Zurich University of Applied Sciences

Life Sciences and Facility Management

Institute of Natural Resource Sciences

Evidence for hybridization between exotic *Fagus orientalis* and native *Fagus sylvatica* in a forest stand of Switzerland

Bachelor Thesis

By
Mirjam Kurz

Bachelor Degree Course 2015
Environmental Engineering
Submission Date: 8.11.2018

Correctors:
Dr. Fabio Rezzonico
ZHAW (Zurich University of Applied Sciences)
Wädenswil

Dr. Christoph Sperisen
Swiss Federal Research Institute WSL
Birmensdorf

External supervisor:
Katalin Csilléry
Swiss Federal Research Institute WSL
Birmensdorf

Imprint

Author

Mirjam Kurz

Cover picture

Forest stand in Wäldi (TG)

Keywords

Fagus orientalis, Fagus sylvatica, Hybridization, Microsatellite markers (SSRs), Invasive plants

Citation

Kurz, M. (2018) *Evidence for hybridization between exotic Fagus orientalis and native Fagus sylvatica in a forest stand of Switzerland.* ZHAW, Wädenswil.

Institute

Institute of Natural Resource Sciences

ZHAW Life Sciences and Facility Management

Grüental, Postfach

8820 Wädenswil

Wädenswil, 8.11.2018

Abstract

Assisted migration – the intended movement of species and populations to facilitate range expansion – has recently received considerable attention in the face of climate change, since it could serve as a tool to reduce the threats posed to ecosystems and species. Particularly, it is generally expected that trees will not be able to adapt or migrate quickly enough in response to the expected climate change without human help. The topic is, however, controversially discussed, because introducing foreign species to an ecosystem can also have disadvantages, such as displacement of native species, especially when a species becomes invasive. Hybridization between introduced and native plant species is one important factor in the evaluation of invasive plants and can be a threat to biodiversity.

European beech (*Fagus sylvatica)* is one of the economically most important broadleaved trees in Europe and is expected to experience a major shift in its natural area as a consequence of climate change. Therefore, its close relative F. orientalis (*Fagus orientalis*) has been proposed as an alternative for the future. But it has to be taken into consideration that these two species are known to hybridize in their contact zone in Eastern Europe.

The goal of this study was to evaluate whether hybridization has occurred between planted *F. orientalis* and native *F. sylvatica* in a forest stand of Switzerland. The stand is located in Wäldi, Canton Thurgau, where about 100 years ago ten *F. orientalis* trees were planted. Eight of them still grow at the site today, surrounded by F. sylvatica. Sixteen microsatellite markers were applied to tell apart the two species and identify individuals with intermediate genotypes.

The microsatellite markers provided adequate resolution to distinguish between the two species. The analysis of offspring strongly suggests the occurrence of hybridization, since nearly half of the sampled saplings and young trees showed intermediate genotypes. In addition, the results indicate that the hybrids are a result of gene flow from *F. sylvatica* to *F. orientalis* and that hybridization has occurred several times during the history of the stand.

For the future it is important to find out whether gene flow also takes place from *F. orientalis* to *F. sylvatica*, in what frequency hybrids occur and whether morphological features could contribute to the evaluation in the field. In Germany, *F. orientalis* is already being promoted for test plantings because the species is regarded to be climatically pre-adapted. A great danger for the ecosystems in Switzerland is not expected, since *F. orientalis* can be found in very similar plant communities. However, plantations must be monitored for plant growth and diseases in both adult trees and offspring, and the introduction of *F. orientalis* should only be carried out if the advantages clearly outweigh all possible disadvantages.

Zusammenfassung

Unterstützte Migration - die Bewegung von Arten und Populationen zur Erleichterung der natürlichen Arealausdehnung - hat in letzter Zeit angesichts des Klimawandels grosse Aufmerksamkeit erregt, da es als Instrument zur Verringerung vieler Bedrohungen für Ökosysteme und Arten dienen könnte. Es wird insbesondere erwartet, dass sich Bäume nicht schnell genug anpassen oder migrieren können, um ohne menschliche Hilfe auf den erwarteten Klimawandel zu reagieren. Das Thema wird jedoch kontrovers diskutiert, da die Einführung fremder Arten in ein Ökosystem auch Nachteile mit sich bringen kann. Zum Beispiel die Verdrängung einheimischer Arten, welche insbesondere wenn eine Art invasiv wird auftritt. Die Hybridisierung zwischen fremden und einheimischen Pflanzenarten ist ein wichtiger Faktor bei der Bewertung invasiver Pflanzen und kann eine Bedrohung für die Biodiversität darstellen. Die Rotbuche (*Fagus sylvatica*) ist einer der wirtschaftlich bedeutendsten Laubbäume Europas und wird voraussichtlich durch den Klimawandel eine starke Veränderung ihres natürlichen Areals erfahren. Daher wurde die nahe verwandte Orientbuche (*Fagus orientalis*) als Alternative für die Zukunft vorgeschlagen. Dabei ist jedoch zu berücksichtigen, dass diese beiden Arten in ihrer Kontaktzone in Osteuropa bekanntlich hybridisieren.

Ziel dieser Studie war es, zu untersuchen, ob eine Hybridisierung zwischen den gepflanzten *F. orientalis* und den einheimischen *F. sylvatica* in einem Waldbestand der Schweiz stattgefunden hat. Der Stand befindet sich in Wäldi, Kanton Thurgau, wo vor rund 100 Jahren zehn *F. orientalis*-Bäume gepflanzt wurden. Acht davon wachsen noch heute am Standort, umgeben von *F. sylvatica*. Sechzehn Mikrosatelliten-Marker wurden eingesetzt, um die beiden Arten zu unterscheiden und Individuen mit intermediären Genotypen zu identifizieren.

Die Mikrosatelliten-Marker zeigten eine ausreichende Auflösung, um zwischen den beiden Arten zu unterscheiden. Die Analyse der Verjüngung deutete stark auf das Auftreten einer Hybridisierung hin, da fast die Hälfte der untersuchten Setzlinge und Jungbäume intermediäre Genotypen aufwiesen. Darüber hinaus deuten die Ergebnisse darauf hin, dass die Hybride ein Ergebnis des Genflusses von *F. sylvatica* nach *F. orientalis* sind und dass die Hybridisierung in der Geschichte des Standes mehrfach vorgekommen ist. Für die Zukunft ist es wichtig herauszufinden, ob auch der Genfluss von *F. orientalis* nach *F. sylvatica* stattfindet, in welcher Frequenz Hybriden auftreten und ob morphologische Merkmale zur Bewertung im Feld beitragen könnten. In Deutschland wird *F. orientalis* bereits für Probeanpflanzungen gefördert, da die Art als klimatisch voradaptiert gilt. Eine grosse Gefahr für die Ökosysteme in der Schweiz ist nicht zu erwarten, da *F. orientalis* in sehr ähnlichen Pflanzengesellschaften zu finden ist. Allerdings müssen die Pflanzungen sowohl bei erwachsenen Bäumen als auch bei Nachkommen auf Pflanzenwachstum und Krankheiten überwacht werden. Die Einführung von *F. orientalis* sollte nur dann erfolgen, wenn die Vorteile alle möglichen Nachteile deutlich überwiegen.

Acknowledgment

I would like to express my very great appreciation to

Fabio Rezzonico for the extraordinary supervision and the introduction and help in the laboratory.

Christoph Sperrisen for the many encouraging discussions, the help with the planning and evaluation of the project and the helpful inspections of the location as well as the financing of parts of the project.

Katalin Csilléry for the many great suggestions, the tips and support with the evaluation, and the additional inspection of the site.

Peter Brang for the proposal, the making possible and financing of parts of the project.

Sebastian Bänteli and his forester team, for the insightful first tour of the stand and help with sampling.

Wilhelm Schenk for his thoroughly researched information on the site and the accompanying of the first sighting.

Rene Graf for his fantastic help with the binning.

Joel Pothier for writing the very valuable script to restructure the data.

Rahel Friedeberg for her excellent language proofreading.

Contents

1 Introduction

Movement of species by man has a long history. For millennia, humans have improved their quality of life by relocating for example edible and medicinal plants (Vitt, Havens, Kramer, Sollenberger & Yates, 2010). In forestry, trees have long been planted outside their natural growing areas in order to promote timber production (Brang, Küchli, Schwitter, Bugmann & Ammann, 2016).

The intended movement of species and populations to facilitate range expansion, has now received renewed attention in the face of climate change and a new term, assisted migration, has been coined (Vitt et al., 2010). It is argued that assisted migration may serve as a tool to reduce the threats posed to ecosystems and species by the rapidly changing climate. It is likely that long-lived species, such as trees, will not be able to adapt or migrate quickly enough in response to the expected climatic changes in order to continue to provide the required services without human help (Allgaier Leuch, Streit, & Brang, 2017; Ledig, Rehfeldt, & Jaquish, 2012).

Consequently, forest tree species are highlighted most often in the discussion about assisted migration, also due to their economic value (Williams & Dumroese, 2013). Decisions about assisted migration programs have scientific, economic, political and societal aspects, which often result in heated debates about this topic. The scientific community in Europe is divided between supporters who urge to help nature adapt to human-induced change and opponents who call for leaving nature alone and reducing human impacts. The discussion is greatly influenced by moral judgements and believes making it difficult for science to propose solutions (Sarewitz, 2011).

The introduction of foreign species, here focused on trees, can have both advantages and disadvantages for the recipient ecosystem. Non-native tree species, for example, from more southern regions, may be pre-adapted to the future climatic conditions of today's still cooler and more humid regions, and thus may bring advantages for timber production, contribute to tree species diversity (Neuner, Beinhofer & Knoke, 2013) and help to maintain ecosystem processes and services. On the other hand, introducing species can also lead to the displacement of native species (Kowarik & Rabitsch, 2010), undesirable soil changes or the introduction of pathogens and parasites (Reif, Aas & Essl, 2011).

