service tree juice). The service tree brandy has been discovered much more recently—people first started making it during 18th century (Fig. 6. a).

Service tree fruits are valued for their nutritional value and their healing properties. The latter is the reason why they are still cared for in some places and why there is still at least some interest in them. From a medical point of view, the fruits have a mild diuretic, tonic, laxative, anti-rheumatic, and antipyretic properties; they also act as a source of vitamins and cholagogue, and a strong medicine for digestive problems. Mentions of service tree fruits used as a medicine can be found in documents written in the Ancient Greece and Ancient Rome eras (see the chapter on history). Back then, they were usually used to treat diarrhoea, dysentery, and an upset stomach; they were also used to strengthen the stomach functions (in that case, they were harvested, cut in half, and dried in the sun). Even the first Czech printed herbarium (written by Jan Černý-Niger in 1517) mentions the beneficial effects of these fruits: "These fruits represent a good meal for watery stomach and bowels; they cure ailments brought on by fat and wet heat, and prevent the heat from invading the head. They also prevent choking on blood and vomiting caused by chills. They harden a meal if eaten before and soften it when eaten after, because their tartness contracts the stomach." (Černý, 1517). In 1940, H. Leclerc published findings documenting the positive effects of the regular consumption of service tree marmalade (100 g per day)—the fruits help against bowel irritation and persistent diarrhoea. When consumed in reasonable doses, the fruits can help with many such conditions; if one were to eat too much, however, it would lead to acute constipation (Lieutaghi, 1975). Today, service tree fruits are still used in traditional folk healing as a medicine for stomach ailments and diarrhoea, but also for loss of appetite. According to the old documents, diarrhoeas were stopped with dried fruits, whereas fresh fruits were more suitable as a medicine for constipation, since they have a slight laxative effect.

Fig. 6.. a) Sorb-apple products – Liqueur Cormier and cake with jam from service tree, b) Preserved sorb apples at the Service Tree Festival in Strážnice in 2005

The brandy tastes similar to pear brandy from older cultivars, with a hint of rowan and a slight bitter taste on palate. It has a delicious aroma, often with spicy finish. Brandy, called "oskerušovice" in Moravia, is typical and unique. Pure service tree brandy is often attributed medicinal properties. It helps prevent and treat digestion problems, regulates and clears lymphatic and blood system, and helps with low blood pressure. Its medicinal properties are also currently used to prevent several lifestyle diseases. The curative effects of this distilled liquor are also supported by great interest of healthcare professionals in the entire region of Central Europe. This interest started when the fruit was first being processed and lasts until present time. A bottle of this high quality alcoholic spirit costs around 40 EUR per litre. Samples that have won awards at various tasting events ("košty") can reach up to 100 EUR per litre (Kausch-Blecken von Schmeling, 2000). In the Czech Republic, the price is around 700 to 1000

CZK. On the other hand, the service tree fruit is virtually never used for brandy preparation in the majority of Mediterranean countries, such as Croatia, Italy and Spain (Moinet, 2009). On the Moravian-Slovakian border, the vast majority of private-owned service tree production is used to make brandy. Selected brands are available to the general public at popularization tasting events ("košty") near Strážnice (Fig 6. B).

Aims of the thesis

Sorbus domestica L. is one of the rarest European tree species, of which mainly wood and fruits from the tree were used to. However distribution species, chorological analyses and molecular variability in Central of Europe was not detail and complexly studied yet. Patterns of genetic diversity were uncovered only recently for the part of Central Europe (George *et al.* 2015) and there are still more questions than answers in this field. Therefore, this thesis aims to contribute to our understanding of distribution in Czech Republic. Uncover relationships, between dendrometrical characteristic and fruit types. Furthermore, by analysing the genotypic diversity we aimed at understanding the relationship between and among Moravian populations and selected European populations. The thesis consists of the following parts:

CHAPTER 2: *Sorbus domestica* L. at its northern Pannonian distribution limits: distribution of individuals, fruit shapes and dendrometric characteristics

This chapter concentrates on detailed distribution service tree in the White Carpathians. The chorologic data are discussed in relation to climatic data and further to dendrometric characteristics and morphology of fruits. Indirect evidences for anthropogenic origin of populations as well as need for conservation is disccussed.

CHAPTER 3: Distribution maps and comments *Sorbus domestica,* et Distributions of vascular plants in the Czech Republic. Part 3

This chapter describes in detail distribution of service tree in Czech Republic. Furthermore, focus on origin archeotypes (spontaneous escapes or deliberately planted in the countryside and uncertain). It extends the Chapter 2 with discovered localities in Bohemia and Moravia.

CHAPTER 4: Genotypic variability of *Sorbus domestica* in Central Europe suggests its anthropogenic origin.

This part describes patterns of genotypic variability of Central European populations (with emphasis to Czech Republic) and compares it with selected European populations. Absence of significant population structure suggests its long-term and continuous cultivation.

CHAPTER 2:

Sorbus domestica L. at its northern Pannonian distribution limits: distribution of individuals, fruit shapes and dendrometric characteristics

Zdeněk Špíšek
Andrea Uherková
Marek Svitok
Radim J. Vašut
Timothy F. Sharbel
Bohumil Travniček

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Abstract:

Fruit species play an important role in human nutrition. For this reason, they have been cultivated for millennia. Their cultivation and domestication have impacted species distribution considerably. Wild relatives of such species are often rare in Europe and are threatened by loss of habitat and landscape fragmentation. Knowledge of the distribution and biological characteristics of populations is crucial for further species conservation. We investigated the detailed distribution of the service tree (*Sorbus domestica* L.) in the White Carpathians, which represents the largest occurrence of the species at its northern distribution limit in Central Europe. We recorded 473 individuals in the studied region, compared their habitats, fruit type, dendrometric characteristics and the climate conditions at the sites. Our data suggest that the occurrence of the species is most likely of human origin and that the vast majority of trees grow in orchards, vineyards or on open landscape (72.7%). The comparison of fruit types has not revealed a strong pattern, although fruit types have apparently been selected by growers. Although most documented trees probably have an anthropogenic origin, they represent an important element in the landscape of Central Europe that requires protection.

Introduction

Collecting fruits of wild plants has played an important role in the livelihoods of people since the Palaeolithic era, long before plant domestication (Harlan, 1975). The domestication of the tree fruit species started several millennia after the domestication of cereals (Janick, 2005), overlapping with the early cultivation of wild fruit species. Fruits were an important source of nutrition and energy, especially during famine or migrations (Goldschmidt, 2013). The development of pomiculture progressed considerably during the late Neolithic and Bronze Ages between 6000 and 3000 BC, since the Mediterranean fruits were cultivated (Zohary & Spiegel-Roy, 1975; Janick, 2005). The vast majority of fruit trees originated in the Middle East (Tischler, 1965) and later spread to Europe during the agricultural expansion or later with ancient Greek or Roman civilisations. Evidence of ancient use of fruits is provided by art, wherein depicting fruit motifs was common in ancient civilizations such as in the Sumerians, Egyptians, and Mesopotamians; the oldest pictorial evidence of fruit growing comes from recent Iraq dating approximately 3000 BC (Janick, 2005). The fruit-species cultivation and domestication shaped not only their species genomes via selection and hybridization (e.g., in *Malus*; Velasco et al., 2010; Nikiforova et al., 2013), but also impacted the species distribution. Distribution of woody fruit species and their wild relatives in Europe usually reflects human influence. Specifically, species such as *Prunus cerasifera*, *Malus domestica* or *Pyrus communis* occur frequently on ruderal or semi-ruderal sites in cultural landscape, whereas species such as *Pyrus pyraster*, *Malus sylvestris*, *Prunus brigantina* and other relatives of domesticated fruit species have either geographically limited or scarce distribution in their natural biotopes due to their disappearance and landscape fragmentation. *Sorbus domestica* (a service tree) is a species that has been cultivated for fruit for millennia and has a scarce distribution in both cultural landscape and natural biotopes.

The broad genus *Sorbus* belongs to the apple tribe (*Maleae*, syn. *Pyreae*) of the Rosaceae family, which is known for its young evolutionary origin and reticulate

Fig. 1. Habitus of the *Sorbus domestica* tree. Left: old tree with broad tree crown growing in the garden (orchard). Right: young tree with the high trunk and absent branches growing in forest

evolution (Robertson et al., 1991; Campbell et al., 2007; Potter et al., 2007). The genus *Sorbus* includes approximately 127 species in Europe and North Africa and approximately 250 species widespread in the northern hemisphere (Aldasoro et al., 2004). Moreover, the genus *Sorbus* is paraphyletic with complex evolutionary and controversial taxonomy (Robertson et al., 1991; Campbell et al., 2007; Potter et al., 2007), and the species traditionally classified in this genus are split into five genera (*Sorbus* s.str., *Aria*, *Chamaemespilus*, *Torminaria* and *Cormus;* Robertson et al., 1991; McAllister, 2005). The apple tribe genera easily hybridize among themselves (including *Sorbus* s.l.) except a few taxa (such as *S. domestica*), which do not hybridize even with the closest relatives (Robertson et al., 1991).

Sorbus domestica can be grouped in the monotypic genus *Cormus* if the phylogenetic approach is applied on the genus *Sorbus* s.l. Unlike other *Sorbus* s.l. species, *S. domestica* is taxonomically homogeneous, not forming any hybrids or apomictic accessions (Kárpáti, 1960; Warburg & Kárpáti, 1968; Scheller et al., 1979; Nelson-Jones et al., 2002). Today, the species is rare in Europe, with the highest frequency of occurrence in the Mediterranean Europe (Balkans, Italy, southern France) and a scattered distribution across Central and Western Europe, extending to Crimea in Ukraine, eastwards, and Northern Africa, southwards (Bignami & Cammilli, 1998; Moinet, 2009; Drvodelić et al., 2015; George et al., 2015; Poljak et al., 2015). It has a two-millennia-long tradition of cultivation in the Mediterranean region dating back to ancient Rome (Brütsch & Rotach, 1993), with the oldest record from Theophrastos (371–287 BC) in ancient Greece (Kausch-Blecken von Schmeling, 2000). The service tree is tolerant to xerothermic climate conditions and water deficit (Rotach, 2003; Pagan & Paganová, 2000; Paganová, 2008; Paganová et al., 2015). Fruits are used in pharmacology, folk medicine, fresh consumption and processing or honey and cider production (Kausch-Blecken von Schmeling, 2000; Végvári, 2000; Termentzi et al., 2006).

Species occurrence in Central Europe (including Slovakia, Austria and Czechia) is divided into several discontinued areas and is a northern limit of its distribution area in this part of Europe (Enescu et al., 2016). In Czechia, it grows only in two large meta-populations in Central Bohemia (Bohemian Central Uplands) and in the south-eastern Moravia, which shares a border with Slovakia (the White Carpathians) (Lepší et al., 2016). Several scattered and small populations are found in the other regions of Moravia (Úradníček et al., 2009). The occurrence in the White Carpathians extends across the border with Slovakia and continues across the Western Carpathian Mountains. In Slovakia, they occur in the warmer foothills of the Carpathians (especially the White Carpathians, Small Carpathians, Štiavnické Vrchy mountains, Strážovské Vrchy mountains, Tokai region – Miko & Gažo, 2004; Paganová et al., 2015)

The aim of this study was to evaluate the distribution of the true service tree in the White Carpathians, specifically in the region having the largest occurrence in Central Europe. Further, we aimed to explain the role of humans and their impact on the species distribution here based on regional climate, ecology and dendrometric parameters. We researched whether there is pattern in fruit shape indicating selection by humans for attractive fruit shapes, and whether the biotope and dendrometric characteristics can explain the origin of individuals in the studied region.

Materials and Methods

Study site

The study area is located in the White Carpathians, which is the westernmost part of the Western Carpathian Mountains. Its unique nature and landscape are protected as the Protected Landscape Area (PLA) and Biosphere Reserve. Characteristic landscape of the White Carpathians comprises species-rich semi-dry meadows (*Bromion erecti* alliance) often with scattered trees, occurring mainly in the south-western part, extensive areas of beech forests in the central and north-eastern part, and oak-hornbeam forests in the south-western part. The lowland and low situated slopes have a warm climate, slopes of upper locations have mild warm climate, and only top part of the White Carpathians has a mild cold climate. The mean annual temperatures fluctuate from 6.6 to 8.7°C, and the annual precipitation ranges from 665 to 835 mm (Lapin et al., 2002; Tolasz et al., 2007).

In the studied area, *S. domestica* occurrences in the White Carpathians are known in two ecologically/phytogeographically contrasting regions: the thermophilous steppes and the mesophilous forests. On the White Carpathians slopes of the range the species has diffused distribution and can be found mainly in agricultural landscape, affected by man for centuries (Tetera et al, 2006), and usually grows solitary or in small groups, as is typical for this species (Mikic et al., 2008).

Data collection and analyses

The study was carried out during the vegetation period from 2008 through 2016. The study of this tree was focused within the PLA, including the individuals situated out of the border. The field research included both the residential and rural landscape as well forest and non-forest biotopes. The localities of the field research include the whole area of the White Carpathians. The localization of individuals was recorded by GPS GARMIN eTrex 10. The total of 473 individuals was determined and measured. Fruits were collected from various positions throughout the area from August through October during all mapping seasons. The circumference of each sampled tree was measured with a tape-measure to calculate the DBH (diameter at breast height) at 1.3 m above the ground. Tree height was measured by a Suunto PM-5/360 PC hypsometer. Since the species occurs in different types of biotopes, the localities with *S. domestica* occurrence were selected based on the field work and the presence of important landscape elements and divided into six categories: open landscape (124 individuals, 26.3%), orchard/garden (178 individuals, 37.7%), forest exterior (61 individuals, 12.9%), forest interior (24 individuals, 5.1%), balk (44 individuals, 9.3%) and vineyard (42 individuals, 8.7%). Fruits were classified into six categories based on the shape (according to Bignami & Cammilli, 1998): flattened, spheroidal, pyriform, conical, egg-shaped and elliptical (see Fig. 2). The shape was determined on fruits randomly collected on all parts of the tree crown prior to full ripening (i.e. before turning brown and soft). If the fruit shape was variable within individual, it was determined as an average of the prevailing shape. The size of the fruit was not considered because the variability in size is influenced by abiotic factors (see e.g. Miletić & Paunović, 2012).

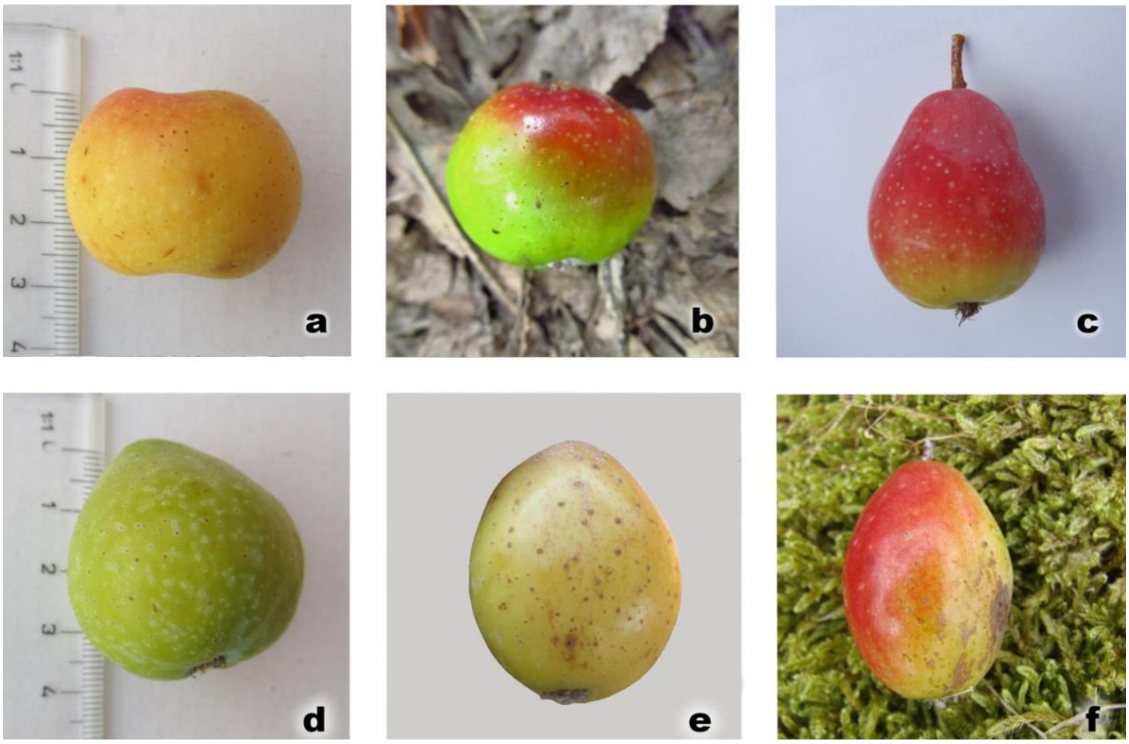


Fig. 2. Fruit shapes of *Sorbus domestica* in the White Carpathians (according to Bignami & Cammilli, 1998): a) flattened, b) spheroidal, c) pyriform, d) conical, e) egg-shaped, f) elliptical

The map data were prepared and the orientation slopes were processed in Geographic Information Systems – Arc View version 3.1. The maps basis was with an obtained digital geographic database ArcČR® 500 v 3.3 for climatic regions (Květoň & Voženílek, 2011). The analysis comprising the altitude and orientation slopes was made in NCSS 9 Statistical Software (2013, Kaysville, UT, USA). Analysis of covariance (ANCOVA) was used to investigate the relationships between height, DBH and the location of service trees. Before analysis, the data on height and DBH were log transformed to linearize data and stabilize variances. The relationship between fruit shape and tree location was fitted using a multinomial model via neural networks (Venables & Ripley, 2002). The analyses were performed in R (version 3.2.3; R Core Team, 2015).