One of the main concerns of assisted migration is that the introduced species may become invasive, which may harm the functioning of the recipient ecosystem (Ricciardi & Simberloff, 2009; Vitt et al., 2010). A non-native species is considered "invasive" when it is endangering native ecosystems, habitats or species. (Wittenberg, 2006). Hybridization of introduced plant species with native plants is considered an important factor in the evaluation of invasive plants and can be a threat to biodiversity (Bleeker, Schmitz & Ristow, 2008; Hails & Morley, 2005; Levin, Francisco-Ortega & Jansen, 1996). While the role of hybridization in herbaceous plant invasions has been extensively studied, (Schierenbeck & Ellstrand, 2009) little is known about the invasiveness of tree species. Trees are increasingly considered

as significant invaders and therefore studies of hybridization in trees are highly relevant (Richardson & Rejmánek, 2011). The invasiveness of a tree can be enhanced by hybridization for various reasons: hybrid-derived genotypes can show increased fitness compared to parental genotypes (Ellstrand & Schierenbeck, 2000) such as increased fecundity and size (Hovick & Whitney, 2014). Hybridization may also contribute to increasing the genetic diversity after a founding event, thus increasing the potential for adaption (Schierenbeck & Ellstrand, 2009). For example, mating of F1s or backcrossing with parental genotypes can increase introgression and thus the number of hybrids in a population, (Gaskin, 2016). Gaskin (2016) has identified 20 hybrid invasive tree taxa and in seven of these taxa hybrids were better invaders than either of the parental species.

In conclusion, the cultivation of foreign tree species requires thorough consideration, in order to avoid considerable risks for ecosystems and species. Nevertheless, non-native tree species can potentially secure timber production and the protective function of the forest. Overall, more scientific knowledge is required and different values and goals need to be clearly defined in order to manage assistant migration of foreign tree species in an adequate way.

Species of the genus *Fagus* are among the most abundant trees of temperate deciduous broad-leaved forests. The genus includes ten primary species that are found in Europe, North America and Asia (Denk, 2003). Diversity is highest in East Asia with six different species (Fang & Lechowicz, 2006).

In Europe, two species occur, European beech (*Fagus sylvatica* LINNAEUS) and Oriental beech (*Fagus orientalis* LIPSKY). *F. sylvatica* is one of the ecologically and economically most important broad-leaved trees. It has a wide distribution range, covering almost the entire temperate and warm to temperate zones of Europe. Its natural area, shown in Figure 1, is mainly limited by the species low tolerance to frost and long dry periods (Roloff, Iisgerber, Lang, & Stimm, 2010). In a small region of southeast Europe, *F. sylvatica* is replaced by *F. orientalis,* whose main range is in west Asia (Northern Turkey, the Caucasus and Northern Iran) (see Figure 2).

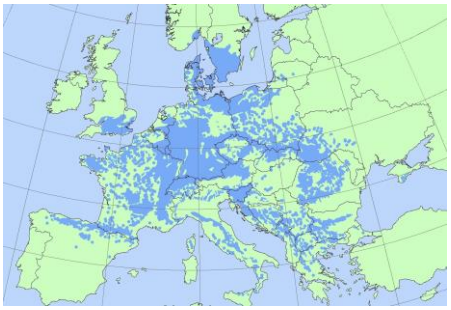

Figure 1: Natural area of *F. sylvatica* (http://www.euforgen.org/species/fagus-sylvatica/)

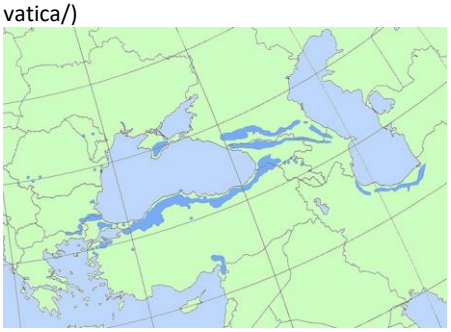

Figure 2: Natural area of *F. orientalis* (http://www.euforgen.org/species/fagus-orientalis/)

The two beech species are closely related and have been suggested to hybridize in their zone of contact in the Balkan peninsula (Gömöry et al., 1999; Papageorgiou et al., 2008). The taxonomic status of *F. sylvatica* and *F. orientalis* is still unclear. Traditionally, they are classified as two separate species (Tutin et al., 1964). Later systematic-morphological comparisons have led to the conclusion that there is only one species that can be divided into two subspecies: *F. sylvatica* ssp. *sylvatica* (sensu Denk) and *F.*

sylvatica ssp. *orientalis* (LIPSKY) GREUTER et. BURDET (Denk, 1999). A third (sub-) species called *F. moesiaca* (*F. sylvatica* ssp. *moesiaca* (K. MALY) CZECZOTT) shows intermediate morphological characteristics and is regarded as a hybrid between *F. sylvatica* and *F. orientalis* (Papageorgiou et al., 2008). For the sake of simplicity, the terms *F. sylvatica* and *F. orientalis* are used for this paper.

Despite their close genetic relationship, the two species inhabit different climatic niches. In comparison with *F. sylvatica*, *F. orientalis* grows at warmer and drier sites (Fang & Lechowicz, 2006), and therefore is regarded as better adapted to warmer and drier climate.

As a consequence, *F. orientalis* has been proposed as an alternative for *F. sylvatica* to mitigate the impacts of climate change (Brang et al., 2016; Schmiedinger, Bachmann, Kölling & Schirmer, 2010). In fact, *F. sylvatica* is expected to experience a considerable shift in its natural area due to climate change (Geßler et al., 2006): In Switzerland, for example, *F. sylvatica* dominates the Swiss Plateau today, but it will most likely retreat to higher elevations (Zimmermann, Schmatz & Psomas, 2013). Maintaining under a warming climate the ecosystem services that *F. sylvatica* provides, such as timber production and protection against natural hazards, is of high ecological and economical importance. The introduction of *F. orientalis* could locally secure these ecosystem services in the long term.

Nevertheless, when considering introducing *F. orientalis* to Switzerland, the question must be clarified as to whether the two species will hybridize as they do in Eastern Europe. In 1921, ten *F. orientalis* trees of unknown origin have been planted in Wäldi (TG). Eight reproductive individuals surrounded by *Fagus sylvatica* are still growing today. The goal of this project was to evaluate whether hybridization has occurred between planted *F. orientalis* and native *F. sylvatica* in a forest stand of Switzerland.

For the distinction of the two species and for identifying hybrids, genetic markers (Avise, 1994) can be developed and used. Several marker types, such as chloroplast DNA (Magri et al., 2006), isozyme (Comps, Gömöry, Letouzey, Thiébaut & Petit, 2001), AFLP (Gailing & Wuehlisch, 2004) and microsatellite markers (SSRs) (Pastorelli et al., 2003) have already been developed for the genus *Fagus*. Due to their high degree of polymorphism SSRs are especially well suited for detection of hybrids (Streiff et al., 1999) and for paternity analysis (Kalinowski, Taper & Marshall, 2007). Since analyzing large beech populations with various SSR markers can be time-consuming and expensive, Lefèvre, Wagner, Petit, & De Lafontaine (2012) developed two multiplex kits each made of eight SSR markers for *F. sylvatica*, which considerably reduce analyses time and cost.

In this project it was investigated whether the two species *F. sylvatica* and *F. orientalis* can be separated using these sixteen SSR markers. Further, these markers were used to detect putative hybrid progeny at this particular site. By sampling different age classes, the question was addressed, if hybridization has occurred across multiple years or only once. On the basis of these results, recommendations were made for the management of *F. orientalis* in Switzerland.

2 Material and Methods

2.1 Study site

The study site is situated east of the village of Wäldi (610 meters above sea level, 47°37’43’’N, 9°6’14’’E) in the Canton of Thurgau, Switzerland. The area is characterized by several forest patches, dominated by oak (*Quercus*), ash (*Fraxinus*), maple (*Alnus*) and European beech (*F. sylvatica*) (ThurGIS, Kartenportal Kanton Thurgau). In two of these patches, eight *Fagus orientalis* trees occur. According to the local foresters ten *F. orientalis* individuals were originally planted in 1921 with reproductive material of unknown origin.

2.2 Adult and offspring sampling

Adult trees were identified as *F. orientalis* or *F. sylvatica* with the help of the local foresters (Sebastian Bänteli and Wilhelm Schenk) and by morphological characteristics summarized in Table 1. However, these characteristics are influenced by the position of the leaf within a shoot, its exposure to light and its orientation (Bartha & Raisz, 2004).

Table 1: Morphological characteristics of *F. sylvatica* and *F. orientalis* (Böhlmann, 2015; Fitschen, Schmidt & Schulz, 2017).

	F. sylvatica	***F. orientalis***
Leaf shape	Ovoid to elliptic	Elliptically elongated, slightly tilted
Vein pairs	5-8	8-12
Leaf length	5-10 cm	8-17 cm
Leaf base	Wedge-shaped, often running out at an angle	Partially rounded
Leaf stem	0.3-1 cm	0.5-1.5 cm

Leaf material for DNA extraction was collected from the lower part of the crown from all eight adult *F. orientalis* (hereafter referred to as OA1 to OA8) as well as 36 adult *F. sylvatica* trees (hereafter referred to as SA1-SA40 and SE1-SE8 (SE were located in a private forest area)). Locations of all adult trees are marked in Figure 3.

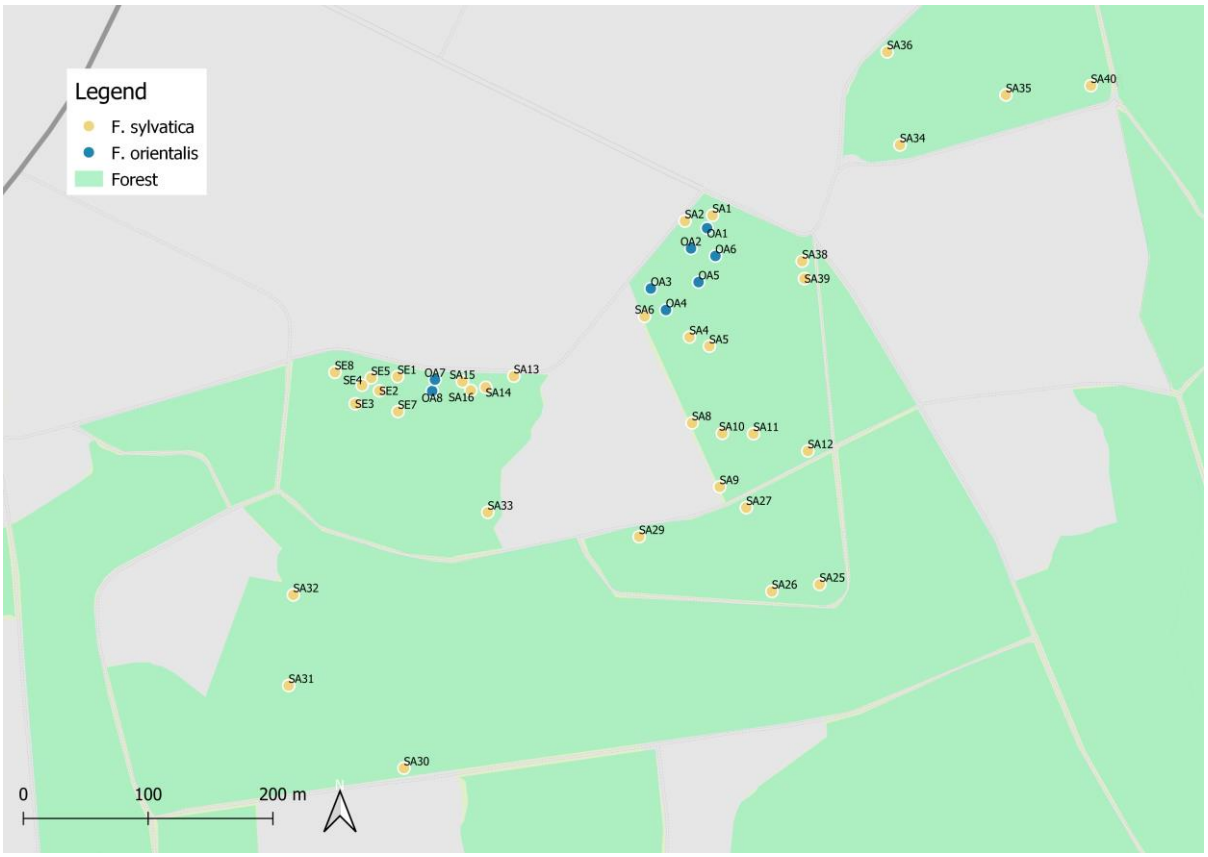

Figure 3: Map of all sampled adults (SA, SE and OA) (created with: QGIS, basemap: Esri World Topo)

Since the goal of the project was to assess if hybridization had occured in this natural setting, saplings and young trees beneath the adult *F. orientalis* trees and a number of adult *F. sylvatica* trees in the vicinity were sampled. The null hypothesis was that hybrids are rare. Therefore, it was planned to preferentially sample individuals with an intermediate morphology type as described by Nielsen & Schaffalitzky de Muckadeli, (1953). This turned out to be more difficult than expected, as a large number of different morphology types were encountered. Therefore, individuals with all different morphology types and in all different age classes present in the forest were sampled.

Saplings and young adult were classified to the following age groups Table 2.

Table 2: Definition of age classes A-D.

Age class	Description
Class A	young saplings, less than a meter high
Class B	saplings, less than three meters high, stem diameter lower than 10 cm
Class C	young trees, stem diameter between 10 and 20 cm
Class D	trees, stem diameter larger than 20 cm

Further, they were divided into Groups 1 to 5 according to location. The groups are visualized in Figure 4.

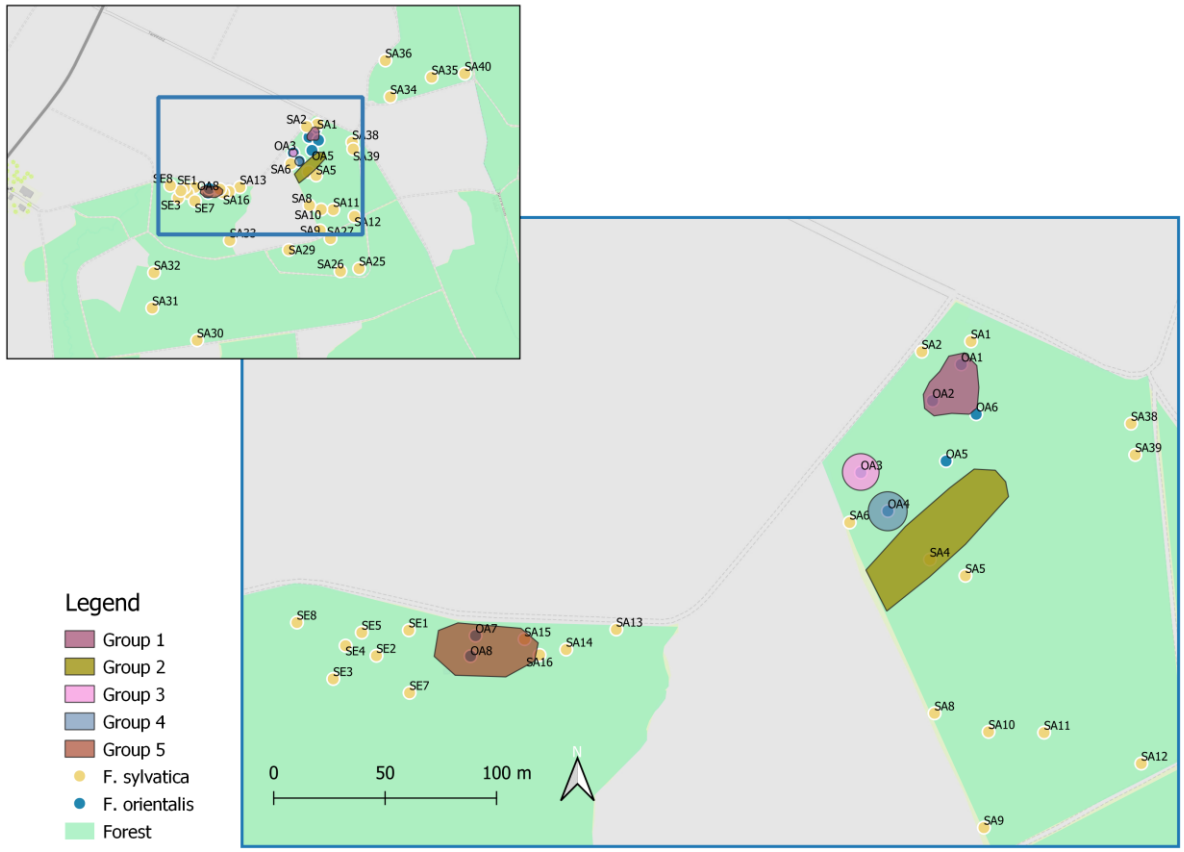

Figure 4: Map of sapling/young tree groups 1-5. (created with: QGIS, basemap: Esri World Topo)

In Group 1, situated beneath the two largest *F. orientalis* (OA1 and OA2), mainly Class A and B individuals were found (see Figure 5). Leaves of 31 saplings of Class A and B along with 5 trees of Class D were collected. Group 2 was located between the sites of OA1-OA6 and the rest of the forest, where numerous *F. sylvatica* were located. It consisted mostly of young trees and Class B saplings (see Figure 6). Eleven samples of each Class B and C as well as two samples of Class D were sampled.

Figure 5: Section of Group 1.

Figure 6: Section of Group 2.

In Group 3 beneath OA3 (see Figure 7) and Group 4 beneath OA4 (see Figure 8) only very young saplings (Class A) were growing. For Group 3 twelve saplings and for group 4 17 saplings were sampled.

Figure 7: Section of Group 3.

Figure 8: Section of Group 4.

In the second site where OA7 and OA8 stand, saplings and young trees in all age classes were found. The many high-grown young trees with low trunk diameters were noticeable here, as can be seen in Figure 9. For this Group 5 eight very young saplings (Class A), twelve Class B saplings and two young trees (Class C) were sampled.

Figure 9: Section of Group 5.

In Table 3 a summary of all sampled saplings and young trees of Group 1-5 is shown. The samples are hereafter referred to as described in the table ("sample labels"). The "V" in the sample labels was derived from the German word for rejuvenation (=Verjüngung). The number after the "V" is the same as the corresponding group, except for "V6". These samples were taken later, than "V1" and were therefore given a separate name. Samples labelled with "H" (e.g. V1H1) were morphologically difficult to classify, while samples labelled with "O" (e.g. V6O1) were morphologically classified as *F. orientalis* in the field.

Table 3: Number of individuals sampled in each Group (1-5) and age Class (A-D). Coloring of the groups corresponds to coloring in Figure 4.

	Class A	Class B	Class C	Class D	Total/Group	Sample labels
Group 1	14	17	-	5	36	V1H1-V1H14, V6H1-V6H9, V6O1-V6O4
Group 2	-	11	11	2	24	V2H1-V2H16, V2O1-V2O8
Group 3	12	-	-	-	12	V3H1-V3H6, V3O1-V3O6
Group 4	17	-	-	-	17	V4H1-V4H11, V4O1-V4O6
Group 5	8	12	2	-	22	V5H1-V5H14, V5O1-V5O8
Total	51	40	13	7	111	

In addition to the five groups, two Class D trees morphologically assigned to *F. sylvatica* (hereafter referred to as SM1&2) and seven Class D trees morphologically assigned to *F. orientalis* (hereafter referred to as OM1-OM7) that were situated between the OA1-OA6 were sampled (not in the map). Summarizing, a total of 120 saplings and young adult trees were sampled. Leaf material was collected in June, July and August of 2018 and frozen at -20°C until DNA extraction.