Results

Geographical distribution of service trees

During the study, 473 individuals of the service tree at the Czech and Slovak sites of the White Carpathians were documented. Their distribution is plotted in Fig. 3.

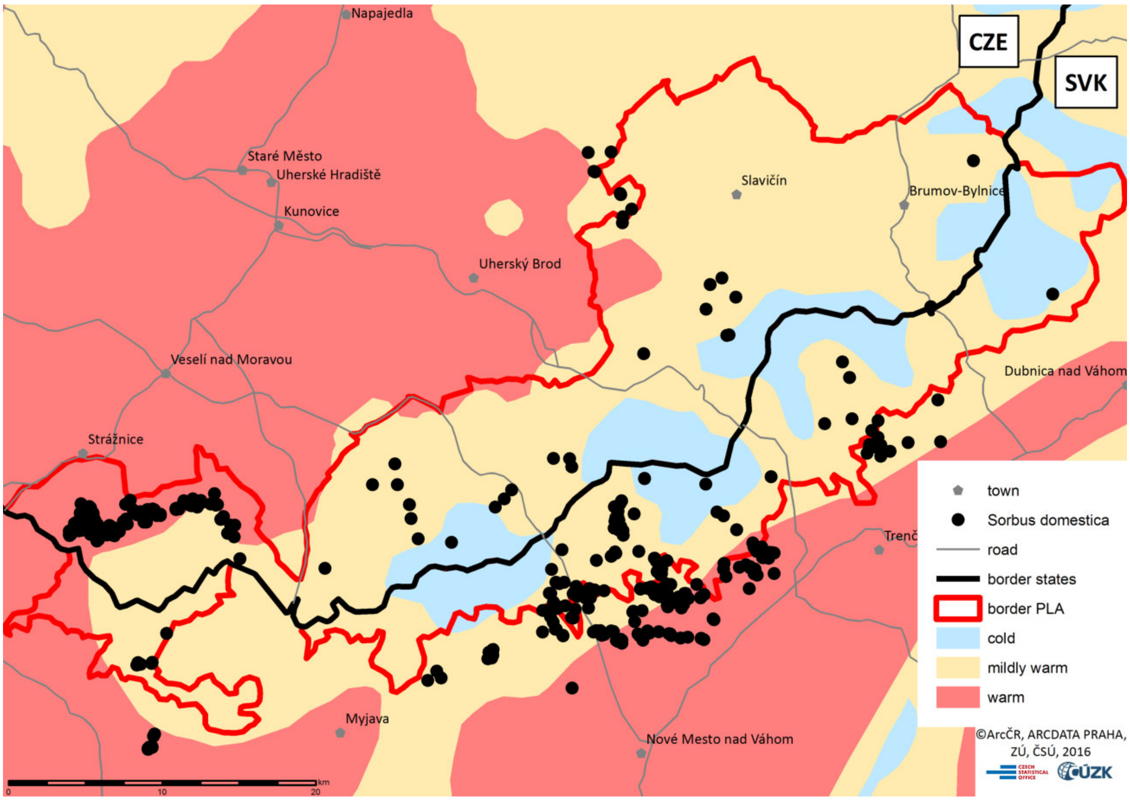


Fig. 3. Climate regions and *Sorbus domestica* distribution in the White Carpathians and their surroundings

The individuals of *S. domestica* forming the largest occurrence were located in the South Moravian region at the Czech site as well as at the foothills of the middle part of the White Carpathians at the Slovak site. According to the climate map, the individuals grow mainly in the mildly warm and moist climate region (48%) and in the warm, very dry or mildly wet regions (51%). Only 1% of the recorded trees were situated in the cold region. The “hot spot” of the service tree occurrence is in the S W at the Czech site of the mountain range, at the Žerotín hill, which lies in the in warm, very dry or mildly wet region; 31.6% of all recorded individuals grow in this region.

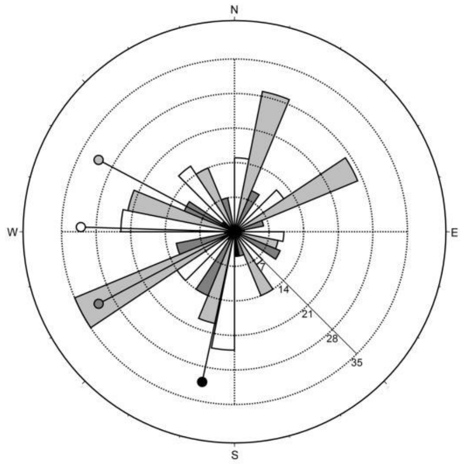


Fig. 4. S – W altitude and orientation slopes of *S. domestica*.
Altitudinal levels: □ 200–299 m a.s.l., ■ 300–399 m a.s.l.; ■ 400–499 m a.s.l.; ■ 500–599 m a.s.l.

Most localities (44.5%) were on altitude 200–299 m a.s.l. (Fig. 4). The most frequent slope exposure in this altitude is west, but many trees grow on south slopes. The second most frequented category of the localities (32.1%) is at the altitude 300–399 m a.s.l. with the most frequent slope exposure towards the west and north-west, but trees often grow on south-west and northeast slopes. Less frequent occurrences (19.5%) were on the altitude 400–499 m a.s.l. with the most frequent slope exposure towards the south-west exposure. Only small part of localities (3.9%) are situated on the altitude 500–599 m a.s.l. and the only single individual was found at an altitude higher than 600 m a.s.l., on the Kykula hill (Chocholná-Velčice village in Slovakia, 662 m a.s.l.), with the southward exposure.

Distribution of fruit types

The site of service trees significantly affects the shape of fruits ($\chi2_{(25)} = 40.8$, p = 0.024). The greatest diversity of fruit shapes was recorded in the forest interior, where all types were discovered (Fig. 5). Flattened fruits were not recorded in the vineyards and balks while elliptical fruits were restricted to vineyards, forests and orchards/gardens.

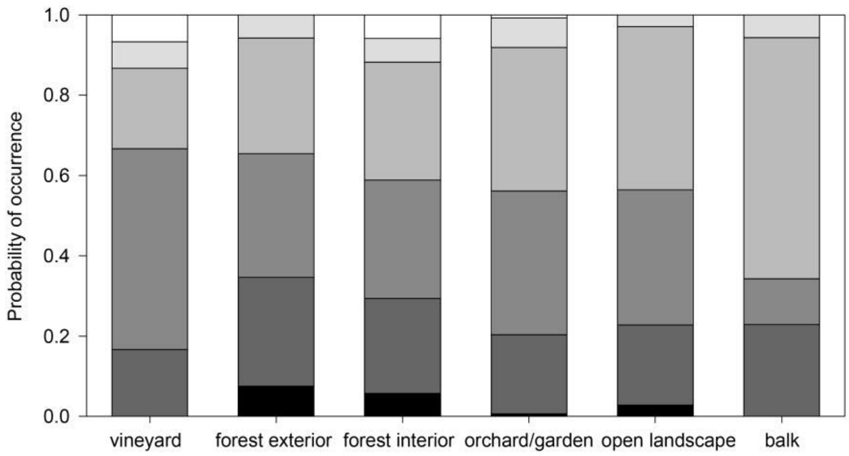


Fig. 5. Fruit shape types of *S. domestica* in different site types. The highest density of fruit shape types was in the region of the Žerotín hill (near Strážnice). The most frequent shapes were the conical (37.1%), pyriform (32.7%) and spheroidal (21.1%). The other types of fruit shapes were rare. Fruit shapes: ■ flattened; ■ spheroidal; ■ pyriform; ■ conical; ■ egg-shaped; □ elliptical

Dendrometric characteristics

The average height of individuals was 11.5 m and the tallest tree was found in the forest interior (approximately 25 m). DBH of the investigated individuals ranged from 0.15 up to 1.45 m. More than a half of the individuals fell within the DBH range 26–75 cm. Some very large trees of *S. domestica* with the DBH more than 1 m (5.9%) were present in this area, and many were still fertile. Supposedly young individuals (DBH < 25 cm) were less frequent (13.2%).

ANCOVA revealed a significant positive relationship between the DBH and height of service trees ($F(1,455) = 142.82$, $p < 0.001$), and this effect was independent of the sampling location (location × height: $F(5,455) = 1.83$, $p = 0.106$), i.e., the rate of height increase with tree DBH was similar at each location with minor exception of forest interiors (Fig. 6). However, location significantly influenced the height of trees

(F(5,455) = 9.00, p < 0.001). The ANCOVA model explained 29% of the variability in tree height.

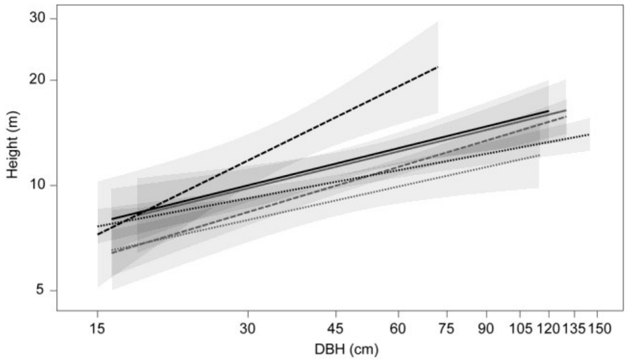


Fig. 6. Results of ANCOVA showing DBH-height relationships for service trees growing at 6 different locations. Least-squares regression lines are displayed along with 95% confidence intervals (grey area). Note the log-scaling of axes. Location: — balk; — forest interior; --- forest interior; --- open landscape; ··· orchard/garden; ··· vineyard.

There was a considerable variation in dendrometric parameters among localities. Notably, shape (DBH-to-height ratio) of the trees growing in forest interiors was significantly different from the otherlocations (Fig. 7). According to the evaluated DBH categories and different localities (Fig. 7), there was a tendency of increase in quantity of trees with an increase in the DBH category in the open landscape. The same pattern was found for individuals growing in the forest exterior. The largest individuals, with a DBH greater than 101 cm, grew mainly in the open landscape and in orchards/gardens (37.5% in both categories); 17.9% of these largest trees were growing in the forest edge, while only a few were found in the forest interior or in the balks.

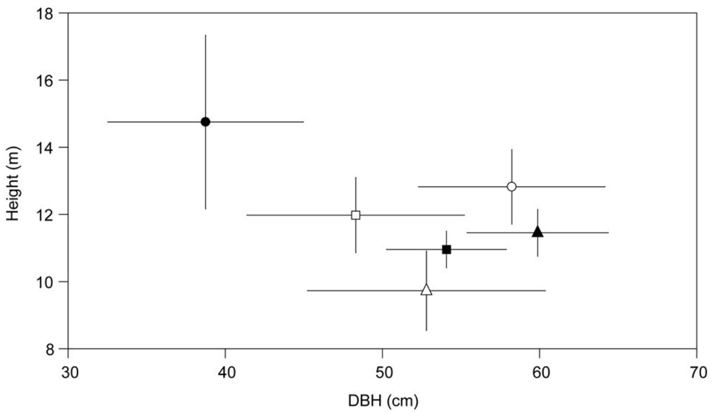


Fig. 7. The effect of tree location on the DBH. Circles represent mean values, and error bars are 95% confidence intervals. Note the log-scaling of the ordinate.

Location: □ balk; ○ forest exterior; ● forest interior; ▲ open landscape; ■ orchard/garden; △ vineyard.

Discussion

Sorbus domestica mainly grow in warm and dry climatic regions (51%) or mildly warm and moist climatic regions (48%) with most occurrences at the colline altitude between 200 and 399 m a.s.l. Notably, occurrences of the northern slopes of the White Carpathians belong to a warmer climatic region than those ones in the southern slopes of the studied hills. From a phytogeographic point of view, at least some occurrences (especially in the dry climatic regions) might resemble the autochthonous population; however, our data on the distribution patterns and the morphological data primarily (discussed below) suggest an anthropogenic origin of studied populations.

Service tree in the White Carpathians

The occurrence in the White Carpathians represents the northern limit of the species distribution area in this part of Europe (Kausch-Blecken von Schmeling, 2000). Although the populations are small and scattered across the studied region, they represent the largest and the most vital metapopulation of the service tree in Central Europe. This service tree prefers warm or mild warm climate regions, and a limiting factor for its distribution is spring temperature: late frosts in May (during blooming) can seriously hamper the reproduction ability of the species.

In the White Carpathians, the service trees prefer areas with altitudes between 200 and 600 metres above sea level, and only 23.4% of the *S. domestica* individuals grow in the altitude between 400 and 599 m a.s.l. These data concur with its documented requirements for the dry and xerothermic biotopes. Approximately 90% of the formerly researched *S. domestica* occurrences (Paganová, 2008) are located at a similar altitude, but those in more continental climate grow up to 400 m a.s.l. In the northernmost part of its natural distribution area in Saxony-Anhalt (Germany), the service tree grows at low altitudes between 140 and 300 m a.s.l. In the southern parts of Europe, it grows in higher altitudes, such as in Switzerland (between 380 and 700 m a.s.l.; Kamm et al., 2009), Bavaria near Münich (up to 800 m a.s.l.) or the Balkans (between 600 and 900 m a.s.l.). In the warmest regions of the Mediterranean, it has been documented in the higher mountainous altitudinal level, specifically 1350 m a.s.l. (Kausch-Blecken von Schmeling, 2000) or 1400 m a.s.l. in Spain (Mikic et al.,, 2008). In the White Carpathians individuals of *S. domestica* are scattered as is typical for this species, with the densest occurrence in warm climate regions. The most distinct population grows in the larger area of the Žerotín hill (nearly 32% of documented individuals). The hill slopes host fragments of the natural thermophilous oak forests of *Quercus pubescens* (Jongepierová, 2008; Chytrý et al., 2010), but its foothills are covered with centuries-old vineyards. Due to the large number of service tree individuals and natural characters of the forests here, the autochthonous origin for the populations in this area was hypothesized; however, our data suggest an anthropogenic origin. A key argument for the non-natural origin of the Žerotín population is the spatial distribution. Many individuals grow in an agricultural landscape, particularly as single individuals or groups of a few plants between the fields and vineyards. Occurrences in the forest biotopes here are scarce and probably represent a spontaneous dispersion from the agricultural landscape than a relic occurrence of former natural populations.

The juice from unripe service tree fruits is used for wine clarification and stabilization (Hrdoušek et al., 2014). The vine-planting tradition in the Žerotín hill has been known since the 15th century. The occurrence here follows its historical use as a fruit tree, mainly cultivated in orchards, gardens or between vineyards. The occurrence in the Žerotín hill illustrates the overall distribution in the area. The Czech populations, 8.7% in the vineyards and even more in gardens and orchards (37.7%) were compared. The service tree in the studied agricultural landscape usually grows with other fruit trees, which strongly supports its non-natural origin. Similarly, a high proportion of solitary single individuals (26.3%) growing in the meadows, between fields, confirms the anthropogenic origin of this important landmark tree.

The occurrence of trees in the agricultural landscape alone is not evidence for the non-natural origin of trees. The analysis of the service tree population distribution in the Tokai hills in Hungary revealed that very old trees scattered in the agricultural landscape represent a relic occurrence of trees (Rapaics, 1940; Nyári, 2010). During the transformation of the forested landscape to the agricultural landscape, the *S. domestica* trees were retained on sites. Another explanation of natural origin is provided by the local tradition documented, for instance, by Holuby (1888), because people used to plant seedlings or root suckers, from woods (natural sites), in their gardens. This was documented by the local people of the Maršov, Hroznová Lhota villages (Hrdoušek et al., 2014). However, these kinds of natural occurrences do not fit into the spatial patterns of the studied local populations, as *S. domestica* is currently missing in natural oak forests in the whole studied area. Analyses of the morphological characteristics of individuals in the studied populations further support the human origin of cultivated trees in the studied region.

Morphological characteristics of studied individuals

The fruit shape types were compared according to Bignami and Cammilli (1998) to analyse phenotype variation within and among studied individuals, although some authors (Miletić & Paunović, 2012) distinguish only two shape types – apple-shaped (62.4%) versus pear-shaped (37.6%). When we focus on the distribution of different fruit shape types in all areas (Fig. 8), there was no obvious pattern, although there is a presumption that individuals very close to each other have the same fruit shape type.