2.3 DNA extraction and microsatellite analysis

DNA was extracted from leaves using the DNeasy Plant Mini Kit (Qiagen) following manufacturer's instructions. Instead of 100 mg only 30 mg of plant material was used, as too much material clogged the filters and a sufficiently high DNA quantity could still be achieved. For pulverization the leaf material, a 3-mm tungsten bead was added in each tube and the material was frozen in liquid nitrogen for 2 min prior to one cycle of 30 s disruption at 30 Hz using a Qiagen TissueLyser II.

Two multiplex kits consisting each of eight microsatellite markers developed by Lefèvre et al. (2012)were used to genotype all samples. Polymerase chain reactions were carried out using the T100 Thermal Cycler (BIO RAD). The 10 µl PCR mixture consisted of 5µl KAPA robust (Kapa Biosystems), 1.5 µl ddH_2O, 1 µl primer premix (premix consisted of 10 µl of each primer (20µM)) and 2.5 µl template DNA. For both multiplex kits the same PCR conditions were applied: Starting denaturation at 95°C for

5 min was followed by 35 cycles consisting of a denaturation step at 95°C for 30 s, an annealing step at 50°C for 30s and an extension step at 72°C for 30s. The final extension step after 35 cycles was for 1 min at 72°C.

For the subsequent genotyping step on the ABI-3500 Genetic Analyzer (Applied Biosystems, USA) 4µl PCR product per sample were first washed using a Milipore MultiScreen PCR µ96 filter plate and then resuspended with 20 µl of ddH_2O. 0.5 µl of each washed sample were added to 9.25 µl of formamide plus 0.25 µl of LIZ600 Marker (Thermo Fisher Scientific), incubated for 10 min at 95°C and then denatured on ice. Binning was carried out using the AUTOBIN function on GeneMapper software (Thermo Fisher Scientific). A list of all markers can be seen in Table 4.

Table 4: Name, sequence, reference, dye, motif and size of the applied microsatellite marker Kits 1 and 2 by Lefèvre et al. (2012).

	Locus	Primer sequences (5'-3')	Reference	Dye	Motif	Size (bp)
Kit 1	**csolfagus_31**	TCTATTGACACAAGAATAAGAACACC CTTGGCAAGAAAAGGGGATT	G.G. Vendramin, personal communication	VIC	$(AG)_{12}$	104–126
	sfc_1143	TGGCATCCTACTGTAATTTGA ATTCCACCCACCATCTGTC C	Asuka et al. (2004)	NED	$(AG)_{21}$	112–130
	csolfagus_05	GGTTTCTAGCAAAATTGGCATT CCCAAAAGGCCCTACTACAA	G.G. Vendramin, personal communication	NED	$(GA)_{10}$	167–179
	FS1_15	TCAAACCCAGTAAATTTCTCA GCCTCAATGAACTCAAAAAC	Pastorelli et al. (2003)	PET	$(GA)_{26}$	95–137
	sfc_0036	CATGCTTGACTGACTGTAAGTTC TCCAGGCCTAAAAACATTTATAG	Asuka et al. (2004)	FAM	$(TC)_{23}$	94–112
	csolfagus_06	GTTGTTGCTCACAGCAGTCG ACGCTTGGTCTTCTTGCACT	G.G. Vendramin, personal communication	PET	$(AG)_{13}$	203–221
	csolfagus_19	TGCCCATGAGGTTTGTATCA GCCGAATAACCCAGAAAACA	G.G. Vendramin, personal communication	VIC	$(TC)_{13}$	154–182
	csolfagus_29	CACAACCTGCATTCCCTTTC GTTTGGCACTTTGGCTTGTT	G.G. Vendramin, personal communication	FAM	$(CT)_{11}$	132–148
Kit 2	**EEU75_A_O**	TTCCAAACCAACCCTTTATCC GACGGAGATTGAGGAAGAACA	Lefèvre et al. (2012)	VIC	$(CT)_{10}$	91–111
	DUKCT_A_O	GCCTCTCGCAGCTCCTATAA GATCTAATGTGGGTTTGGTTTTG	Lefèvre et al. (2012)	PET	$(AC)_{14}$	75–95
	EJV8T_A_O	CCTGTTCTCACACTTGGGTCTA TGCATTACAAAGCCTGAAACA	Lefèvre et al. (2012)	NED	$(TC)_{10}$	143–155
	EMILY_A_O	GACCCCAAGGTTACAGTGCT CGTACAATTGCACCCACATC	Lefèvre et al. (2012)	FAM	$(GA)_{11}$	142–152
	ERHBI_A_O	TGCAACAACTTAGCACTTTGA GCGTGTGGCTTATCCAAAAT	Lefèvre et al. (2012)	PET	$(AG)_{9}$	159–167
	DZ447_A_O	GGTGCAATACTTCACTTTAGGACA ATAGGAGTGGGACGGCTAGG	Lefèvre et al. (2012)	NED	$(TC)_{10}$	186–194
	concat14_A_O	TGAAGAAATTCACAACCCAACA GGGTTGTTTACGATGGTGGA	Lefèvre et al. (2012)	VIC	$(TC)_{9}$	173–197
	DE576_A_O	TCTCCTTAGATCCACAATCACA AGCTCTTCATTGCTCAGAACG	Lefèvre et al. (2012)	FAM	$(CAA)_{10}$	211–232

2.4 Data analysis

In order to exclude loci with non-amplifying alleles, the presence of null alleles was estimated using the *Cervus* software version 3.0 (Kalinowski et al., 2007). *Cervus* uses an iterative algorithm based on the observed and expected frequencies of the various genotypes to identify null alleles (Summers & Amos, 1997). As subsequent analyses assume Hardy–Weinberg equilibrium (HWE) the two adult (i.e. pure *F. sylvatica* and pure *F. orientalis*) populations were also tested for departures from it (Guo & Thompson, 1992) (Markov chain Monte Carlo exact test) using *Arlequin* software version 3.5.2.2. (Excoffier & Lischer, 2010). The genetic diversity for the two adult populations was characterized using the total number of alleles, the number of private alleles (i.e. alleles that are present only in one population), observed heterozygosity (H_O) and expected heterozygosity (H_E) using *Arlequin* software.

Analysis of molecular variance (AMOVA) was applied using *Arlequin* software to divide the variance in allele frequencies to between and among group components in and between the adult populations and the sapling/young-adult generations. The inter-population component is the fixation index F_{ST}, which is a measure of differentiation in the allele frequencies between two populations (Weir & Cockerham, 1984). Locus by locus F_{ST} values were calculated to detect so-called diagnostic loci, i.e. loci that can distinguish between the two species

The Bayesian clustering method implemented in the software *STRUCTURE* version 2.3.4 (Pritchard, Stephens & Donnelly, 2000) was used to assign individuals to K populations (in our case, to the two species) and to detect potential hybrids among the saplings and young adults. *STRUCTURE* was run assuming an admixture model with a 30´000 burn-in iterations followed by 30`000 iterations for estimation. Potential clusters (K) from two to four using five independent Markov Chains for each were tested. *STRUCTURE HARVESTER* 0.6.94 program (Earl & von Holdt, 2012) was applied to determine the most likely number of K and the results were averaged across the five runs using *CLUMPP* (Jakobsson & Rosenberg, 2007).

Since saplings below adult trees were sampled, it is likely that their mother is one of the adult trees above. Thus, a likelihood-ratio test was used, implemented in the software *Cervus* 3.0 (Kalinowski et al., 2007), to identify if saplings situated below *F.orientalis* adults have two *F. orientalis* parents or if one of the parents (father) is a random *F. sylvatica* tree from the forest. Ten-thousand simulations were performed to derive a critical value for the likelihood-ratio tests given the data set. For the simulations, following assumptions were made: 25% of the candidate parents sampled, 0.01 genotyping error rate, 95% as the strict and 85% as the relaxed confidence level and 200 individuals as probable candidate parents. For the parentage analysis (parent pair (sexes unknown)) relaxed confidence level with a critical LOD score of 0.69 for single parent was used.

3 Results

3.1 Microsatellite loci

DNA was successfully extracted from leaf material of 164 samples (36 adult *F. sylvatica*, 8 adult *F. orientalis* and 120 saplings and young trees). Due to lack of amplification of loci or problems with binning, 38 samples were removed (5 adult *F. sylvatica* and 33 saplings and young trees) from further evaluation. Null alleles were confirmed at locus FS1_15, which therefore was excluded from following analysis.

There were significant departures from HWE ($P < 0.05$) at two loci (ERHBI, csolfagus_19) in the *F. orientalis* population, at one locus (EJV8T) in the *F. sylvatica* population and at three loci (EMILY, csolfagus_19, sfc_1143) in the progeny (see Appendix A). Nevertheless, these loci were integrated into the analysis, since the small sample size and high levels of polymorphisms (see Genetic diversity) did not allow for a precise assessment of HWE. Subsequent population genetic analyses were therefore performed with results from 126 samples and 15 loci.

3.2 Genetic diversity

The number of alleles per locus across all sampled adults ranged from 5 (csolfagus_09) to 13 (EEU75, sfc_1143) with a mean number of 8.8. For the adult *F. sylvatica* group the total number of alleles ranged from 3 to 11, averaging 6.8 per locus and for the adult *F. orientalis g*roup a range of 2-8 with an average of 5.3 per locus was found. Loci from Kit 1 with a mean number of alleles per locus of 9.9 were more polymorphic than those from Kit 2 which showed a mean number of alleles of 7.9 (see Appendix C).

Expected heterozygosity in all three populations ranged from 0.36 to 0.87 and the observed heterozygosity from 0.25 to 1 (Figure 10 and Figure 11.).

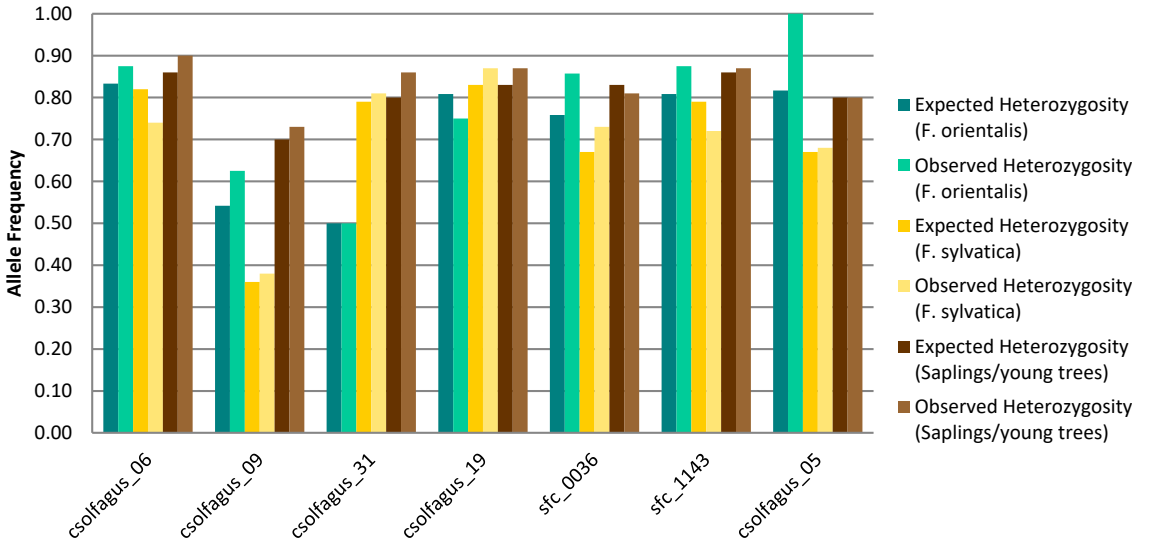

Figure 10: Expected (H_E) versus observed (H_O) heterozygosity for all markers in Kit1 for the adult groups (*F. sylvatica and F. orientalis*) and saplings/young trees group.

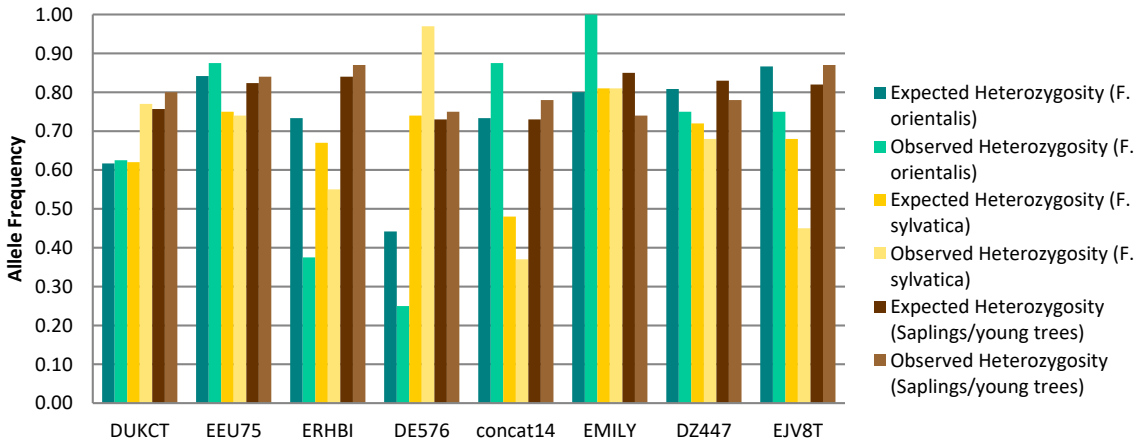

Figure 11: Expected (H_E) versus observed (H_O) heterozygosity for all markers in Kit 2 for the adult groups (*F. sylvatica* and *F. orientalis*) and saplings/young trees group..

In the adult *F. orientalis* group mean observed and expected heterozygosity did not differ (Mean H_O und H_E = 0.73), while in the adult *F. sylvatica* group mean observed heterozygosity was slightly lower than mean expected heterozygosity (H_O = 0.68, H_E = 0.69). The saplings/young trees group showed the highest heterozygosity with the observed heterozygosity being slightly higher than the expected one (H_O = 0.82, H_E = 0.8) (see Appendix B).

3.3 Genetic differentiation

The AMOVA conducted for the two adult groups only (*F. orientalis* and *F. sylvatica)* revealed that most variation in allele frequencies is present within populations and less among populations see Table 5).

Table 5: Percentage of variation among and within populations for adult populations (*F. sylvatica* and *F. orientalis*) and Fixation Index (F_{ST})

Percentage of variation among populations	23,28
Within populations	76,72
Fixation index (F_{ST})	0,23283

If all three groups (*F. sylvatica* adults, *F. orientalis* adults and saplings/young trees) were considered together, the highest variation is still found within populations and a lower percentage of variation among populations is observed, compared to when only the two adult populations were included (see Table 6).

Table 6: Percentage of variation among and within populations for all three populations (*F. sylvatica*, *F. orientalis* and saplings/young trees) and fixation index (F_{ST})

Percentage of variation among populations	7,19
Within populations	92,81
Fixation Index (F_{ST})	0,0719

Locus by locus AMOVA with the two adult populations revealed that several loci involve private alleles for either *F. sylvatica* or *F. orientalis*. A total of 30 alleles to be unique for *F. orientalis* and 52 alleles unique for *F. sylvatica* were found. It was also shown that csolfagus_09 from Kit 1 contributed the most to the variation between the two adult populations (56.2%) (see Appendix D). The allele frequencies per locus are shown in Figure 12, the data is listed in Appendix E. The loci are ordered by highest to lowest contribution to the variation.

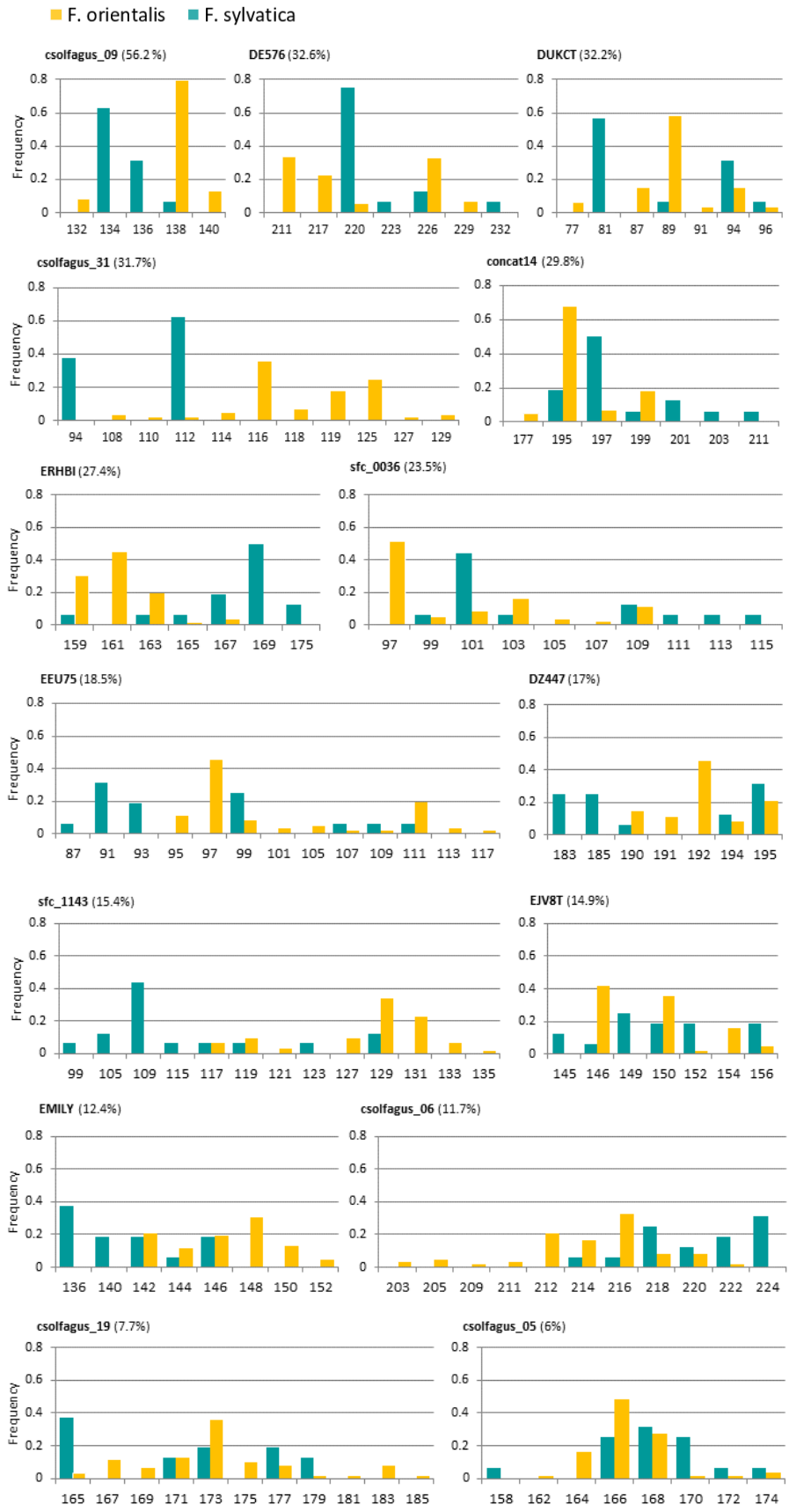

Figure 12: Allele frequencies for the applied microsatellite markers in Kit 1 and two. Next to the name of the loci, the corresponding % of variation is listed. x-axis: Alleles.