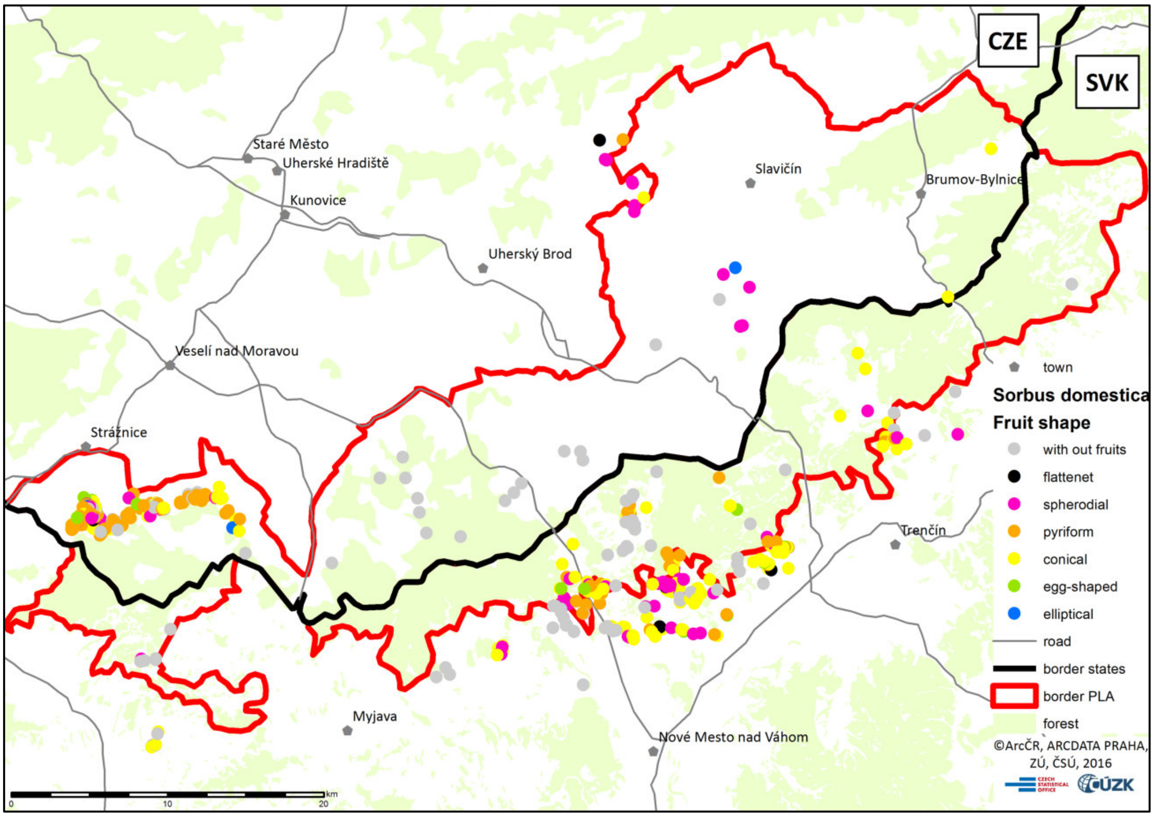


Fig. 8. Spatial distribution of the *S. domestica* individuals according to fruit shape

Trees with elliptical fruits individuals were found to be very rare in the studied area (1.1% out of all known samples). These phenotypes probably originated from the spontaneous dispersion and their low frequency is probably a result of negative selection by a man. Another factor supporting the non-natural origin of studied localities is the fact that only the biotope of the forest interiors has all fruit-shapes at the locality. However, these sites do not represent the natural oak forests; they are usually semi-ruderal forests often consisting of pioneer woody species (like *Prunus avium, Prunus spinosa, Fraxinus excelsior* and *Acer platanoides*). The character of such populations indicates spontaneous dispersion (especially by birds) from occurrences in an agricultural landscape.

The contrasting pattern offers a distribution of fruit types at non-natural sites (orchards and vineyards). The most favourite fruit shape types for human use are the pyriform and conical, both providing seemingly larger fruits than previously mentioned types. Both fruit-shape phenotypes were documented with high frequency, notably in orchards and gardens, specifically conical fruit-shape phenotype in 37.1% and pyriform one in 32.7% of all documented individuals. Combining the fact about the character of sites (single trees or group of few trees in orchards or among fields) and high proportions of phenotypes selected by humans for use (nearly 70%) at such localities, supports the hypothesis for anthropogenic origin. The limit of phenotype comparison is the fact that trees (especially when they are more than 100 years old) set seeds every 2–3 years only. Further, it is known that individual trees have some variation in fruit shape depending on their health conditions or on the weather in a particular year (Kausch-Blecken von Schmeling, 2000). Although there can be an error in our data due to the phenotypic plasticity of individuals, we documented strong patterns favouring human-selected phenotypes at the studied sites.

Previous studies in Slovakia showed a similar, human-influenced pattern in the distribution of human-preferred fruit shape types. Among 97 trees in six regions of Slovakia, the egg-shaped (56.7%) and conical (23.4%) fruits were the most frequent types. Historically, the fruits were selected and cultivated based on their size, colour, taste, maturation period, and their resistance against diseases (Kausch-Blecken von Schmeling, 2000; Nyári, 2010). Therefore, the biggest fruits occur in places with a long history of service tree cultivation such as in Southern and Central Italy, Central France, Central Germany and in Crimea (Bignami & Cammilli, 1998; Kausch-Blecken von Schmeling, 2000; Miko & Gažo, 2004; Tetera et al., 2006, Benediková, 2009; Brindza et al., 2009).

We further analysed the DBH of individuals and their heights, which we found that there is a continued proportion between the DBH. Further, the DBH is continuously correlated among the biotopes. Only a weak (not significant) higher proportion of larger (putatively older) trees were documented for the agricultural landscape, not providing any strong evidence for their origin from the natural forest from periods before the agricultural use of the landscape. The proportion of the DBH and the height is not significantly obvious within the individuals growing in the forest interior because of their different strategy in the canopy, which forces them to be tall. We predict that the origin of these forest individuals is natural and is not affected by humans. The natural reproduction could be ensured by the large amount of fruits, and thus, the seeds, mainly during seed years. Steiner et al. (2009) observed higher rates of natural regeneration of *S. domestica* at particular sites in the Vienna Woods hills: clearcuttings (8 young plants per hectare) and on deer-free sites (6 plants/ha). The species is a light demanding plant and on sites with open canopy it successfully competes for light with other woody species. It has the optimum conditions for growth in the open land or scattered woodlands (as it is known from the Mediterranean populations) and these artificial clear cuttings help the young plants successfully overcome the insufficient condition in fragmented Central European oak forests. Although we did not study this factor in detail, it likely plays an important role at our sites too. Forest biotopes at studied localities represent rather closed forests (see example on Fig. 1) and not the natural oak forests with scattered distribution of trees.

The role of ruminants has to be considered as well, although we have not collected such data in the field. Generally speaking for whole Czechia, the cloven-hoofed game is alarmingly overpopulated in the region and causing damage to forests (see e.g. Annuals Reports on the Environment of the Czech Republic issued by the Ministry of the Environment of the Czech Republic; www.mzp.cz).

According to our research, most individuals in the White Carpathians grow on the western and southern orientation of the slopes, but trees that grow at a lower altitude do not have a preferential orientation of the slopes. The most significant is the human impact on planting. The higher the altitude, the bigger the probability of the trees occurrence in S–W or S exposition. Generally, the service tree prefers slopes with plenty of sunlight facing west-, southwest-, south-, and south-eastward. Local differences in the species composition may, therefore, be primarily explained by human settlement (Jongepierová, 2008).

Conclusions

For this part of Europe, the occurrence of the species in the White Carpathians represents the northern distribution limit of the natural area of distribution (Kausch-Blecken von Schmeling Blecken, 2000; Enescu et al., 2016). The occurrence of the species here is scattered; however, it is relatively frequent compared with other regions of eastern Central Europe. Our data suggest that studied occurrences are most likely of anthropogenic origin. However, the largest populations (such as the Žerotín hill) can be dated to two centuries ago only as a result of the advent of vine cultivation in the region. Since the natural origin of *S. domestica* was continuously discussed and considered of an archaeophytic origin, it is not listed in the Red Lists of both Czechia and Slovakia (Grulich, 2012; Feráková et al., 2001). However, it is an important species from a cultural point of view. The long-time tradition of its use in cultivation, important landscape-mark tree, or its ornamental value (large, broadly branched tree) makes the species important for its conservation in nature. There is a documented decline in the species frequency in the White Carpathians since the 19th century. It is due to intensive forest planting followed by the landscape damaging due to socialistic agricultural managements by field consolidation in the 50s decade of the 20th century (Hrdoušek et al., 2014; Jakubec et al., 2014). Recently, there is only limited regeneration of the surviving old trees (often having bad health conditions) in the regions. The younger individuals are usually planted in the gardens or orchards but are missing in the open landscape. The decline of the occurrence of species is a general problem documented in most European countries due to an overall reduction in the number of individuals, habitat fragmentation and isolation of populations, lack of natural regeneration, and disturbance of the natural metapopulation structure due to human impact (Young et al., 1996; Rotach, 2003; Enescu et al., 2016).

Sorbus domestica is a prospective fruit species with a high value for the landscape; thus, it is important to protect the populations of this species, even if they are not of natural origin. Cultivated individuals might represent interesting traits for future use as well as a reservoir of genetic variability of the highly fragmented population in Europe.

CHAPTER 3:

Distribution maps and comments *Sorbus domestica.* Distributions of vascular plants in the Czech Republic. Part 3

Martin Lepší

Petr Lepší

Zdeněk Špíšek

Karel Kubát

Lepší M., Lepší P., Špíšek Z. & Kubát K. (2016): Distribution of *Sorbus domestica* in the Czech Republic. - In.: Kaplan Z., Danihelka J., Lepší M., Lepší P., Ekrt L., Chrtek J. jr., Kocián J., Prančl J., Kobrlová L, Hroneš M & Šulc V., Preslia 88: 459–544, pp. 5515, 517-518.

Introduction

Since the project of mapping plant distributions in the Czech Republic was launched in 2014, a modern plant record database Pladias has been established and 162 grid distribution maps have been produced by taxonomic experts, based on critically evaluated and sorted records, and published in two papers (Kaplan et al. 2015, 2016). The ultimate aim of this effort, started within the PLADIAS project (www.pladias.org) and planned to continue as a series of publications, is to prepare the basis for a complete atlas of the distribution of vascular plants in the Czech Republic.

From April to August 2016 the Pladias database has increased by about 2,900,000 new records. Of these almost 11,000 records resulted from critical examination of herbárium specimens by taxonomic experts.Maps of further 105 taxa were finished at the beginning of August 2016 and these are published in this paper. These maps include both native and alien species, rare species confined to small geographic areas as well as widespread species, and endangered as well as common species. About one third of the Czech endemics (Kaplan 2012), which is a group of plants that deserves the highest attention and conservation priorities, are mapped. A great majority of the maps resulted from recent detailed revisions of taxonomically critical groups, such as *Amelanchier* (Lepší & Lepší 2008), *Asplenium* (Ekrt 2008, Ekrt & Štech 2008), *Cerastium* (Letz et al. 2012, Vít et al. 2014), *Hieracium* (e.g. Chrtek 2004, Chrtek et al. 2007), *Lemna* (Kaplan 2010), *Sorbus* (e.g. Lepší et al. 2015) and *Symphytum* (Kobrlová et al. 2016), which have refined taxonomic concepts and the delimitation of taxa, and in some cases also led to the discovery of new species or first country records.

Materials and methods

Taxonomic scope

The following groups of vascular plants are mapped: native taxa, naturalized aliens and most casuals, and selected hybrids. Distribution maps are produced for species and subspecies, and in exceptional cases also for varieties or infrageneric taxa (e.g. sections). Plants of species groups that are difficult to assign to species may be mapped as species aggregates. Field crops and plants deliberately cultivated in gardens and parks are not included in the mapping project. Nomenclature, taxonomic concepts and delimitation of 460 *Preslia 88: 459–544, 2016* species aggregates mostly follow Danihelka et al. (2012), with differences indicated where necessary. For taxa not included in that checklist, a taxonomic reference is given. Publication of maps does not follow any alphabetical or systematic order but those maps that have resulted from recent revisions are printed preferentially.

Data sources

All relevant floristic data sources are used. Major national herbaria and some local and foreign collections, incl. BRA, BRNL, BRNM, BRNU, CB, CBFS, CESK, CHEB, CHOM, FMM, GM, HOMP, HR, KHMS, LIM, LIT,MJ,MMI,MP,MZ, NJM, OH, OL, OLM, OMJ, OP, OSM, OVMB, PL, PR, PRA, PRC, ROZ, SAV, SOB, SOKO, SUM, VM, WRSL, WU and ZMT (acronyms follow Thiers 2016), were consulted as the main source of taxonomically revised records. Most records for maps of common and easy-toidentify taxa come from the recently developed Pladias database (hosted at the Institute of Botany, Průhonice), which has integrated all available records on the distribution of the vascular plants in the Czech Republic. Among the most important incorporated databases are the Database of the Distribution of Vascular Plants in the Czech Republic (FLDOK), the Czech National Phytosociological Database (CNPD), plant records from the Floristic Summer Schools and other activities of the Czech Botanical Society, the Species Occurrence Database of the Nature Conservation Agency of the Czech Republic (NDOP) and the Database of Forest Typology of the Forest Management Institute of the Czech Republic (DLT). Unpublished field records previously entered into the Pladias database by the authors of maps or regional contributors were also considered.

Procedure of mapping

All records used for mapping are entered into the Pladias database and geographically sorted according to the traditionally used CEBA (Central European Basic Area) grid template (Niklfeld 1999) divided into quadrants of 5 × 3 arc minutes (corresponding to approximately 5.5 × 5.9 km). The territory of the Czech Republic is covered by 2551 quadrants, of which 2181 are completely within the border of the country. Individual records as well as the whole distribution pattern of each taxon are checked and evaluated by the author of a particular map in a web-based mapping interface of the Pladias database. Maps of taxonomically critical groups are based solely or mainly on herbarium records revised by taxonomic experts; these cases are indicated in the text accompanying the particular map. Maps of all other taxa are based on records from databases, literature and herbaria, which were scrutinized by the authors of the respective maps. Records used for producing maps are listed in Electronic Appendices 1–105. In selected maps, native versus introduced occurrences are distinguished and corresponding records in the database classified accordingly. Draft distribution maps and the background records are released in a web-based review process for scrutiny to field botanists, regional collaborators and members of the Czech Botanical Society. Their comments and additional records are collected in the database and returned to the responsible specialists for consideration before producing final distribution maps.

Final maps and comments

The treatment of each taxon consists of a grid distribution map and an accompanying text; authors ofmaps are indicated in the figure captions, and they also took the major part in preparing the first drafts of the respective texts. Maps are displayed using spherical Mercator projection (EPSG:3857) where meridians and parallels are shown perpendicularly, and the mapping CEBA grids are thus nicely displayed. The background relief was derived from the SRTM data (http://www2.jpl.nasa.gov/srtm/, the version provided by http://srtm.csi.cgiar.org), and the river network was adapted from data provided by CENIA (www.cenia.cz). When appropriate, different symbols are used in the maps in order to distinguish one of the following attributes of the plant distribution records: (1) recent versus old records, (2) native occurrences versus introductions, or (3) records based on revised herbarium specimens versus all other records. These classifications of records are used only for those taxa where such distinction provides important information and, in addition, the amount and quality of records are sufficient. The mapping symbols used to indicate the different attributes of the records in the particular grid cell are shown in Table 1. Symbols specific to individual maps are explained in their captions. To save space, rare taxa of the genera *Hieracium* and *Sorbus* with distinct distributions are shown in maps in groups of 2–4, with symbols and annotations of individual taxa in the maps distinguished using different colours. In the caption to each map, counts of occupied quadrants are indicated according to the symbols used in the map; uncertain occurrences are not included in the counts. The accompanying text includes the accepted scientific name, a brief outline of the total distribution, information on habitats occupied by the species and a description of its distribution in the Czech Republic. Where appropriate, comments on the taxonomy, biology and details of the spatial and temporal dynamics of the distribution are given.

Distribution maps and comments

Sorbus subg. *Cormus*

Sorbus domestica (Fig. 62)

Sorbus domestica, the only member of *S.* subg. *Cormus*, is distributed in central and southern Europe from eastern Spain to southern Great Britain, northern France, Germany, Slovakia, Hungary and the Balkan Peninsula, with outposts in the Black Sea area, Anatolia and in Morocco and Algeria in northern Africa (Rotach 2003, George et al. 2016). The species has been planted in some warm areas of the Czech Republic as a fruit tree since the Medieval period (Pyšek et al. 2012) and it has become widely naturalized in the České středohoří Mts in north-western Bohemia and in several parts of southern Moravia (e.g. the Pavlovské vrchy, Ždánický les, Chřiby and Vizovická vrchovina hills and the Bílé Karpaty Mts). The southernmost and easternmost localities in Moravia are close to the northern limit of its assumed native distribution area in Slovakia or Hungary (Kurtto 2009) and perhaps some of them may be native. However, direct evidence of its native occurrence in southern Moravia is lacking. In the České středohoří Mts it is almost solely confined to areas where *Quercus pubescens* also grows. Because it has been grown not only in villages but commonly also planted in vineyards and elsewhere, it is often difficult to distinguish intentionally planted individuals from bird-sown escapes. The map therefore distinguishes spontaneous escapes and naturalized populations from trees of uncertain origin, including those planted outside settlements. The trees planted in gardens and parks are not mapped. The escaped plants are found in thermophilous oak and open hornbeam forests, forest edges and scrub. Most of the records are from the planar to colline, rarely up to the supracolline vegetation belts, with an altitudinal maximum at 470 m. *Sorbus domestica* is classified as a casual archaeophyte in the Czech Republic (Pyšek et al. 2012).