The population pairwise F_{ST} was highest between the adult *F. orientalis* and *F. sylvatica* populations at 0.228. The F_{ST} values between the saplings/young trees group and the two adult populations were lower: 0.062 for *F. sylvatica* and 0.049 for *F. orientalis* (Table 7).

Table 7: Population pairwise F_{st}

	F. orientalis	*F. sylvatica*	Saplings/young trees
F. orientalis	0		
F. sylvatica	0,22767	0	
Saplings/young trees	0,04919	0,06191	0

A total of 126 samples were analyzed in *STRUCTURE.* The samples were sorted by age Class A to D. The two genetic clusters that provided the best fit to the data (according to *STRUCTURE HARVESTER* and CLUMPP) corresponded to the two species (*F. sylvatica* and *F. orientalis*). *STRUCTURE* estimates a probability of *F. sylvatica* or *F. orientalis* ancestry for each sample. Figure 13 shows that all adult individuals (OA and SA) have a pure probability of ancestry to one of the clusters. Thus, the blue cluster corresponds to *F. orientalis* and the yellow cluster to *F. sylvatica*.

Based on the two adult individuals (SA16, OA6) that have 20% ancestry from the other cluster, an individual was classified as hybrid if its ancestry for both clusters was higher than 20%.

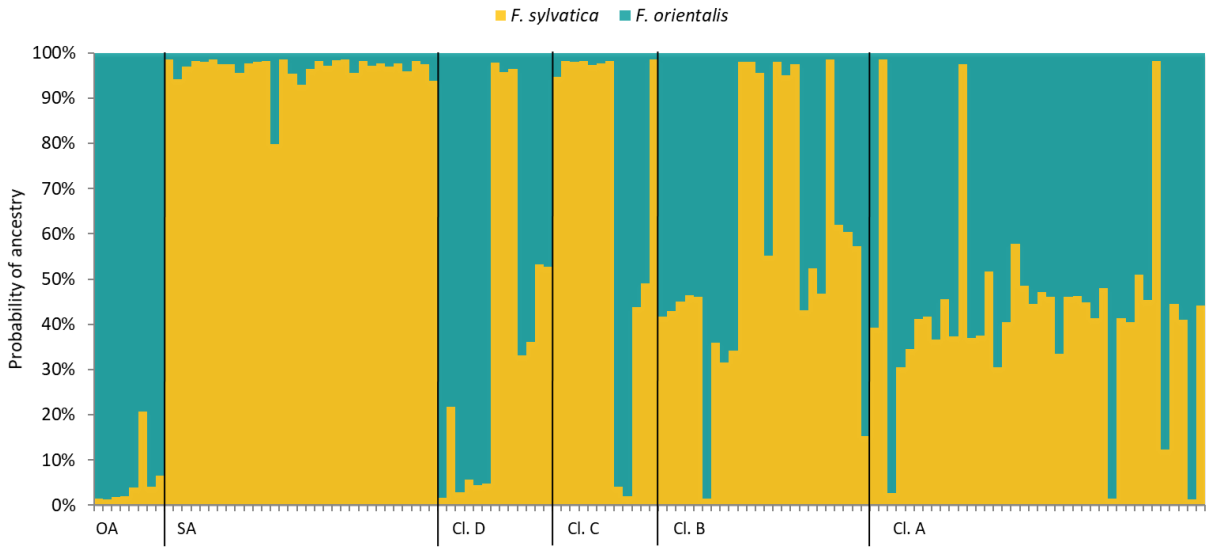

Figure 13: Results of the genetic assignement based on the Bayesan method implemented in the program *STRUCTURE* for all genotyped samples. Each individual is represented by a vertical line, which is partitioned into two colored segments that represent the individual's probability of belonging to the cluster with that color. Saplings and young trees are sorted by age Class 1-4 (Cl. 1- Cl. 4).

Potential hybrids were mostly found in age Class A and B, as can be seen in Table 8.

Table 8: Number of individuals in age Classes A to D. *F. sylvatica* = Individuals who have been assigned more than 80% probability of ancestry to the *F. sylvatica* cluster. *F. orientalis* = Individuals who have been assigned more than 80% probability of ancestry to the *F. orientalis* cluster. Hybrid = individuals who have been assigned a probability of ancestry higher than 20% to both clusters.

Age Class	*F. orientalis*	*F. sylvatica*	Hybrid
Class D	6	3	4
Class C	2	8	2
Class B	1	7	18
Class A	4	2	30

In Figure 14 the *STRUCTURE* results are split into the sampling groups 1 to 5 and placed in the map at their sampling site. In the following, the results of the parentage analysis by *Cervus* are integrated as well. For all saplings and young trees, *Cervus* selected the most likely parents from all sampled adults. For a total of 51 individuals, the LOD score was higher than the critical value (0.69). A table of all positive LOD scores can be found in Appendix F.

Figure 14: Results of the genetic assignement based on the Bayesan method implemented in the program *STRUCTURE* split into saplings/young tree groups 1-5. Each individual is represented by a vertical line, which is partitioned into two colored segments that represent the individual's probability of belonging to the cluster with that color.

In Group 1 beneath OA1, OA2 and OA6 all samples were assigned a hybrid-genotype, except for five individuals, as can be seen in Figure 14. The parentage analysis by *Cervus* indicated that OA1 is the most likely parent to nearly all individuals sampled here. Only the two young individuals V1H1 and V1H8, which *STRUCTURE* grouped to *F. sylvatica*, are most likely to be the offspring of the most nearby European beech (SA1). For two of the pure *F. orientalis* saplings (V1H20 and V6O2) OA1 and OA2 were the two most likely parents.

Similar results were found in Group 3 below OA3 and Group 4 below OA4, where *STRUCTURE* analysis suggested that all samples are potential hybrids except for one sample (V4O1). Again *Cervus* was able to determine the closest mature *F. orientalis* OA3 and OA4 as parents of mostly all samples in the respective rejuvenation Group (no positive LOD scores: V3H3, V4H10, V4H11, V4O6). Only the pure sample V4O1 was assigned OA1 and OA4 as parents.

Fewer hybrids were found in Group 2 than in the other groups. Most samples were attributed to *F. sylvatica*, while only two individuals showed to be pure *F. orientalis*. Nevertheless, also here five samples were found with a crossed genotype. Parentage analysis by *Cervus* resulted in only a few positive LOD scores, seen in Appendix F.

Hybrids were also detected in Group 5 situated in the other forest patch under OA7 and OA8. Three of the young trees showed to be pure *F. sylvatica*. *Cervus* was only able to assign parents to the pure *F. sylvatica* offspring. Accordingly, V5H4 is the offspring of SA27 and SE6, and V5H8 is that of SA11 and SE7.

4 Discussion

The main goal of this study was to evaluate whether there is genetic evidence for hybridization between *F. sylvatica* and *F.orientalis* in the forest stand in Wäldi (TG). The results of the microsatellite analysis allowed me to draw several major conclusions:

- The applied 15 microsatellite markers provide adequate resolution to distinguish between *F. sylvatica* and *F. orientalis*.
- The analysis of saplings and young trees strongly suggests the occurrence of hybridization between the two species, since numerous individuals with admixture proportions typical for F1 hybrids were identified.
- The presence of hybrid individuals belonging to different height classes indicates that hybridization has occurred during several years.
- The identified hybrid individuals are the results of gene flow from *F. sylvatica* to *F. orientalis*.

4.1 Evaluation of Microsatellite Markers

I tested the applied microsatellite markers for null alleles and deviation from HWE, so problematic markers could be excluded from the analysis. Among the 16 microsatellites tested, *Cervus* identified null alleles for a single marker, FS1_15. Because this marker amplified rather poorly, it is well possible, that the null alleles are due to genotyping errors. Based on these findings, I excluded this marker.
Further, five markers showed deviation from HWE either in the two adult populations or the young trees. Although deviation from HWE was assessed with an exact test, reported to be less sensitive to small sample sizes than the Pearsons's chi-square goodness-of-fit test (Wang & Shete, 2012) it is plausible to suggest, that the deviations are due, at least in part, to the small sample sizes in this study, especially that of the adult *F. orientalis* population (Li & Leal, 2009). Therefore, I retained the markers.
The resulting 15 microsatellite loci were highly polymorphic with 5-13 alleles per locus. The loci of Kit 1 were more polymorphic than those of Kit 2, a finding that is in accordance with the study of Lefèvre et al. (2012). An explanation may lie in the different repeat numbers of the microsatellite motifs. The average repeat numbers of the microsatellite motifs were higher in Kit 1 (16.1), then in Kit 2 (10.4). Loci with greater number of repeats generally show higher mutation rates and lead to higher levels of polymorphism (Petit et al., 2005).

4.2 Genetic differentiation of *F. sylvatica* and *F. orientalis*

The results of this study show that the applied microsatellite markers have an adequate resolution to distinguish the two species and detect hybrids. The genetic analysis with *STRUCTURE* software identified two genetic clusters, to fit the data (according to *STRUCTURE HARVESTER* and *CLUMPP*), which corresponded to the two species. All adult trees were assigned to their species, with a membership proportion of at least 80%. This strongly supported the presence of the two species *F. sylvatica* and *F. orientalis* at the site.

Genetic differentiation between the two adult populations as estimated by F_{ST} was relatively high (F_{ST} = 0.2328) and higher than that described for *F. sylvatica* populations in two other studies (F_{ST} = 0.058, F_{ST} = 0.0978) (Buiteveld, Vendramin, Leonardi, Kamer & Geburek, 2007; Ciocîrlan, Sofletea, Ducci & Curtu, 2017).