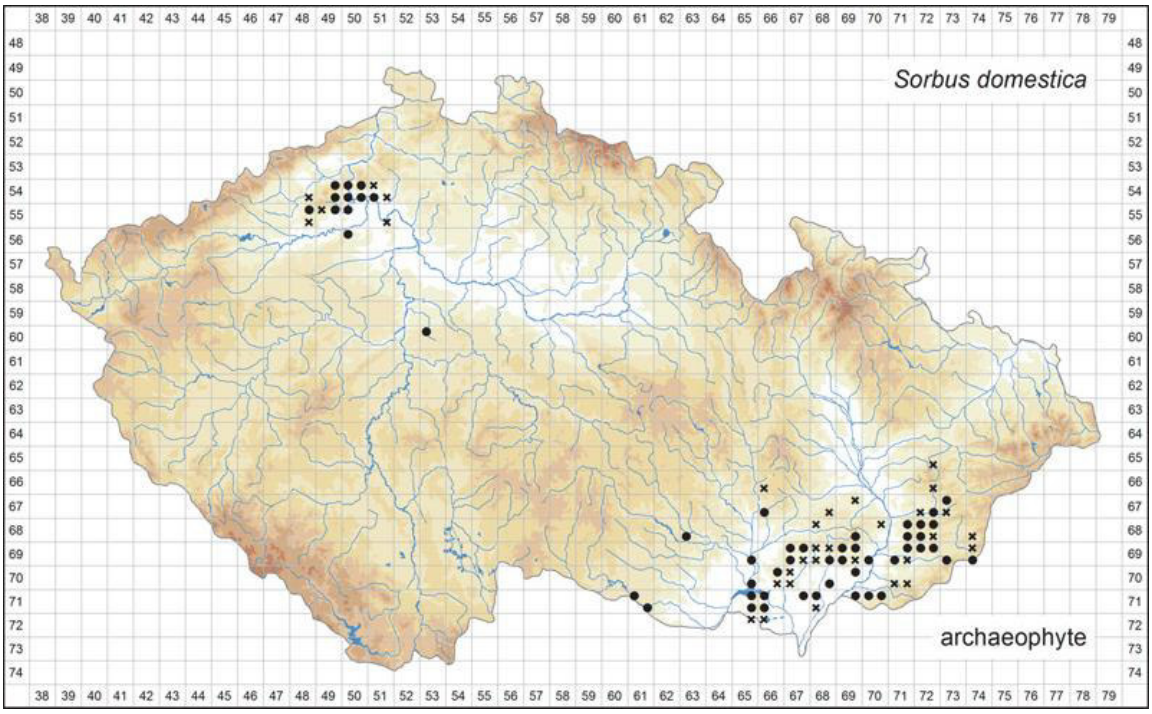


Fig. 62. – Distribution of *Sorbus domestica* in the Czech Republic: _ spontaneous escapes (52 quadrants), × deliberately planted in the countryside and uncertain origin (32 quadrants). Prepared by Martin Lepší, Petr Lepší, Zdeněk Špíšek & Karel Kubát.

CHAPTER 4:
Genotypic variability of *Sorbus domestica* in Central Europe suggests its anthropogenic origin.

Zdeněk Špíšek

Radim J. Vašut

(in prep.)

Introduction

The service tree (*Sorbus domestica* L.) is a deciduous tree and it is one of European wild fruit species. Similarly to species such as *Pyrus pyraster*, *Malus sylvestris*, *Prunus brigantinna* has limited and scattered distribution with the highest frequency in warm parts of Europe. It is expected that the overall distribution and population structures of such cultural tree species are under long-term influence of human.

Taxonomically, *Sorbus domestica* is traditionally classified within the broad genus *Sorbus* (*Rosaceae*, tribe *Maleae*, apple tribe) having more than 250 species occurring in the northern hemisphere and 91 species in Europe (Phipps et al. 1990; Aldasoro et al. 2004). More recently, total 201 taxa of *Sorbus* s.l. is listed for Europe (Sennikov & Kurtto 2017). The tribe as well the broad genus *Sorbus* are known for very complex taxonomy due to reticulate evolution and recent occurrence of extensive (often intergeneric) hybridization and/or apomixis (Robertson et al. 1991; Campbell et al. 2007; Potter et al. 2007). However, the service tree has somehow distinct position within the *Sorbus* s. l. (and whole tribe), i.e. it is fully sexual allogamous species never hybridizing with any other species of the whole tribe. From the phylogenetic point of view, it is better to classify it as *Cormus domestica* (a separated monospecific genus), however we adopt here the traditional but phylogenetically incorrect classification as *Sorbus domestica*, because the new phylogenetic approach (Robertson et al. 1991; Sennikov & Kurtto 2017) is still not generally accepted.

Species is considered rare and the genetic diversity is shaped by human activity (Enescu et al. 2016, George et al. 2015). Its infrequent distribution covers mainly the Mediterranean Europe (Enescu et al. 2016), with further scattered distribution in adjacent regions, i.e. from the Western Europe (Galicia in Spain, northern Portugal) to Eastern Europe (Crimea in Ukraine) and Asia Minor (north-western Turkey), from Central Europe (Germany, Czechia) and Great Britain (likely allochthonous origin) to Northern Africa (Morocco, Algeria and Tunisia). Its distribution in Central Europe (the northern distribution limit in this area) is fragmented in several discontinued areas (Enescu et al. 2016, Špíšek et al. 2018). Species prefers warm to mild climate and it is drought as well cold tolerant (Paganová 2008).

In Central Europe, the species extends its northern limit here and is divided in several areas (Enescu et al., 2016, Caudullo et al. 2017). The most northerly distribution is represented by two smaller areas in northern Bohemia (Czechia) and roughly Saxony-Anhalt (Germany), whereas the major area is spanning along the Pannonia (Eastern Austria, South-eastern Moravia in Czechia, southern Slovakia and the most of Hungary). Distribution area in Czechia consists of two major areas (metapopulations): one in Central Bohemia (Bohemian Central Uplands) and second in the south-eastern Moravia, which shares a border with Slovakia (the White Carpathians) (Lepší et el. 2017, Špíšek et al. 2018). Few additional minor populations are found in other regions of Moravia (Lepší et el. 2017).

Genetic structure of the service tree populations confirms its endangered status among European tree species. An extreme case represents the isolated occurence in Great Britain (putatively of natural origin), which shows a very low number of individuals, low diversity in populations and relatively higher genetic diversity in whole British metapopulations (George et al. 2016). On the contrary, three major European regions (Italy, France, and Austria) shows quite high genetic diversity with just moderate genetic differentiation (George et al. 2015). The Austrian population formed a distinct cluster, however showed low differentiation among population suggesting previous gene-flow or human influence on seed dispersal (George et al. 2015). The species has ability for long-distance gene flow over fragmented landscape (Kamm et al. 2009), which probably causes the observed pattern.

The aim of this study was to reveal the population structure of the Czech populations. We emphasised the population of the Bílé Karpaty hills (White Carpathians), which represents the major occurrence in Czechia and Slovakia (see also Špíšek et al. 2018). We further compared it populations in northern Bohemia and other European populations (France, Germany, Croatia and others). Our major goal was to provide a platform for further plant species conservation in the region and provide arguments on the origin of populations in this part of Central Europe.

Material and Methods

Plant material and DNA extraction

We studied a total of 189 individuals of *Sorbus domestica* from 3 large Czech population and additional 11 European populations. The number of individuals considerably varies among populations, the largest sample represents the White Carpathian occurrence with 54 samples (Table 1, Table S1, Figure 1). Sampling at Czech localities represents the frequency of the species in regions, additional sampling from other European regions is collected primarily as outgroup. The detailed characteristics of the White Carpathian metapopulation are described by Špíšek et al. (2018).

For further DNA extraction, fresh leaves were collected and consequently dried and stored in silica gel. Genomic DNA was extracted according to modified CTAB (Cetyl Trimethyl Ammonium Bromide) protocol described by Doyle and Doyle (1987) using ca. 50 mg of dried leaf tissue. The DNA extraction was evaluated on a 1.5% agarose gel stained with ethidium bromide and measured with the Nanodrop 100 spectrophotometer (Thermo Scientific).

SSR analyses

Out of 9 tested microsatellite loci were finally employed 5 of them, i.e. MSS-3, MSS-5, MSS-6, MSS-13, MSS-16 (Oddou-Muratorio et al. 2001) under published PCR conditions with minor individual modifications. The thermal cycling consisted of initial denaturation step (2 min at 95°C), followed by 30 number of cycles (1 min at annealing temperature) and 2 min of 72°C, ended by final extension (10 min at 72°C). Amplification was performed at Thermal Cycler DNA (MJ Research PTC-200) using 10 µl reaction volumes containing 5 ng of genomic DNA. Reaction mixtures were prepared according to the manufacturer's protocol (Promega) containing 1× GoTaq (Promega) reaction buffer, 0.2 mM dNTP (each), 1 µM of primer (each) and 0.25 U of GoTaq polymerase. PCR products were visualized using on the CEQ™ 8000 Genetic Analysis System (Beckmann Coulter), fragment lengths were detected by using 400 bp size standards.

Data analysis

Standard descriptive population genetic characteristics (such as average number of alleles per locus, *A*, and the observed and expected heterozygosity, *F*- and *ρ*-statistics) were calculated using R-package *adegenet* (Jombart 2008), POPGENE (ver. 1.32; Yeh et al. 1999) and GENEPOP (ver. 4.0.11; Raymond & Rousset 1995, Rousset 2008), the latter with 10,000 dememorisation iterations; 200 batches; and 10000 iterations using MCMC simulations. The level of differentiation among populations was analysed by AMOVA (analysis of molecular variance) using Arlequin 3.5 (Excoffier & Lischer 2010). The UPGMA, PCoA and DAPC clustering was performed using the R-packages *adegenet*, ade4, *hclust* and *ape* (Paradis et al. 2004, Popescu et al. 2012).

To analyse the population structure, we used Bayesian clustering approach implemented in the STRUCTURE (ver. 2.2; Pritchard et al. 2000). The analysis was performed with admixture model with *K* ranging between 1 and 20 with 4 replicate runs for each *K*, 80 000 burn-in iteration followed by 800,000 MCMC iterations. The Δ*K* statistics (Evanno et al. 2005) was used in order to find appropriate number of cluster in the STRUCTURE output files using the STRUCTURE HARVESTER (Earl & von Holdt 2012). For the graphical interpretation of clustering for the appropriate *K*, the software programmes CLUMPAK (Kopelman et al. 2015) and STRUCTURE PLOT (v2.0; Ramasamy et al. 2014) were used.

Table 1. Number of collected individuals analysed in this study. For detailed information on origin of plants see the Table S1 in the Suplementary data.

POPULATION	Number of individuals
Czechia	135
White Carpathians	*54*
České Středohoří	*41*
Moravia (south-central)	*40*
United Kingdom (England)	3
France	10
Corse	*2*
Provence	*8*
Slovakia (White Carpathians)	9
Turkey (Cappadokia)	3
Ukraine (Crimea)	4
Croatia (Dalmatia)	6
Austria	1
Italy (Sicily)	2
Germany	7
Slovenia	7

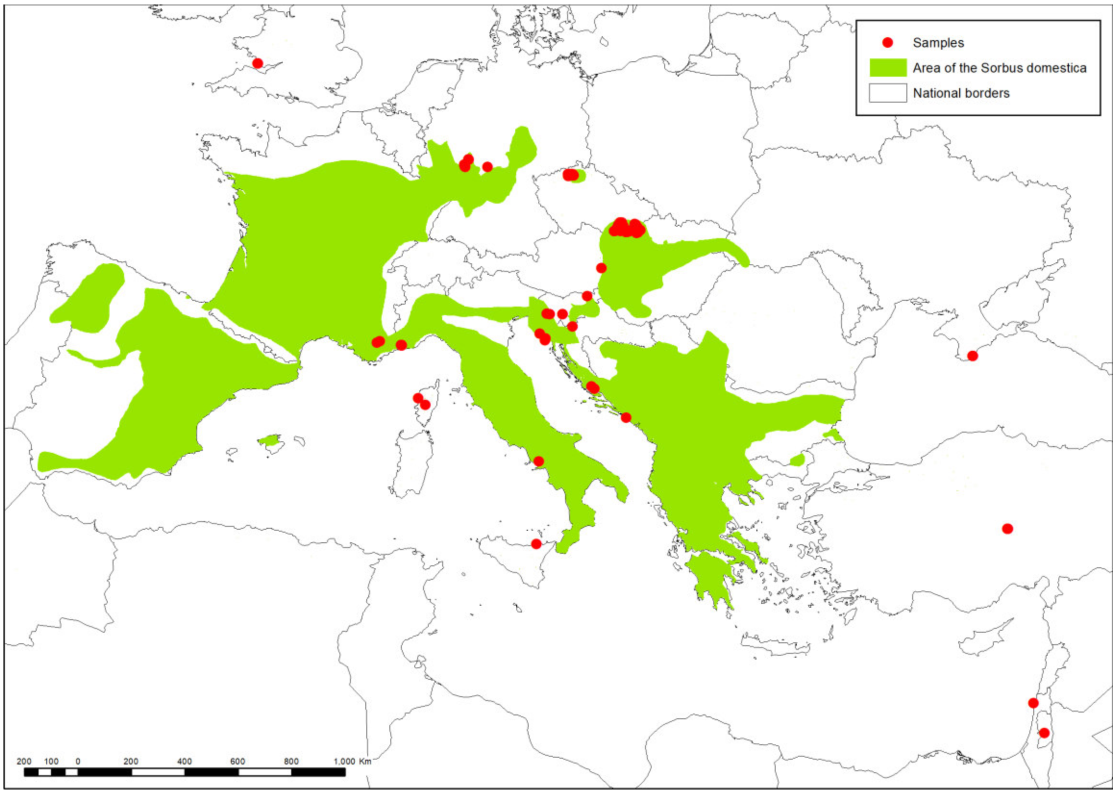


Figure 1. Map of collected samples of *Sorbus domestica* in Europe and adjacent regions. Red dots represent collected samples analysed in our study. Green area depicts the expected natural distribution of *Sorbus domestica* according to Enescu et al. (2016).

Results

Analysis of microsatellites

All 5 loci amplified well for all samples, with exception of *mss-6* for sample #029 from Dubrovnik (Croatia) and sample #002 from Adamovske Kochanovice (Slovakia). For most of analyses were these samples used with indicated missing value (as -9), but all 189 samples were included. Analysed loci were highly heterozygous, i.e (H_o/H_e): mss-5 (0.92/0.77), mss-13 (0.9/0.55), mss-6 (0.72/0.68) and mss-3 (0.84/0.67) only mss-16 showed expected heterozygosity (0.63/0.65) and generally indicates high genotypic variability within populations. Total number of identified alleles is 38 and it varies among assigned groups of localities between 11 (UK - England) and 25 (CZ-BK – White Carpathians). It is strongly affected by the population sample, however, even samples with low number of collected individuals exhibit genotypic variability. Number of alleles among loci varies between 4 (mss-3) and 12 (mss-6). The overall characteristics of loci is summarized in Table 2.

Genetic differentiation among populations

Pairwise F_{ST} indices (see Table 3) revealed weak to strong genetic differentiation. Values range between 0.003 and 0.270. Generally, neighbouring populations showed very weak differentiation, whereas distant population revealed strong differentiation, i.e. Turkey (up to 0.268), Crimea in Ukraine (up to 0.227) and Israel (up to 0.270). All Pannonian populations shows very weak genetic differentiation, but outlying population from the České Středohoří hills (Central Bohemia, Bohemian Massif) has moderate differentiation with weakest differentiation to populations in Slovakia (0.058) and Germany (0.066). Unfortunately, some of these values are not significant due to low number of sampled individuals (Italy, Crimea, Israel).

Different hierarchical clustering approaches showed similar pattern of not-well differentiated populations. The UPGMA (Figure 2) revealed distances mostly related to distant geographic distribution showing as the most distant populations in Turkey, Crimea and UK. However, further clustering revealed no clear distribution- or population-based pattern. Samples from all population are distributed across all 4 major distinguished clades, although some samples from the White Carpathians or České Středohoří hills tend to cluster together. The AMOVA revealed very high intra-population variation and decreased inter-population variation even on large geographic distance (Table 4).

Similar pattern was obtained by DAPC. The PCoA diagram was fit best at 4 major groups, which are weakly separated (Figure 3a) having some individuals tidily neighbouring with individuals from other cluster. Inferred clusters include mostly individuals from more than single natural population (Figure 3b), with minor exceptions of populations with low number of individuals (such as Italy, Crimea, Israel and England). Samples from the České Středohoří Mts. are prevailingly clustered in cluster/group #2, which shows moderate differentiation. All geographically distant populations (such as Israel, Turkey, Crimea) are clustered in cluster/group #4 along with individuals with most of sampled populations. Another best-fitting number of clusters was set at 10 having similar pattern of 8 groups not-well differentiating from each other (not shown here).