The high distinctiveness of the two clusters was also supported by a large number of private alleles, 52 from 102 alleles in *F. orientalis* and 30 from 80 alleles in *F. sylvatica*. The observed number of alleles can be affected by different sample sizes (Müller et al., 2018). With only eight *F. orientalis* samples and 31 *F. sylvatica* samples, the sample size varied for the two adult populations

4.3 Evidence for hybridization between *F. sylvatica* and *F. orientalis*

Hybridization is a common feature in natural plant populations. Its occurrence depends on genetic, physiological and environmental factors (Howard, Britch, & Braswell, 2003). Closely related species tend to hybridize more frequently, since their mating system compatibility is higher (Boavida, Silva & Feij, 2001). As already mentioned, hybridization between the two closely related beech species *F. sylvatica* and *F. orientalis* is well-known from there contact area in Eastern Europe (Gömöry et al., 1999; Papageorgiou et al., 2008). Nevertheless, the expectation of finding hybrids in the beginning of this project was low, since *F. sylvatica* and *F. orientalis* can differ in flowering phenology (Wagner et al., 2010). My analysis with *STRUCTURE* strongly indicated the existence of hybrids between *F. sylvatica* and *F. orientalis*, since I detected many genetically intermediate individuals. Notably, about half (52 out of 120) of the sampled saplings and young trees showed a hybrid genotype. For many of these individuals, the proportion of both clusters was close to 50%, as would be expected for F1 hybrids.

I further observed high levels of genetic diversity in all three groups of trees: for the *F. orientalis* group, the mean observed and expected heterozygosity was 0.73; for the *F. sylvatica* group, they were 0.68 and 0.69, respectively. Other studies of beech found similar levels (Bilela et al., 2012; Müller et al., 2018; Vornam, Decarli & Gailing, 2004). The highest values were detected in the saplings/young trees group: observed heterozygosity was 0.82 and expected heterozygosity was 0.8. This can be attributed to the fact that the offspring group is composed of *F. orientalis*, *F. sylvatica* and mainly crossbred saplings.

As a conclusion of the listed results, I can answer the initial question of whether the two beech species *F. sylvatica* and *F. orientalis* also crossbreed in Switzerland in the affirmative. Further, the results reveal that the two species must flower simultaneously under the climatic conditions currently prevailing in Wäldi (TG).

However, I identified hybridization in one direction only: pollination of *F. orientalis* mothers by *F. sylvatica* fathers. According to Nielsen & Schaffalitzky de Muckadeli (1953), hybridization in the other direction is likewise possible. For reasons of limited time and resources, my sampling strategy focused on offspring beneath *F. orientalis* individuals and therefore I cannot give any evidence as to whether *F. sylvatica* mothers were pollinated by *F. orientalis* fathers as well. Since Westerly wind dominates at the investigated site (Windatlas, 2018), pollen distribution of *F. orientalis* pollen towards *F. sylvatica* is also very likely. Still, it has to be considered that *Fagus* pollen has a short dispersal distance (<57.3 m) (Oddou-Muratorio, Klein, Vendramin & Fady, 2011) and the search for hybrids beneath *F. sylvatica* individuals should be restricted to that radius.

The extent to which *F. orientalis* have produced pollen must also be taken into account. *F. orientalis* generally begin fruiting at age 60 (Wagner et al., 2010). The individuals on site have been planted around 100 years ago, so it is possible that they have been fruiting for the last 40 years. Pidek et al. (2010) have investigated pollen production in the genus *Fagus* and suggested with reservations that both species (*F. sylvatica* and *F. orientalis*) produce approximately the same amount of pollen. Further, they found that pollen production is strongly dependent on climate and less on the location of trees in a forest stand. The year 2005 had peak pollen production in Switzerland in *F. sylvatica* and also in *F. orientalis* in Eastern Europe (Pidek et al., 2010). Many sampled individuals in the rejuvenation at the investigated stand are roughly ten years old and it is possible that crossbreeding events took place in the high pollen year of 2005. It can therefore be assumed, that the *F. orientalis* individuals also showed high pollen production in the afore mentioned year and hybridization in the other direction also took place. However, this needs further investigations.

Due to my sampling strategy, I cannot make any statements about the precise rate of hybridization. Firstly, my results can be biased with hybrids appearing more frequently, than in the average population of descendants, because I sampled according to qualitative morphological traits and often chose intermediate morphology types. Furthermore, natural selection and chance determine the rate of pure or hybrid genotypes in the sampled saplings and young trees (Tomiuk & Loeschcke, 2017). Therefore, the found offspring does not represent the original genetic composition of the fruits and the rate at which *F. orientalis* was pollinated by *F. sylvatica*. To answer this question, beech nuts would have to be sampled and genotyped. Nevertheless, based on our results I can still say that hybridization is not rare and has occurred in various years, since I found genetically intermediate individuals in different age classes.

As an addition to the *STRUCTURE* analysis, I used *Cervus* software to try and assign possible parents to the offspring. In most cases, the closest adult *F. orientalis* individual was identified as the most likely parent. This is in correspondence with the fact that seed dispersal distance of Fagus is only about 10 meters (Oddou-Muratorio et al., 2011). Assigning the most likely parent in the *F. sylvatica* population was more challenging as not all adult individuals in the vicinity were sampled. Therefore, this analysis could only provide more information about hybridization in a few individuals. Nevertheless, this analysis could partially confirm the attribution of saplings and young trees to the correct species. By sampling more adult *F. sylvatica* in the vicinity, the analysis could provide further valuable information on pollen dispersal distance and hybridization between *F. orientalis* and *F. sylvatica*.

4.4 Significance for forestry and nature conservation

As mentioned in the Introduction, hybrids between exotic and native plant species can have positive as well as negative effects for forestry and nature conservation. Since *F. orientalis* is not native to Switzerland, it's invasiveness has to be investigated. Hybridization between exotic and native plants is considered as a risk for biodiversity, because it can stimulate invasiveness of exotic plants (Bleeker et al., 2008; Hails & Morley, 2005; Levin et al., 1996). In the case of *F. orientalis* and *F. sylvatica* the risk can, however, be considered as low. This is because the two species are genetically similar and the overall species composition and floristic differentiation patterns within *F. orientalis* forests are not fundamentally different from *F. sylvatica* forests (Willner et al., 2017).

An advantage of hybridization could be that the *F. sylvatica* population might obtain alleles coding for traits regarding drought tolerance from *F. orientalis* through introgression, which could result in accelerated adaptation of *F. sylvatica* to the changing climate (Martinsen, Whitham, Turek & Keim, 2001). However, there is a possibility that beneficial genes are linked with unfavorable genes, which could break down adaptation complexes, which would make hybrids less resistant to diseases, herbivores or fungi.

Concerning the stand in Wäldi (TG), it is especially important to investigate if there is gene flow from *F. orientalis* to *F. sylvatica* as well. As mentioned before, it would also be interesting to study the rate as well as the direction of hybridization in order to gather more information about the invasiveness of *F. orientalis*. For detecting introgression much older *F. orientalis* stands would have to be considered as well. The investigation of fertility in hybrids and ecological differences in *F. orientalis* and *F. sylvatica* could also respond to the right approach to managing the exotic species *F. orientalis* and assess the potential of this species in climate change.

In Germany *F. orientalis* is already being promoted for test plantings (Schmiedinger et al., 2010) and I assume that in regions such as the Swiss Plateau, where *F. sylvatica* will most likely disappear (Zim-

mermann et al., 2013) *F. orientalis* can well be cultivated in industrial forests to ensure timber production. However, it is essential that future plantings are well monitored, since still little is known about the spread of alleles of foreign species to native taxa and how they may affect the adaption of a species or ecosystem functions (Levine et al., 2003). Furthermore, forestry can face challenges where the identification of species is problematic (like it is in *F. orientalis* and *F. sylvatica* and their hybrids), since this complicates implementation of clear policies (Richardson & Rejmánek, 2011).

4.5 Outlook

In order to assess the risk of hybridization and thus the introduction of *F. orientalis* in Switzerland, further investigations are necessary. As already mentioned, direction of gene flow and rate of hybridization are important parameters to evaluate, as they indicate how fast and far the genes of *F. orientalis* can spread. In addition, it would be advantageous if further plantations of *F. orientalis* in Switzerland or surrounding countries were examined, because the flowering phenology can be different depending on the origin of *F. orientalis*. In doing so, the comparison of growth and health of *F. orientalis* with that of the *F. sylvatica* and their hybrids would be central. In the case of *F. orientalis* showing a more vigorous growth, there is a possibility that *F. sylvatica* will be suppressed.

Further research could be facilitated by an evaluation of morphological features in the two species and their hybrids. The differentiation of *F. orientalis* and *F. sylvatica* by the application of the 16 microsatellite markers showed promising results, but microsatellite analysis is cost and time intensive.

The results of this project show, that the subject of assisted migration remains without a general solution. My opinion on further treatment of this topic is reflected in a concept introduced by McLachlan et al. (2007) called “constrained assisted migration”. According to this concept, assisted migration can be an effective tool for species conservation with many potential benefits for species and ecosystems as well as potential risks, which need to be carefully addressed. I agree with the proposal of a case-by-case decision making process, where assisted migration is only chosen when the potential benefits clearly outweigh the potential risks. This concept should also be applied to the possible introduction of *F. orientalis* in Switzerland to support *F. sylvatica* in the changing climate.

Literature

Allgaier Leuch, B., Streit, K. & Brang, P. (2017). *Naturnaher Waldbau im Klimawandel. Merkblatt für die Praxis, 59.1.* Eidg. Forschungsanstalt WSL, Birmensdorf.