Bayesian clustering approach revealed not well-differentiated (clustered) pattern between populations. The rate of change of the likelihood distribution revealed a value of $K = 9$ as the best fitting number of clusters. Additionally, $K = 3$, $K = 11$ and $K = 12$ appeared to be another possible number of most-likely number of clusters (Figure 4a). No unique genetic background was detected for any population; all populations consisted of individuals with admixed genetic composition. Only population from the České Středohoří Mts. and distant populations (Turkey, Israel, Crimea) show slightly distinct partial differentiation from other populations. Mediterranean populations include this component in admixed genetic background as well (Figure 4b).

Table 2. Characteristics of studied loci.

	Na	*Ho*	*Hs*	*Ht*	*Dst*	*Htp*	*Dstp*	*Fst*	*Fstp*	*Fis*	*Dest*
mss-5	9	0.92	0.69	0.81	0.12	0.82	0.13	0.15	0.16	-0.33	0.41
mss-16	8	0.48	0.58	0.65	0.07	0.66	0.07	0.10	0.11	0.17	0.18
mss-13	5	0.94	0.58	0.70	0.11	0.71	0.12	0.16	0.17	-0.62	0.30
mss-6	12	0.77	0.65	0.77	0.12	0.78	0.13	0.16	0.17	-0.18	0.37
mss-3	4	0.75	0.60	0.64	0.04	0.65	0.05	0.07	0.07	-0.25	0.12

Table 3. Pairwise F_{ST} indices for studied populations and population groups. Values in regular font are significant (significance of differentiation P<0.05) ,values in italic font are non-significant. Abbreviated populations: CZ (BK) = Czechia (White Carpathians), CZ (SM) – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, CZ (CS) – Czechia (České Středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom, IL – Israel, TR – Turkey, UA – Ukraine (Crimea)

POP	CZ (BK)	CZ (SM)	SK	AT+SI	HR	CZ (CS)	DE	FR	IT	UK	IL	TR	UA
CZ (BK)	0,000												
CZ (SM)	0,032	0,000											
SK	0,023	0,003	0,000										
AT+SI	0,033	0,037	-0,013	0,000									
HR	0,062	0,069	0,040	0,014	0,000								
CZ (CS)	0,073	0,093	0,058	0,088	0,125	0,000							
DE	0,078	0,053	0,011	0,034	0,036	0,066	0,000						
FR	0,074	0,052	0,030	0,016	0,056	0,139	0,060	0,000					
IT	*0,030*	*0,016*	*-0,043*	*-0,012*	*-0,042*	*0,058*	*0,017*	*-0,003*	*0,000*				
UK	0,241	0,236	0,206	0,209	0,130	0,251	0,121	0,209	*0,141*	0,000			
IL	0,262	0,232	0,177	0,187	0,146	0,270	0,149	0,177	*0,062*	*0,211*	0,000		
TR	0,200	0,184	0,183	0,124	0,143	0,268	0,150	0,095	*0,130*	*0,230*	*0,079*	0,000	
UA	0,227	0,190	0,141	0,146	0,147	0,219	0,165	0,086	*0,014*	0,225	*0,017*	0,124	0,000

Table 4. AMOVA (analysis of molecular variance) results of 5 SSR loci based on F_{ST}

Source of variation	**d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among groups	4	37.280	0.08767	5.13
Among populations within groups	8	25.933	0.09729	5.70
Within populations	365	561.916	1.52239	89.17
Total	377	625.130	1.70736	

Figure 2. UPGMA consensus tree. Abbreviated populations: BK = Czechia (White Carpathians), MOR – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, Stred – Czechia (české Středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom (England), IL – Israel, TR – Turkey (Cappadocia), UA – Ukraine (Crimea).

Figure 3. DCPA with 4 major groups. Inferred 4 clusters of PCoA (**a**) are consisting of individuals across different populations (b). Abbreviated populations: CZ (BK) = Czechia (White Carpathians), CZ (SM) – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, CZ (CS) – Czechia (České Středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom, IL – Israel, TR – Turkey, UA – Ukraine (Crimea)

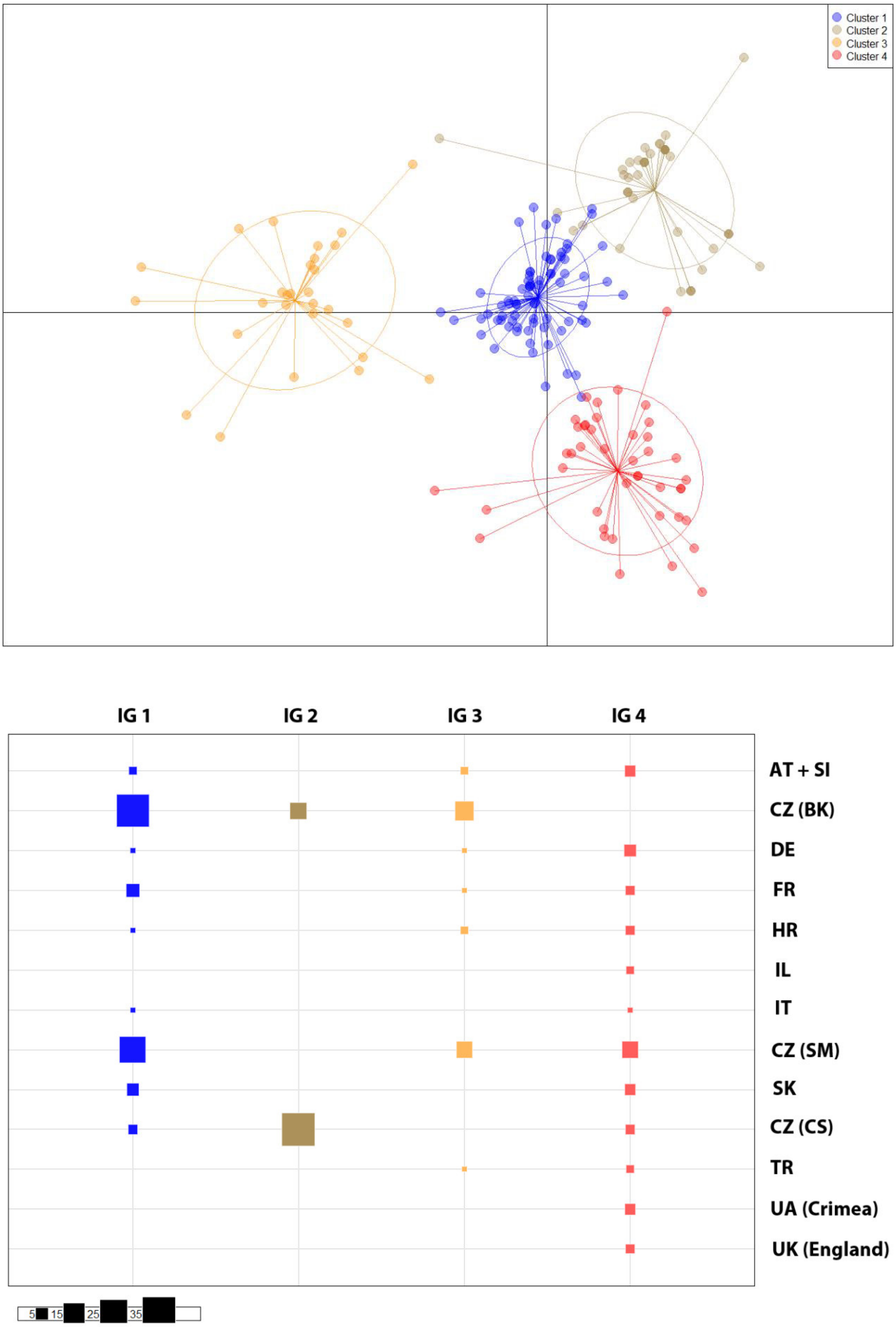
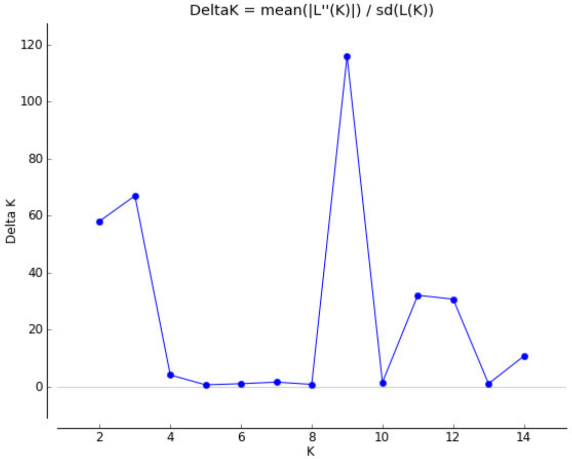
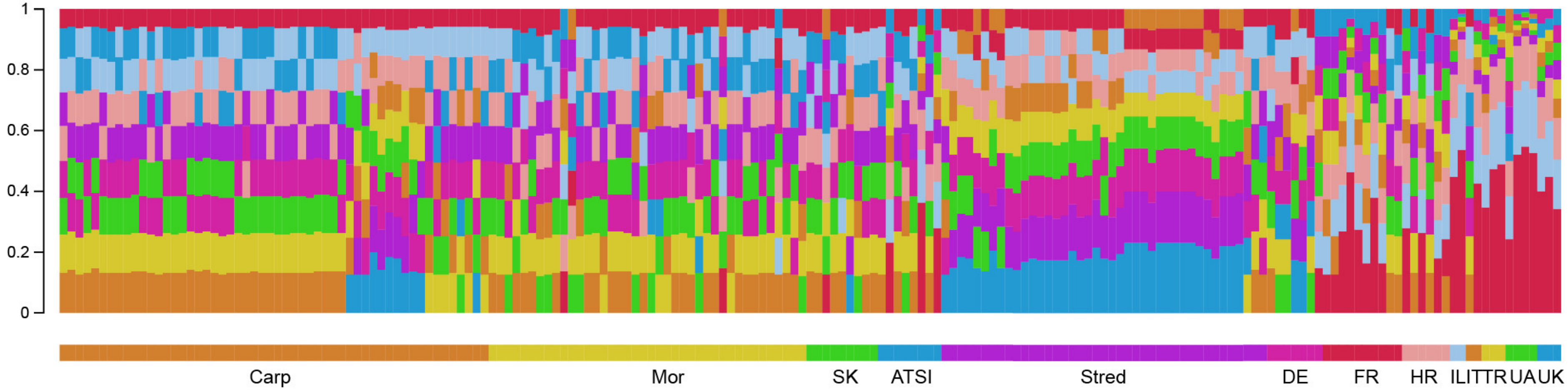


Figure 4. Bayesian assignment of populations by STRUCTURE. Results for K=9 are shown, along with the deltaK.





Discussion

Genetic diversity of Sorbus domestica

All studied populations have high genetic variability diversity, both at loci level (Table 2) as well as at population level (not presented here). Analyses were affected by low number of individuals, however even within such populations high allelic diversity was observed. This methodological issue is related to natural behaviour of the species: it has very scattered distribution and even large population samples in our study are represented by more or less scattered individuals on larger geographic area, which is contrast to population studies on rare woody species in fragmented landscape we performed in past (e.g. Sochor et al. 2013). Unlike in usual studies, in this study we work more with scattered individuals rather than populations located to spatially discrete location. In the largest population, i.e. in the White Carpathians are subpopulations often consisted of individual trees in cultural landscape (Špíšek et al. 2018). However, in this study we consider a population on large geographic scale due to facts that *S. domestica* is obligate sexual species with any evidence of apomixis; and that rosaceous closely related taxa are self-incompatible outbreeders, which was confirmed not only for *Sorbus* s.l. (Aguiar et al. 2013, Ludwig et al. 2013, Jankowska-Wroblewska et al. 2016a) but also other genera within the tribe *Maleae*, such as *Pyrus* or *Malus* (Hoebee et al. 2012, Aguiar et al. 2015). Further, *Sorbus* species are capable of long distance pollen dispersal (Oddou-Muratorio et al. 2003, 2004; Kamm et al. 2009). The observed genetic and allelic variability in our study can also be attributed to outbreeding (see F_{IS} values in Table 2). Similar patterns supporting the idea of importance of the long-distant pollen dispersal in combination with self-incompatibility were observed in other related taxa. Nearly same pattern of high genetic (allelic) diversity was already documented in *S. domestica* on sample from 17 populations across western and southern Europe (George et al. 2015). The decline in allelic richness was observed on south-north gradient, from potential refugia in the Mediterranean towards the northern distribution limits (S France → NW France; Serbia → Austria). Rather scattered occurrence with low number individuals is typical for *Sorbus torminalis*, which has in Switzerland considerable genetic variability on spatial scale with large number of genotypes, despites it capability to clonal reproduction (Hoebee et al. 2006). Similarly, on the northern distribution limits of *S. torminalis* in Poland population of scattered individuals shows high genetic variability (Jankowska-Wroblewska et al.

2016a, 2016b). Relatively high genetic variability was documented also in facultative apomict *Sorbus collina* (Feulner et al. 2017), which is in contrast to other facultative apomicts such as *Rubus* with low intraspecific variation within species (Šarhanová et al. 2017) and indicating that high genetic variability is more related to biological behaviour of the genus *Sorbus* s.l. rather than facultative sexuality. Increased genetic variability due to long-distance pollen dispersal can be observed not only in natural populations, but also in clonal populations of orchards: offspring the *S. domestica* cultivated clonally (by grafting) in the orchard reveals significant increased genetic variability due to pollinated from distant plants cultivated in alley or further in the landscape (Czernikarz et al. 2016). Pollen dispersal from plants brought by human to orchards probably influenced the high genetic diversity of the Moravian plants.

Population differentiation

The general differentiation among populations seems weak to moderate. Based on F_{ST}, it is comparable to other studied related species with the rosacean tribe *Maleae*, such as *S. domestica* (George et al. 2015), *S. torminalis* (e.g. Angelone et al. 2007, Jankowska-Wroblewska et al. 2016a, 2016b) or *Malus sylvestris* (Cornille et al. 2012). George et al. (2015) hypothesise the observed pattern comes from a combination of long-distance pollen dispersal in combination with human impact on populations. In our previous study, we showed that Central-European populations are strongly shaped by human activities (based on characters of distribution, demography, ecology). The weak genetic differentiation can probably be explained by the distant outbreeding (see citations above), however in combination with demographic facts (occurrence in cultural landscape, absence "normal" population structure and the importance for the viticulture) the human impact cannot be excluded.

This idea of anthropogenic influence on *S. domestica* populations in Central Europe is supported by our results from clustering analyses. Both, DAPC and STRUCTURE were not unequivocal. The STRUCTURE has the most likely number of clusters at value K = 9, however K = 3 and K = 11/12 very likely too. DAPC revealed the best fitting number of clusters at value 4, however 9/10 clusters were also likely. Any of the clustering method revealed unique and clear cluster pattern, but all inferred clusters shows that either individuals have admixed genetic background or populations are mixed.

One of the most remarkable patterns from our data suggests that distant populations from Asia (and one from Croatia) are remarkable genetically different have the marginal position on the tree (Figure 2). On the other, they cluster together with individuals across Central Europe (Figure 2 and especially Figure 3b – see the Inferred group 4). The STRUCTURE shows that these populations contain component that with decreased proportion is present also in East-Mediterranean populations (Croatia) and in Central Europe. It indicates that there is relationship between the most distant populations (UA, TR, IL), the Mediterranean (HR) with a gradient to Central Europe (SI, AT, CZ (BK), CZ (SM) and SK). Other interesting pattern shows that there is just a weak differentiation among Central-European population, suggesting that populations in the Pannonian area have common origin. The high variability absences of obvious cluster pattern among population further suggest not only long-distance gamete dispersal, but also hints influence of human in the cultural landscape. The STRUCTURE did not reveal significant difference between populations from the White Carpathians, Southern Moravia, Slovakia and Austria. However, the DAPC revealed weak differentiation of the White Carpathian population from the "core" cluster of the Mediterranean populations. It can be partly explained by its northernmost position of the distribution area (Špíšek et al. 2018) and probably it can be biased by the population sample. Interestingly, the most differentiating inferred cluster contains individuals from the České Středohoří Mts. – CZ (CS). According to the STRUCTURE analysis it contains a proportion, which is also similarly present in German samples as well as samples from France. Based on the DAPC, it is isolated inferred cluster with only a minor overlap to population of the White Carpathians. It is the only nearly well distinguished cluster. These data suggest that the origin of Bohemian population is likely different from the Pannonian populations in Moravia, Slovakia and eastern Austria. Czech Pannonian populations, i.e. CZ(BK) and CZ (SM) are clearly linked to other Pannonian populations and further to east-Mediterranean population. Om the contrary, it is likely that Bohemian population are linked either to western-European population in Germany or further in France. This pattern can be easily explained by post-glacial migration routes, but also by the historical cultural connections between regions (connections between Bohemia and Bavaria + Saxony on one side, and Moravia and Austria + Hungary (+ Croatia) on other side).

These observed patterns are more or less in agreement with clustering results in *S. domestica* of George et al. (2015). In their study, populations formed a “core” (or basal) cluster including the most of the Mediterranean populations (Italy, Bosnia, Bulgary, Croatia etc.), which is equivalent to the inferred cluster #4 from our study. Only Austrian population and population from NW France formed 2 distinct clusters. Unfortunately, due to different microsatellites used, we are unable to compare our data, however it possible that Austrian group from George et al. (2015) might be linked to inferred cluster #1 or #3 from from our study and possibly the French group to our IG #2. Although it is speculative, we can see in our data and data of George et al. (2015) one common pattern: *i*) a “core” with distinct high genetic variability containing populations from the Mediterranean and Asia (“IG#4” in our study, “Balkan and Mediterranean Group” in George et al. 2015); ii) distinct cluster at the northern limits of the species distribution area – East (“IG#1 and IG#3” in our study and “Austrian group” in George et al. 2015); iii) cluster at the northern limits of the species distribution area – West (“IG #2” and “French group” from George et al. 2015). We must stress that we don’t know the real linkage between groups from our study and groups from George et al. 2015 (i.e. we don’t know true genetic distance between IG#1/3 and “Austrian group” and between IG#2 and “French group”). For both studies it is also true, that populations of these distinct clusters are sampled well, whereas the Mediterranean (and other) populations are underestimated in number of sampled individuals and thus might biased towards distinguishing clear clusters. However, the link (and admixed genetic background) of “northern” population to the Mediterranean ones are in both studies unambiguous.

Conclusions

Our study revealed that scattered pattern of distribution does not automatically lead to decreased genetic variability (allelic richness) and that Czech populations considerable variation. It is probably due to self-incompatibility of species and capability of long-distance pollen dispersal or can be a result of human dissemination due to its use in viticulture. Apparently, the most-likely scenario is combination of both strategies, when populations are consisting of natural genotypes enriched by individuals from orchards or vineyards brought by human from anywhere. Genetic differentiation among populations was not high, especially Pannonian populations of Central Europe shows similar genetic admixed background with several slightly distinct clusters of *i*) White Carpathians and *ii*) Southern Morava (Pálava). These are clearly linked to other Pannonian populations and further Mediterranean populations, which makes a "core" cluster of genetic variability. Interestingly, population form the České Středohoří Mts. forms distinct cluster slightly differing by the admixed genetic background from Pannonian population and more linked to German (or further French) populations. Even the most distant Asian population has genetic link to Mediterranean populations hinting its young origin (probably dissemination by human in past millennia) rather than a relic occurrence. Despites the fact that populations of *S. domestica* are clearly influenced by human, they definitively deserve a protection due to conservation of unique genotypes and due it is value for the landscape.

CHAPTER 5: Summary and conclusions

Summary and conclusions

Title: Populations of service tree (*Sorbus domestica* L.) in Central Europe and their Characteristics

In Europe, solitaire trees are gradually disappearing from the free landscape, especially fruit trees. Landscapes are gradually changing alley, stalks and large field ropes are being cast. My Thesis is monitoring occurrence of service tree in Czechia. A detailed survey showed a predominant occurrence in warm and slightly warm climatic areas (Czech Central Mountains and Southeastern Moravia). The vast majority of trees grow in dominant in orchards, vineyards in the open countryside. The occurrence of trees in the forest is limited, yet the species spontaneously spreads. In the White Carpathian region there is a strong anthropogenic influence on species expansion. However, the comparison of the shape variability of the fruits did not show any statistically significant correlation.

Genetic differentiation among populations was not high, especially Pannonian populations of Central Europe show similar genetic admixed background with several slightly distinct clusters of *i*) White Carpathians and *ii*) Southern Morava (Pálava). These are clearly linked to other Pannonian populations and further Mediterranean populations, which makes a “core” cluster of genetic variability. Interestingly, population form the České Středohoří Mts. forms distinct cluster slightly differing by the admixed genetic background from Pannonian population and is more linked to German (or further French) populations.

Although this thesis brings many new insights into the actual distribution, ecology and genetic variability of species in Europe, there are still many questions to be answered. Besides specific viability of populations, the question which populations might be consisting of putatively natural and autochthonous genotypes and what is the origin of allochthonous genotypes. One of major unresolved questions is the species protection and conservation. As an archaeophyte it is excluded from regional Red lists and protection plans, despites its importace in cultural landscape of Czechia. This thesis opened new reserach question and further reserach can bring new insights in understanding the biology and genetics of *Sorbus domestica* in Czechia and in Europe.

Shrnutí a závěr

Název práce: Charakteristika populací jeřábu oskeruše (*Sorbus domestica* L.) ve střední Evropě

V Evropě postupně mizí solitérní stromy z volné krajiny obzvláště ty ovocné. Krajinný ráz se postupně mění, mizí aleje, remízky i stromořadí a dochází zcelováni velkých polních lánů. Práce mapuje výskyt jeřábu oskeruše v České republice. Detailní průzkum prokázal převážný výskyt v teplých a mírně teplých klimatických oblastech (České středohoří a Jihovýchodní Morava). Velká většina stromů roste v jako dominanty v sadech, vinicích ve volné krajině. Výskyt stromů v lese je omezen, přesto se druh spontánně šíří. V oblasti Bílých Karpat je patrný silný antropogenní vliv na rozšíření druhu. Přesto srovnání tvarové variability plodů neprokázalo žádnou statisticky významnou korelaci.

Genetická variabilita mezi populacemi není nikterak vysoká. Zvláště Panonské populace střední Evropy vykazují geneticky podobné pozadí s několika odlišnými populacemi i) Bílé Karpaty a ii) Jižní Morava (Pálava). Tyto populace jsou navzájem propojeny s Panonskými populacemi. S dalšími středomořskými spoluvytváří „jádro„ genetické variability druhu. Zajímavé je, že populace Českého středohoří vytváří cluster, který se mírně liší od genetického pozadí panonských populací a je více propojen s německými (nebo francouzskými) populacemi.

Ačkoliv tato dizertační práce přináší řadu nových poznatků týkajících se aktuálního rozšíření, ekologie druhu, genetické variability druhu, zůstává v této oblasti stále mnoho nezodpovězených otázek. A to zejména životaschopnost jednotlivých populací, otázka původnosti druhu na našem území: tj. stanovení populací, které mohou obsahovat hypotetické původních autochtonní genotypy, případě jaký je původ alochtonních (nepůvodních) genotypů, kterými jsou naše populace obohaceny. Další zásadní nezodpovězená otázka se týká ochrany druhu, který jako archeofyt není zařazen v červených seznamech a proto není chráněn, přestože by si ochranu jako důležitá součást kulturní krajiny zasloužil (i s ohledem na jeho genetickou variabilitu). Problematika tak není zdaleka vyčerpána a jistě v budoucnu přinese řadu zajímavých poznatků, neboť páce otevřela nové otázky o biologii a genetice druhu u nás i v Evropě.

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Summary of the PhD. Thesis

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Ph.D. thesis was carried out at the Department of Botany, Faculty of Science, Palacký University in Olomouc in 2011 – 2018.

PhD. candidate: **Mgr. Zdeněk Špíšek**

Supervisor: **doc. RNDr. Vladan Ondřej, Ph.D.**
Department of Botany, Faculty of Science,
Palacký University in Olomouc, Czech Republic

Opponents: **Prof. RNDr. Ladislav Havel, CSc.**
Department of Plant Biology, Faculty of Horticulture,
Mendel University in Brno, Czech Republic

doc. Ing. Luboš Úradníček, CSc.
Department of Plant Biology, Faculty of Forestry and Wood Technology,
Mendel University in Brno, Czech Republic

Prof. Ing. Viera Paganová, PhD.
Department of Planting Design and Maintenance,
Slovak University of Agriculture in Nitra, Slovakia

The PhD. thesis has been approved by Prof. Ing. Aleš Lebeda, DrSc., Department of Botany, Faculty of Science, Palacký University in Olomouc.

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The oral defense will take place on 24. 1. 2018 at 9:30 in front of the Commission for Ph.D. thesis of the Study Program Botany at the Department of Botany, Šlechtitelů 27, Olomouc.

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Content

Introduction

Service tree (*Sorbus domestica* L.) is a unique fruit species of rare occurrence in Central and Southern Europe. The Czech Republic represents the northern limit of natural distribution area. In the area, service tree grows in fragmented populations with scattered distribution. Human is responsible for the use of the as a fruit tree. Service tree fruit has been consumed in Southern Europe since the ancient times and it was known to be consumed in Central Europe since the Middle Ages. The main topic of the thesis is related to understanding the patterns of distribution of the species and to what extent is the distribution impacted by human activities. I the theseis, I particularly covered following topics: 1) species prevalence in the White Carpathians including fruit variability, dendrometric parameters and climatic conditions of the site. 2) Detailed species distribution in the Czech Republic including the excerption of historical data from herbarium specimens. 3) Genetic variability of the species in area of its natural occurrence with focus on the Czech Republic.

The study shows that the species distribution in the Czech Republic is predominantly in warm or mild climate regions (central Bohemia and Southeastern Moravia). Our data suggest that occurrence of the species in the White Carpathians is most likely strongly influenced by human activities and we havenot traced any signs of natural occurrence. The majority of the service trees grow at the altitude of 200 – 600 meters above sea level, mostly in orchards, vineyards or on open landscape. The comparison of the fruit types has not revealed any strong pattern, although the fruit types have been selected by the growers supposedly. Genetic differentiation among populations was not high, especially Pannonian populations of Central Europe shows similar genetic admixed background. Interestingly, population from the České Středohoří Mts. forms distinct cluster slightly differing by the admixed genetic background from Pannonian population and more linked to German (or further French) populations. Although most of the documented trees probably have an anthropogenic origin, they represent an important part of the flora in Central Europe and require the protection.

Aims of the thesis

Sorbus domestica L. is one of the rarest European tree species, of which mainly wood and fruits from the tree were used to. However distribution species, chorological analyses and molecular variability in Central of Europe was not detail and complexly studied yet. Patterns of genetic diversity were uncovered only recently for the part of Central Europe (George *et al.* 2015) and there are still more questions than answers in this field. Therefore, this thesis aims to contribute to our understanding of distribution in Czech Republic. Uncover relationships, between dendrometrical characteristic and fruit types. Furthermore, by analysing the genotypic diversity we aimed at understanding the relationship between and among Moravian populations and selected European populations. The thesis consists of the following parts:

***Sorbus domestica* L. at its northern Pannonian distribution limits: distribution of individuals, fruit shapes and dendrometric characteristics**

This part concentrates on detailed distribution service tree in the White Carpathians. The chorologic data are discussed in relation to climatic data and further to dendrometric characteristics and morphology of fruits. Indirect evidences for anthropogenic origin of populations as well as need for conservation is disccussed.

Distribution maps and comments *Sorbus domestica*

This part describes in detail distribution of service tree in Czech Republic. Furthermore, focus on origin archeotypes (spontaneous escapes or deliberately planted in the countryside and uncertain). It extends the previous part with discovered localities in Bohemia and Moravia.

Genotypic variability of *Sorbus domestica* in Central Europe suggests its anthropogenic origin

This part describes patterns of genotypic variability of Central European populations (with emphasis to Czech Republic) and compares it with selected European populations. Absence of significant population structure suggests its long-term and continuous cultivation.

Materials and methods

Chorological data collection, analyses and maps

The study area is located in the White Carpathians, which is the westernmost part of the Western Carpathian Mountains. Its unique nature and landscape are protected as the Protected Landscape Area (PLA) and Biosphere Reserve.

The study was carried out during the vegetation period from 2008 through 2016. The study of this tree was focused within the PLA, including the individuals situated out of the border. The field research included both the residential and rural landscape as well forest and non-forest biotopes. The localities of the field research include the whole area of the White Carpathians. The localization of individuals was recorded by GPS GARMIN eTrex 10. Fruits were collected from various positions throughout the area from August through October during all mapping seasons. The circumference of each sampled tree was measured with a tape-measure to calculate the DBH (diameter at breast height) at 1.3 m above the ground. Tree height was measured by a Suunto PM-5/360 PC hypsometer. The map data were prepared and the orientation slopes were processed in Geographic Information Systems – Arc View version 3.1. The maps basis was with an obtained digital geographic database ArcČR® 500 v 3.3 for climatic regions (Květoň & Voženílek, 2011). Analysis of covariance (ANCOVA) was used to investigate the relationships between height, DBH and the location of service trees. The analyses were performed in R (version 3.2.3; R Core Team, 2015).

Plant material, DNA extraction and SSR analyses

We studied a total of 189 individuals of *Sorbus domestica* from 3 large Czech population and additional 11 European populations (Figure 1.). Sampling at Czech localities represents the frequency of the species in regions, additional sampling from other European regions is collected primarily as outgroup.

For further DNA extraction, fresh leaves were collected and consequently dried and stored in silica gel. Genomic DNA was extracted according to modified CTAB (Cetyl Trimethyl Ammonium Bromide) protocol described by Doyle and Doyle (1987) using ca. Out of 9 tested microsatellite loci were finally employed 5 of them, i.e. MSS-3, MSS-5, MSS-6, MSS-13, MSS-16 (Oddou-Muratorio et al. 2001) under published PCR conditions with minor individual modifications. The thermal cycling consisted of initial denaturation step (2 min at 95°C), followed by 30 number of cycles (1 min at annealing temperature) and 2 min of 72°C, ended by final extension (10 min at 72°C). Amplification was performed at Thermal Cycler DNA (MJ Research PTC-200) using 10 µl reaction volumes containing 5 ng of genomic DNA. Reaction mixtures were prepared according to the manufacturer’s protocol (Promega) containing 1×

GoTaq (Promega) reaction buffer, 0.2 mM dNTP (each), 1 µM of primer (each) and 0.25 U of GoTaq polymerase. PCR products were visualized using on the CEQ™ 8000 Genetic Analysis System (Beckmann Coulter), fragment lengths were detected by using 400 bp size standards.

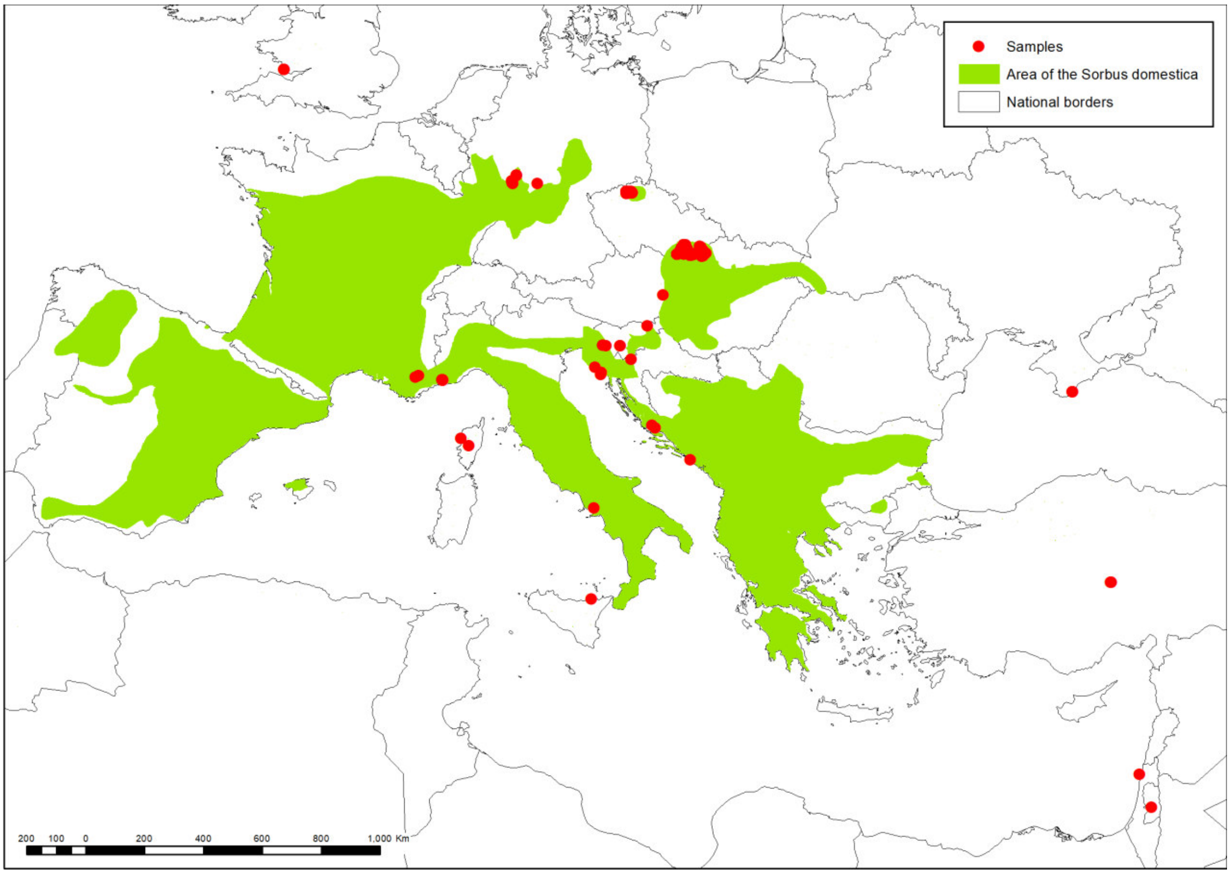


Figure 1. - Map of collected samples of *Sorbus domestica* in Europe and adjacent regions. Red dots represent collected samples analysed in our study. Green area depicts the expected natural distribution of *Sorbus domestica* according to Enescu et al. (2016).

Data analysis

Standard descriptive population genetic characteristics (such as average number of alleles per locus, *A*, and the observed and expected heterozygosity, *F*- and *ρ*-statistics) were calculated using R-package *adegenet* (Jombart 2008), POPGENE (ver. 1.32; Yeh et al. 1999) and GENEPOP (ver. 4.0.11; Raymond & Rousset 1995, Rousset 2008), the latter with 10,000 dememorisation iterations; 200 batches; and 10000 iterations using MCMC simulations. The level of differentiation among populations was analysed by AMOVA (analysis of molecular variance) using Arlequin 3.5 (Excoffier & Lischer 2010). The UPGMA, PCoA and DAPC clustering was performed using the R-packages *adegenet*, ade4, *hclust* and *ape* (Paradis et al. 2004, Popescu et al. 2012). To analyse the population structure, we used Bayesian clustering approach implemented in the STRUCTURE (ver. 2.2; Pritchard et al. 2000). The analysis was performed with admixture model with *K* ranging between 1 and 20 with 4 replicate runs for each *K*, 80 000 burn-in iteration followed by 800,000 MCMC iterations. The Δ*K* statistics (Evanno et al. 2005) was used in order to find appropriate number of cluster in the STRUCTURE output files using the STRUCTURE HARVESTER (Earl & von Holdt 2012).

Survey of results

Geographical distribution of service trees

The species has been grown in some warm areas of the Czech Republic as a fruit tree since the Medieval period (Pyšek et al. 2012) and it has become widely naturalized in the České středohoří Mts in north-western Bohemia and in several parts of southern Moravia (e.g. the Pavlovské vrchy, Ždánický les, Chřiby and Vizovická vrchovina hills and the Bílé Karpaty Mts). The southernmost and easternmost localities in Moravia are close to the northern limit of its assumed native distribution area in Slovakia or Hungary (Kurtto 2009) and perhaps some of them may be native. However, direct evidence of its native occurrence in southern Moravia is lacking. In the České středohoří Mts it is almost solely confined to areas where *Quercus pubescens* also grows.

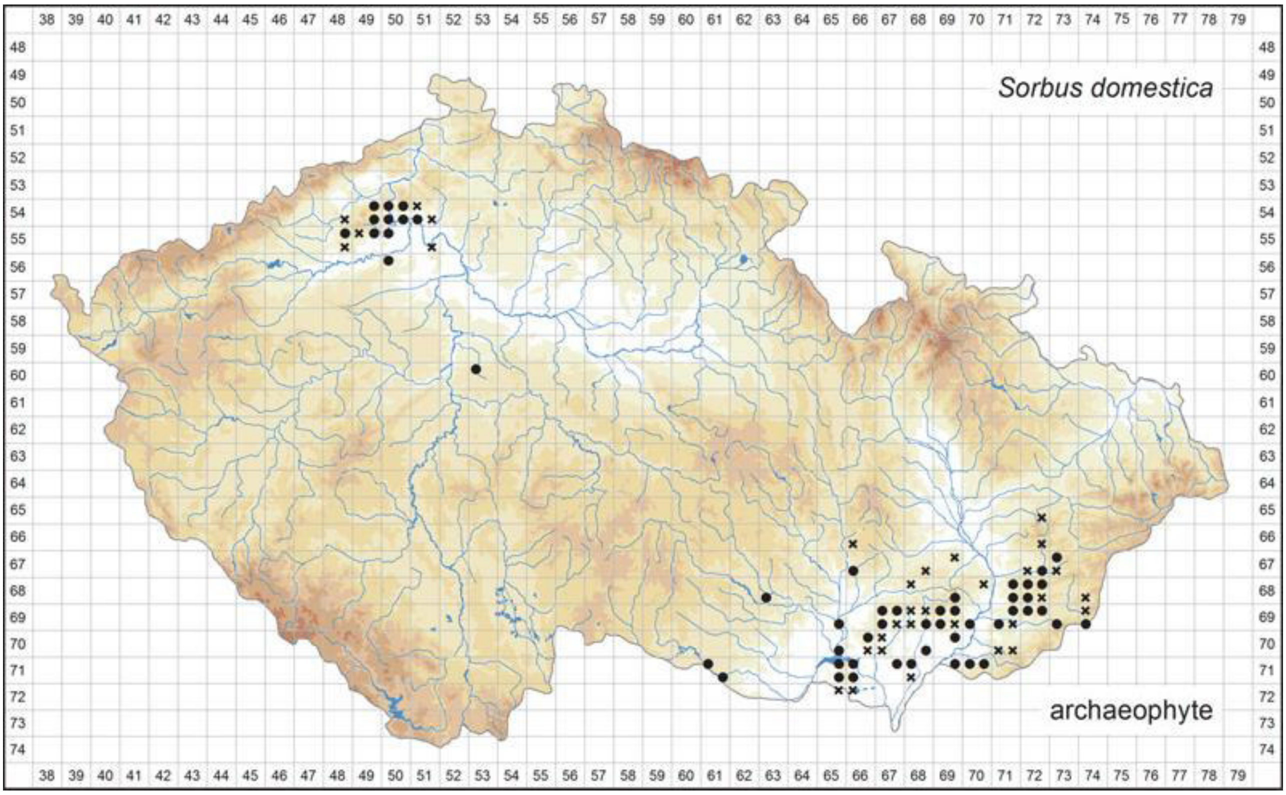


Figure 2. – Distribution of *Sorbus domestica* in the Czech Republic: _ spontaneous escapes (52 quadrants), × deliberately planted in the countryside and uncertain origin (32 quadrants). Prepared by Martin Lepší, Petr Lepší, Zdeněk Špíšek & Karel Kubát.

During the study, 473 individuals of the service tree at the Czech and Slovak sites of the White Carpathians were documented. Their distribution is plotted in Figure 3.

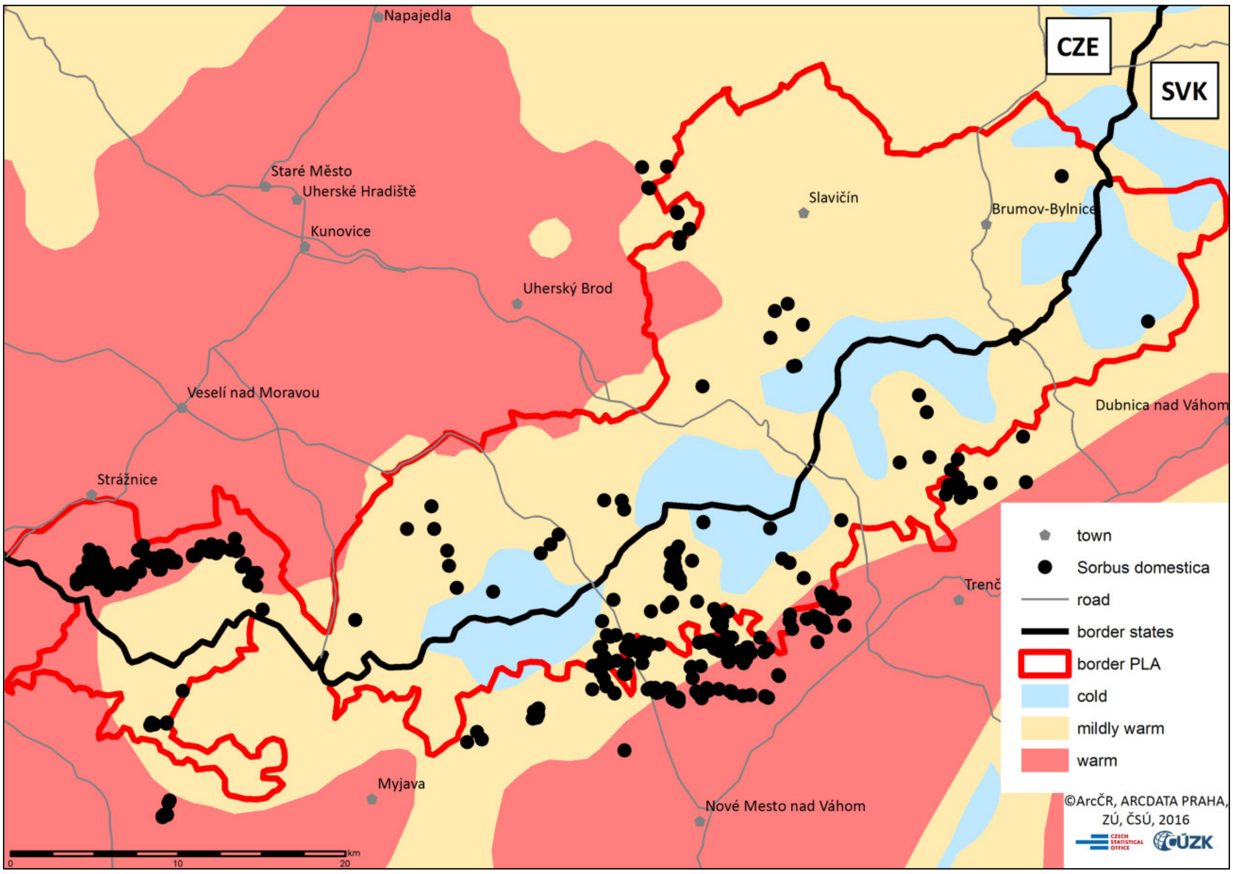


Figure 3. - Climate regions and *Sorbus domestica* distribution in the White Carpathians and their surroundings

The individuals of *S. domestica* forming the largest occurrence were located in the South Moravian region at the Czech site as well as at the foothills of the middle part of the White Carpathians at the Slovak site. According to the climate map, the individuals grow mainly in the mildly warm and moist climate region (48%) and in the warm, very dry or mildly wet regions 51%). Only 1% of the recorded trees were situated in the cold region.

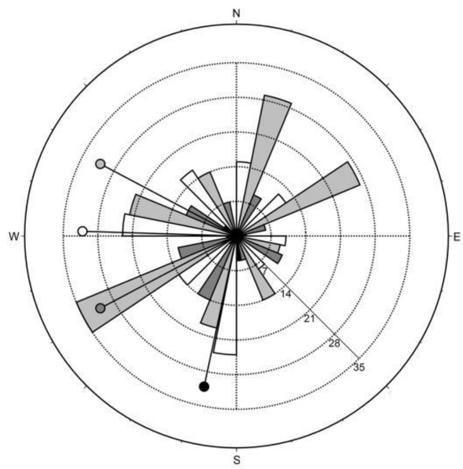


Figure. 4. S – W altitude and orientation slopes of *S. domestica*
Altitudinal levels: □ 200–299 m a.s.l., ▇ 300–399 m a.s.l.; ▇ 400–499 m a.s.l.; ▇ 500–599 m a.s.l.

Most localities (44.5%) were on altitude 200–299 m a.s.l. (Figure 4.). The most frequent slope exposure in this altitude is west, but many trees grow on south slopes. The second most frequented category of the localities (32.1%) is at the altitude 300–399 m a.s.l. with the most frequent slope exposure towards the west and north-west, but trees often grow on south-west and northeast slopes. Less frequent occurrences (19.5%) were on the altitude 400–499 m a.s.l. with the most frequent slope exposure towards the south-west exposure. Only small part of localities (3.9%) are situated on the altitude 500–599 m a.s.l. and the only single individual was found at an altitude higher than 600 m a.s.l., on the Kykula hill (Chocholná-Velčice village in Slovakia, 662 m a.s.l.), with the southward exposure.

Distribution of fruit types

The site of service trees significantly affects the shape of fruits ($\chi^2_{(25)} = 40.8$, $p = 0.024$). The greatest diversity of fruit shapes was recorded in the forest interior, where all types were discovered (Figure. 5). Flattened fruits were not recorded in the vineyards and balks while elliptical fruits were restricted to vineyards, forests and orchards/gardens.

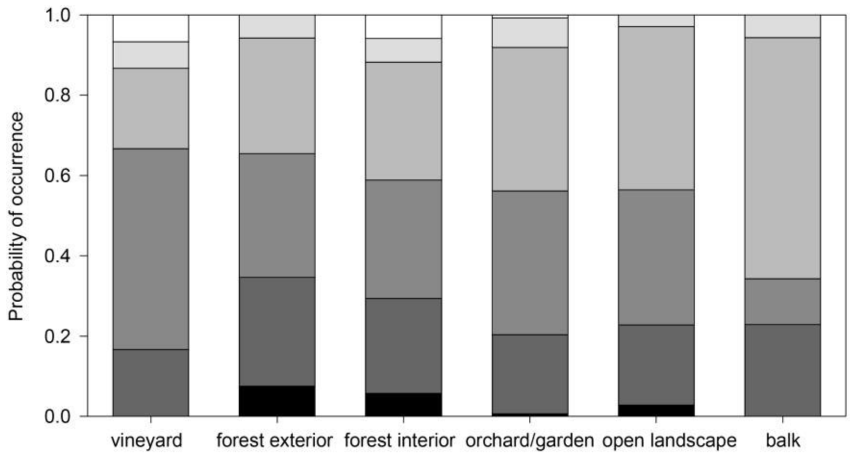


Figure 5. Fruit shape types of *S. domestica* in different site types. The highest density of fruit shape types was in the region of the Žerotín hill (near Strážnice). The most frequent shapes were the conical (37.1%), pyriform (32.7%) and spheroidal (21.1%). The other types of fruit shapes were rare. Fruit shapes: ■ flattened; ■ spheroidal; ■ pyriform; ■ conical; ■ egg-shaped; □ elliptical

Dendrometric characteristics

The average height of individuals was 11.5 m and the tallest tree was found in the forest interior (approximately 25 m). DBH of the investigated individuals ranged from 0.15 up to 1.45 m. More than a half of the individuals fell within the DBH range 26–75 cm. Some very large trees of *S. domestica* with the DBH more than 1 m (5.9%) were present in this area, and many were still fertile. Supposedly young individuals (DBH < 25 cm) were less frequent (13.2%).

There was a considerable variation in dendrometric parameters among localities. Notably, shape (DBH-to-height ratio) of the trees growing in forest interiors was significantly different from the other locations (Figure 6). According to the evaluated DBH categories and different localities (Figure 6), there was a tendency of increase in quantity of trees with an increase in the DBH category in the open landscape. The same pattern was found for individuals growing in the forest exterior. The largest individuals, with a DBH greater than 101 cm, grew mainly in the open landscape and in orchards/gardens (37.5% in both categories); 17.9% of these largest trees were growing in the forest edge, while only a few were found in the forest interior or in the balks.

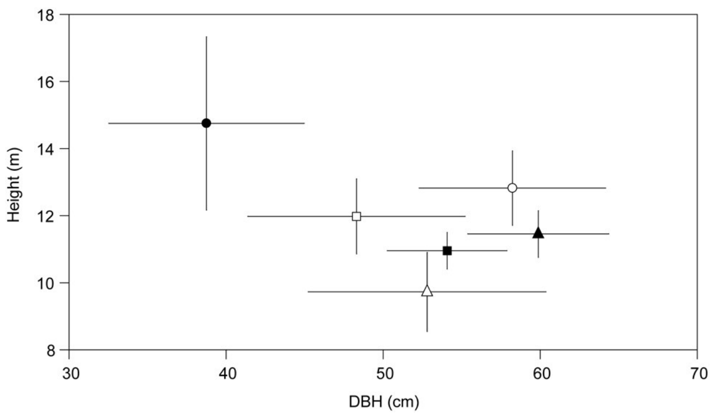


Figure 6. The effect of tree location on the DBH. Circles represent mean values, and error bars are 95% confidence intervals. Note the log-scaling of the ordinate.

Location: □ balk; ○ forest exterior; ● forest interior; ▲ open landscape; ■ orchard/garden; △ vineyard.

Analysis of microsatellites

All 5 loci amplified well for all samples, with exception of *mss-6* for sample #029 from Dubrovnik (Croatia) and sample #002 from Adamovske Kochanovice (Slovakia). For most of analyses were these samples used with indicated missing value (as -9), but all 189 samples were included. Analysed loci were highly heterozygous, i.e (H_o/H_e): mss-5 (0.92/0.77), mss-13 (0.9/0.55), mss-6 (0.72/0.68) and mss-3 (0.84/0.67) only mss-16 showed expected heterozygosity (0.63/0.65) and generally indicates high genotypic variability within populations. Total number of identified alleles is 38 and it varies among assigned groups of localities between 11 (UK - England) and 25 (CZ-BK – White Carpathians). It is strongly affected by the population sample, however, even samples with low number of collected individuals exhibit genotypic variability.

Number of alleles among loci varies between 4 (mss-3) and 12 (mss-6). The overall characteristics of loci is summarized in Table 1.

Genetic differentiation among populations

Pairwise F_{ST} indices (see Table 3.) revealed weak to strong genetic differentiation. Values range between 0.003 and 0.270. Generally, neighbouring populations showed very weak differentiation, whereas distant population revealed strong differentiation, i.e. Turkey (up to 0.268), Crimea in Ukraine (up to 0.227) and Israel (up to 0.270). All Pannonian populations shows very weak genetic differentiation, but outlying population from the České Středohoří hills (Central Bohemia, Bohemian Massif) has moderate differentiation with weakest differentiation to populations in Slovakia (0.058) and Germany (0.066). Unfortunately, some of these values are not significant due to low number of sampled individuals (Italy, Crimea, Israel).

Different hierarchical clustering approaches showed similar pattern of not-well differentiated populations. The UPGMA (Figure 7.) revealed distances mostly related to distant geographic distribution showing as the most distant populations in Turkey, Crimea and UK. However, further clustering revealed no clear distribution- or population-based pattern. Samples from all population are distributed across all 4 major distinguished clades, although some samples from the White Carpathians or České Středohoří hills tend to cluster together. The AMOVA revealed very high intra-population variation and decreased inter-population variation even on large geographic distance (Table 2.).

Similar pattern was obtained by DAPC. The PCoA diagram was fit best at 4 major groups, which are weakly separated (Figure 8a.) having some individuals tidily neighbouring with individuals from other cluster. Inferred clusters include mostly individuals from more than single natural population (Figure 8b.), with minor exceptions of populations with low number of individuals (such as Italy, Crimea, Israel and England). Samples from the České Středohoří Mts. are prevailingly clustered in cluster/group #2, which shows moderate differentiation. All geographically distant populations (such as Israel, Turkey, Crimea) are clustered in cluster/group #4 along with individuals with most of sampled populations. Another best-fitting number of clusters were set at 10 having similar pattern of 8 groups not-well differentiating from each other (not shown here).

Table 1. Characteristics of studied loci.

	Na	*Ho*	*Hs*	*Ht*	*Dst*	*Htp*	*Dstp*	*Fst*	*Fstp*	*Fis*	*Dest*
mss-5	9	0.92	0.69	0.81	0.12	0.82	0.13	0.15	0.16	-0.33	0.41
mss-16	8	0.48	0.58	0.65	0.07	0.66	0.07	0.10	0.11	0.17	0.18
mss-13	5	0.94	0.58	0.70	0.11	0.71	0.12	0.16	0.17	-0.62	0.30
mss-6	12	0.77	0.65	0.77	0.12	0.78	0.13	0.16	0.17	-0.18	0.37
mss-3	4	0.75	0.60	0.64	0.04	0.65	0.05	0.07	0.07	-0.25	0.12

Table 2. AMOVA (analysis of molecular variance) results of 5 SSR loci based on F_{ST}

Source of variation	**d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among groups	4	37.280	0.08767	5.13
Among populations within groups	8	25.933	0.09729	5.70
Within populations	365	561.916	1.52239	89.17
Total	377	625.130	1.70736	

Table 3. Pairwise F_{ST} indices for studied populations and population groups. Values in regular font are significant (significance of differentiation P<0.05) ,values in italic font are non-significant. Abrreviated populations: CZ (BK) = Czechia (White Carpathians), CZ (SM) – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, CZ (CS) – Czechia (České Středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom, IL – Israel, TR – Turkey, UA – Ukraine (Crimea)

POP	CZ (BK)	CZ (SM)	SK	AT+SI	HR	CZ (CS)	DE	FR	IT	UK	IL	TR	UA
CZ (BK)	0,000												
CZ (SM)	0,032	0,000											
SK	0,023	0,003	0,000										
AT+SI	0,033	0,037	-0,013	0,000									
HR	0,062	0,069	0,040	0,014	0,000								
CZ (CS)	0,073	0,093	0,058	0,088	0,125	0,000							
DE	0,078	0,053	0,011	0,034	0,036	0,066	0,000						
FR	0,074	0,052	0,030	0,016	0,056	0,139	0,060	0,000					
IT	*0,030*	*0,016*	*-0,043*	*-0,012*	*-0,042*	*0,058*	*0,017*	*-0,003*	*0,000*				
UK	0,241	0,236	0,206	0,209	0,130	0,251	0,121	0,209	*0,141*	0,000			
IL	0,262	0,232	0,177	0,187	0,146	0,270	0,149	0,177	*0,062*	*0,211*	0,000		
TR	0,200	0,184	0,183	0,124	0,143	0,268	0,150	0,095	*0,130*	*0,230*	*0,079*	0,000	
UA	0,227	0,190	0,141	0,146	0,147	0,219	0,165	0,086	*0,014*	0,225	*0,017*	0,124	0,000

Figure 7. UPGMA consensus tree. Abrreviated populations: BK = Czechia (White Carpathians), MOR – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, Stred – Czechia (České středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom (England), IL – Israel, TR – Turkey (Cappadocia), UA – Ukraine (Crimea).

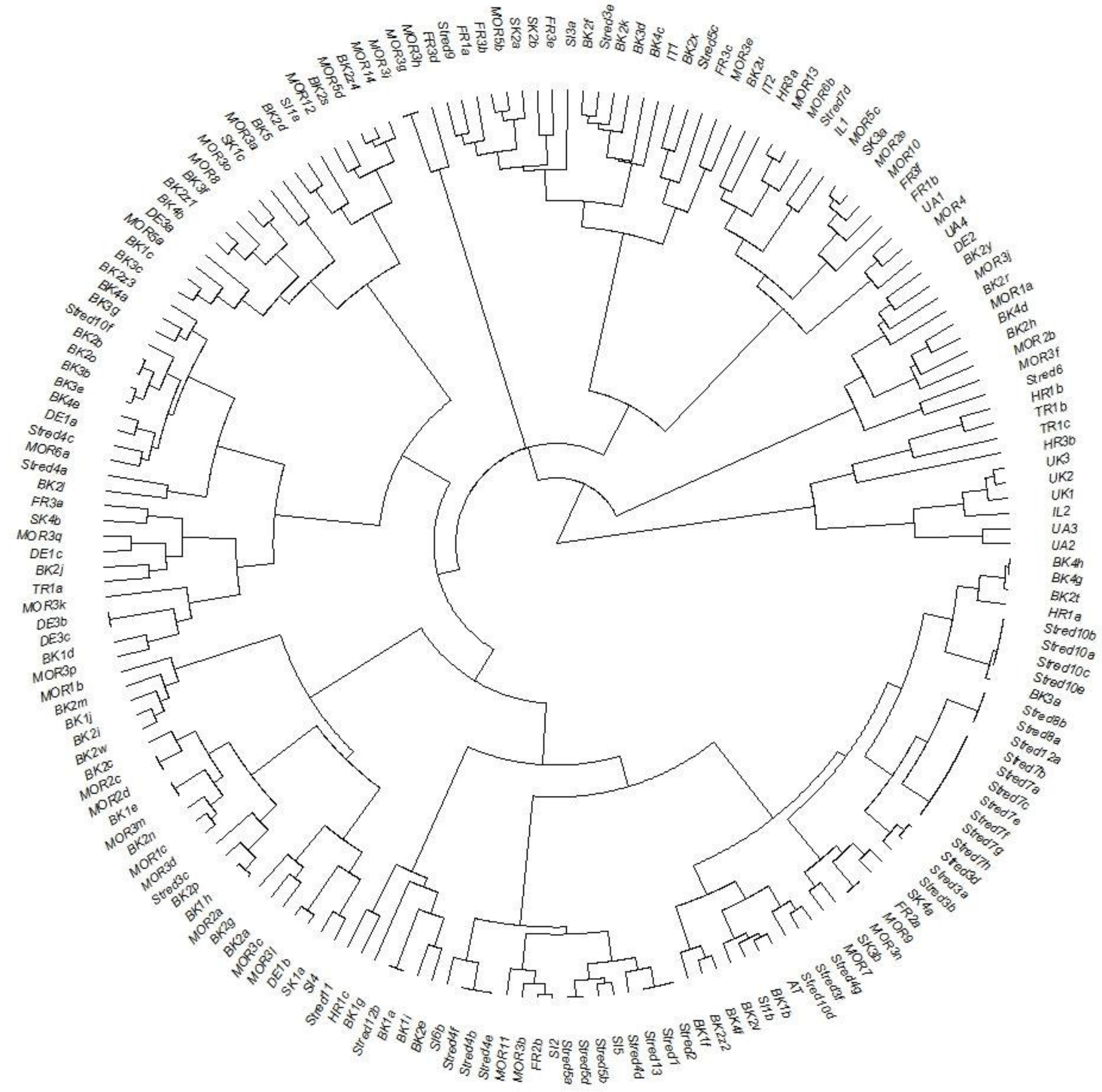
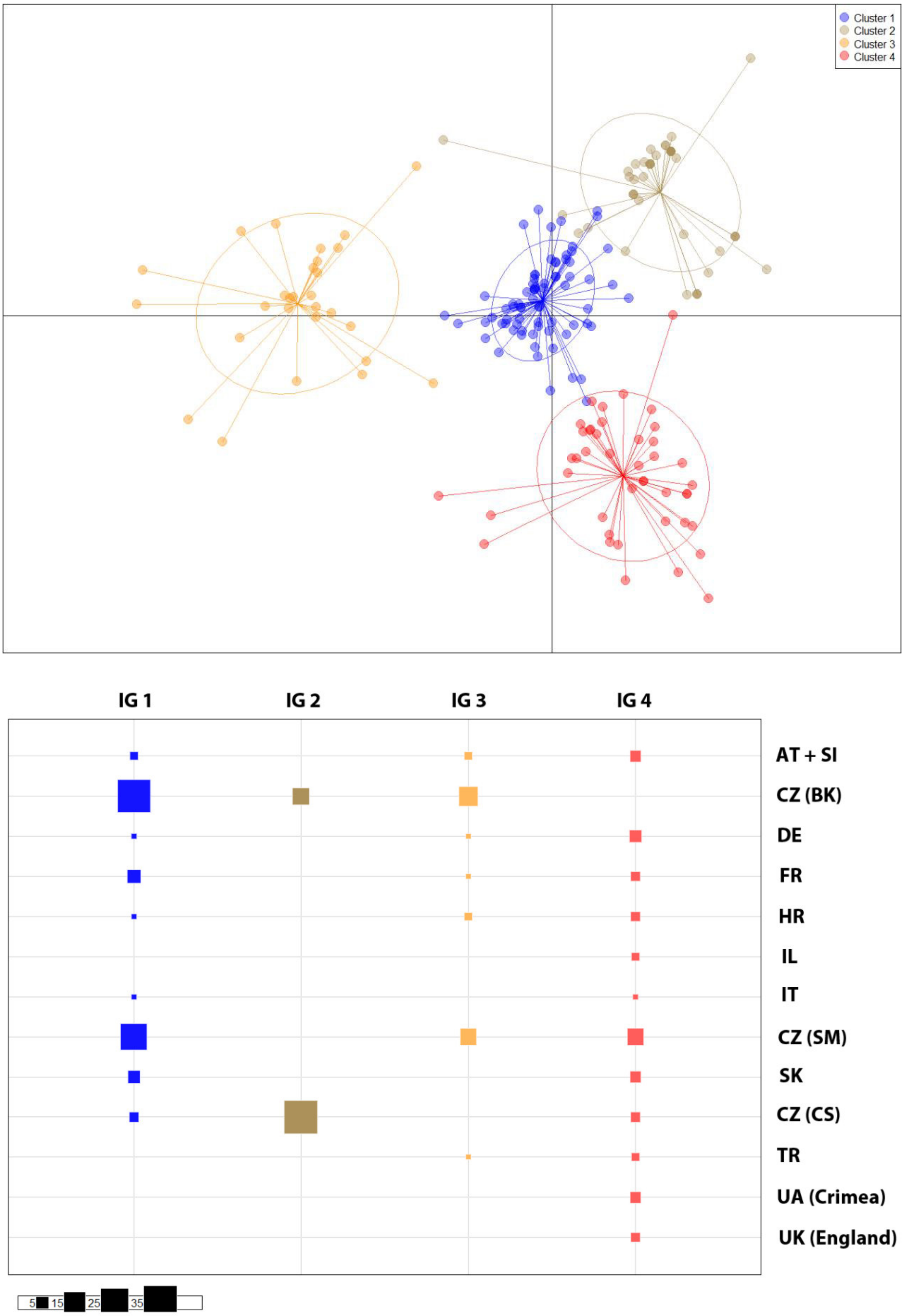


Figure 8. DCPA with 4 major groups. Inferred 4 clusters of PCoA (a) are consisting of individuals across different populations (b). Abrreviated populations: CZ (BK) = Czechia (White Carpathians), CZ (SM) – Czechia (Southern Moravia), SK – Slovakia, AT+SI = Austria & Slovenia, HR – Croatia, CZ (CS) – Czechia (České Středohoří Mts.), DE – Germany, FR – France, IT – Italy, UK – United Kingdom, IL – Israel, TR – Turkey, UA – Ukraine (Crimea)



Summary and conclusions

Title: Populations of service tree (*Sorbus domestica* L.) in Central Europe and their Characteristics

In Europe, solitaire trees are gradually disappearing from the free landscape, especially fruit trees. Landscapes are gradually changing alley, stalks and large field ropes are being cast. My Thesis is monitoring occurrence of service tree in Czechia. A detailed survey showed a predominant occurrence in warm and slightly warm climatic areas (Czech Central Mountains and Southeastern Moravia). The vast majority of trees grow in dominant in orchards, vineyards in the open countryside. The occurrence of trees in the forest is limited, yet the species spontaneously spreads. In the White Carpathian region there is a strong anthropogenic influence on species expansion. However, the comparison of the shape variability of the fruits did not show any statistically significant correlation.

Genetic differentiation among populations was not high, especially Pannonian populations of Central Europe show similar genetic admixed background with several slightly distinct clusters of *i*) White Carpathians and *ii*) Southern Morava (Pálava). These are clearly linked to other Pannonian populations and further Mediterranean populations, which makes a “core” cluster of genetic variability. Interestingly, population form the České Středohoří Mts. forms distinct cluster slightly differing by the admixed genetic background from Pannonian population and is more linked to German (or further French) populations.

Although this thesis brings many new insights into the actual distribution, ecology and genetic variability of species in Europe, there are still many questions to be answered. Besides specific viability of populations, the question which populations might be consisting of putatively natural and autochthonous genotypes and what is the origin of allochthonous genotypes. One of major unresolved questions is the species protection and conservation. As an archaeophyte it is excluded from regional Red lists and protection plans, despites its importace in cultural landscape of Czechia. This thesis opened new reserach question and further reserach can bring new insights in understanding the biology and genetics of *Sorbus domestica* in Czechia and in Europe.

Shrnutí a závěr

Název práce: Charakteristika populací jeřábu oskeruše (*Sorbus domestica* L.) ve střední Evropě

V Evropě postupně mizí solitérní stromy z volné krajiny obzvláště ty ovocné. Krajinný ráz se postupně mění, mizí aleje, remízky i stromořadí a dochází zcelováni velkých polních lánů. Práce mapuje výskyt jeřábu oskeruše v České republice. Detailní průzkum prokázal převážný výskyt v teplých a mírně teplých klimatických oblastech (České středohoří a Jihovýchodní Morava). Velká většina stromů roste v jako dominanty v sadech, vinicích ve volné krajině. Výskyt stromů v lese je omezen, přesto se druh spontánně šíří. V oblasti Bílých Karpat je patrný silný antropogenní vliv na rozšíření druhu. Přesto srovnání tvarové variability plodů neprokázalo žádnou statisticky významnou korelaci.

Genetická variabilita mezi populacemi není nikterak vysoká. Zvláště Panonské populace střední Evropy vykazují geneticky podobné pozadí s několika odlišnými populacemi i) Bílé Karpaty a ii) Jižní Morava (Pálava). Tyto populace jsou navzájem propojeny s Panonskými populacemi. S dalšími středomořskými spoluvytváří „jádro“ genetické variability druhu. Zajímavé je, že populace Českého středohoří vytváří cluster, který se mírně liší od genetického pozadí panonských populací a je více propojen s německými (nebo francouzskými) populacemi.

Ačkoliv tato dizertační práce přináší řadu nových poznatků týkajících se aktuálního rozšíření, ekologie druhu, genetické variability druhu, zůstává v této oblasti stále mnoho nezodpovězených otázek. A to zejména životaschopnost jednotlivých populací, otázka původnosti druhu na našem území: tj. stanovení populací, které mohou obsahovat hypotetické původních autochtonní genotypy, případě jaký je původ alochtonních (nepůvodních) genotypů, kterými jsou naše populace obohaceny. Další zásadní nezodpovězená otázka se týká ochrany druhu, který jako archeofyt není zařazen v červených seznamech a proto není chráněn, přestože by si ochranu jako důležitá součást kulturní krajiny zasloužil (i s ohledem na jeho genetickou variabilitu). Problematika tak není zdaleka vyčerpána a jistě v budoucnu přinese řadu zajímavých poznatků, neboť páce otevřela nové otázky o biologii a genetice druhu u nás i v Evropě.

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Lidové moudro z Moravy

„Romantici sází růže, správní muži oskoruše“