Avise, J. C. (1994). *Molecular Markers, Natural History and Evolution*. New York: Chapman & Hall. Zugriff am 11.10.2018. Verfügbar unter: http://doi.wiley.com/10.1046/j.1420-9101.1994.7060766.x

Bartha, D. & Raisz, A. (2004). Untersuchungen zur Variabilität von Blattmerkmalen innerhalb der Krone bei *Fagus sylvatica* und *Fagus orientalis*. *Beitr. Fortwirtsch. und Landsch. ökol.*, *38*, 169–178.

Bilela, S., Dounavi, A., Fussi, B., Konnert, M., Holst, J., Mayer, H. et al. (2012). Natural regeneration of *Fagus sylvatic*a L. adapts with maturation to warmer and drier microclimatic conditions. *Forest Ecology and Management*, *275*, 60–67. https://doi.org/10.1016/j.foreco.2012.03.009

Bleeker, W., Schmitz, U. & Ristow, M. (2008). Ist Hybridisierung mit Neophyten eine Bedrohung für indigene Pflanzenarten? (Bundesamt für Naturschutz, Hrsg.) *Naturschutz und Biologische Vielfalt*, *60*, 11–16.

Boavida, L. C., Silva, J. P. & Feij, J. A. (2001). Sexual reproduction in the cork oak (Quercus suber L). II. Crossing intra- and interspecific barriers. *Sexual Plant Reproduction*, *14* (3), 143–152. https://doi.org/10.1007/s004970100100

Böhlmann, D. (2015). *Laubbäume temperierter Klimate mit ihrer Artenvielfalt: Nachschlagewerk mit vergleichenden Originalbildern*. Berlin Hannover: Patzer Verlag.

Brang, P., Küchli, C., Schwitter, R., Bugmann, H. & Ammann, P. (2016). Potenzial von Gastbaumarten bei der Anpassung an den Klimawandel (Forum für Wissen). In Bundesamt für Umwelt BAFU, Bern & Eidg. Forschungsanstalt WSL, Birmensforf (Hrsg.), *Wald im Klimawandel: Grundlagen für Adaptationsstrategien* (1. Auflage., S. 143–365). Bern, Stuttgart: Haupt Verlag, Wien.

Buiteveld, J., Vendramin, G. G., Leonardi, S., Kamer, K. & Geburek, T. (2007). Genetic diversity and differentiation in European beech (*Fagus sylvatic*a L.) stands varying in management history. *Forest Ecology and Management*, *247* (1–3), 98–106. https://doi.org/10.1016/j.foreco.2007.04.018

Ciocîrlan, E., Sofletea, N., Ducci, F. & Curtu, A. (2017). Patterns of genetic diversity in European beech *(Fagus sylvatica* L.) at the eastern margins of its distribution range. *iForest - Biogeosciences and Forestry*, *10* (6), 916–922. https://doi.org/10.3832/ifor2446-010

Comps, B., Gömöry, D., Letouzey, J., Thiébaut, B. & Petit, R. J. (2001). Diverging trends between heterozygosity and allelic richness during postglacial colonization in the European beech. *Genetics*, *157* (1), 389–397.

Denk, T. (1999). The taxonomy of *Fagus* in western Eurasia, 1: *Fagus sylvatica* subsp. *orientalis* (= *F. orientalis*). *Feddes Repertorium*, *110*, 177–200.

Denk, T. (2003). Phylogeny of *Fagus* L. (Fagaceae) based on morphological data. *Plant Systematics and Evolution*, *240* (1–4), 55–81. https://doi.org/10.1007/s00606-003-0018-x

Earl, D. A. & von Holdt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4* (2), 359–361. https://doi.org/10.1007/s12686-011-9548-7

Ellstrand, N. C. & Schierenbeck, K. A. (2000). Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences*, *97* (13), 7043–7050. https://doi.org/10.1073/pnas.97.13.7043

Excoffier, L. & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10* (3), 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Fang, J. & Lechowicz, M. J. (2006). Climatic limits for the present distribution of beech (Fagus L.) species in the world. *Journal of Biogeography*, *33* (10), 1804–1819. https://doi.org/10.1111/j.1365-2699.2006.01533.x

Fitschen, J., Schmidt, P. A. & Schulz, B. (2017). *Gehölzflora: ein Buch zum Bestimmen der in Mitteleuropa wild wachsenden und angepflanzten Bäume und Sträucher* (13., vollständig neu bearbeitete und erweiterte Auflage.). Wiebelsheim, Hunsrück: Quelle & Meyer Verlag GmbH & Co.

Gailing, O. & Wuehlisch, G. V. (2004). Nuclear markers (AFLPs) and chloroplast microsatellites differ between *Fagus sylvatic*a and *F. orientalis*. *Silvae Genetica*, *53* (1–6), 105–110. https://doi.org/10.1515/sg-2004-0019

Gaskin, J. F. (2016). The role of hybridization in facilitating tree invasion. *AoB Plants*, plw079. https://doi.org/10.1093/aobpla/plw079

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W. & Rennenberg, H. (2006). Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees*, *21* (1), 1–11. https://doi.org/10.1007/s00468-006-0107-x

Gömöry, D., Paule, L., Brus, R., Zhelev, P., Tomovic, Z. & Akeroyd, J. (1999). Genetic differentiation and phylogeny of beech on the Balkan peninsula. *Journal of Evolutionary Biology*, *12* (4), 746–754. https://doi.org/10.1046/j.1420-9101.1999.00076.x

Guo, S. W. & Thompson, E. A. (1992). Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics*, *48* (2), 361–372. https://doi.org/10.2307/2532296

Hails, R. S. & Morley, K. (2005). Genes invading new populations: a risk assessment perspective. *Trends in Ecology & Evolution*, *20* (5), 245–252. https://doi.org/10.1016/j.tree.2005.02.006

Hovick, S. M. & Whitney, K. D. (2014). Hybridisation is associated with increased fecundity and size in invasive taxa: meta-analytic support for the hybridisation-invasion hypothesis. (J. Gurevitch, Hrsg.)*Ecology Letters*, *17* (11), 1464–1477. https://doi.org/10.1111/ele.12355

Howard, D., Britch, S. & Braswell, W. (2003). Evolution in hybrid zones. *The evolution of population biology*. Cambridge: Cambridge University Press.

Jakobsson, M. & Rosenberg, N. A. (2007). CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23* (14), 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Kalinowski, S. T., Taper, M. L. & Marshall, T. C. (2007). Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment: Cervus likelyhood model. *Molecular Ecology*, *16* (5), 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Kowarik, I. & Rabitsch, W. (2010). *Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa* (2., wesentlich erw. Aufl.). Stuttgart (Hohenheim): Ulmer. https://doi.org/10.1002/mmnz.20040800118

Lefèvre, S., Wagner, S., Petit, R. J. & De Lafontaine, G. (2012). Multiplexed microsatellite markers for genetic studies of beech: Technical advances and genetic ressources. *Molecular Ecology Resources*, *12* (3), 484–491. https://doi.org/10.1111/j.1755-0998.2011.03094.x

Levin, D. A., Francisco-Ortega, J. & Jansen, R. K. (1996). Hybridization and the Extinction of Rare Plant Species. *Conservation Biology*, *10* (1), 10–16. https://doi.org/10.1046/j.1523-1739.1996.10010010.x

Levine, J. M., Vila, M., Antonio, C. M. D., Dukes, J. S., Grigulis, K. & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, *270* (1517), 775–781. https://doi.org/10.1098/rspb.2003.2327

Li, B. & Leal, S. M. (2009). Deviations from Hardy-Weinberg Equilibrium in Parental and Unaffected Sibling Genotype Data. *Human Heredity*, *67* (2), 104–115. https://doi.org/10.1159/000179558

Magri, D., Vendramin, G. G., Comps, B., Dupanloup, I., Geburek, T., Gomory, D. et al. (2006). A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, *171* (1), 199–221. https://doi.org/10.1111/j.1469-8137.2006.01740.x

Martinsen, G. D., Whitham, T. G., Turek, R. J. & Keim, P. (2001). Hybrid populations selectively filter gene introgression between species. *Evolution; International Journal of Organic Evolution*, *55* (7), 1325–1335. https://doi.org/10.1111/j.0014-3820.2001.tb00655.x

Müller, M., Cuervo-Alarcon, L., Gailing, O., K.C., R., Chhetri, M., Seifert, S. et al. (2018). Genetic Variation of European Beech Populations and Their Progeny from Northeast Germany to Southwest Switzerland. *Forests*, *9* (8), 469. https://doi.org/10.3390/f9080469

Neuner, S., Beinhofer, B. & Knoke, T. (2013). The optimal tree species composition for a private forest enterprise – applying the theory of portfolio selection. *Scandinavian Journal of Forest Research*, *28* (1), 38–48. https://doi.org/10.1080/02827581.2012.683038

Nielsen, P. C. & Schaffalitzky de Muckadeli, M. (1953). Flower observations and controlled pollinations in Fagus.

Oddou-Muratorio, S., Klein, E. K., Vendramin, G. G. & Fady, B. (2011). Spatial vs. temporal effects on demographic and genetic structures: the roles of dispersal, masting and differential mortality on patterns of recruitment in *Fagus sylvatica*. *Molecular Ecology*, *20* (9), 1997–2010. https://doi.org/10.1111/j.1365-294X.2011.05039.x

Papageorgiou, A. C., Vidalis, A., Gailing, O., Tsiripidis, I., Hatziskakis, S., Boutsios, S. et al. (2008). Genetic variation of beech *(Fagus sylvatic*a L.) in Rodopi (N.E. Greece). *European Journal of Forest Research*, *127* (1), 81–88. https://doi.org/10.1007/s10342-007-0185-3

Pastorelli, R., Smulders, M. J. M., Van't Westende, W. P. C., Vosman, B., Giannini, R., Vettori, C. et al. (2003). Characterization of microsatellite markers in *Fagus sylvatica* L. and *Fagus orientalis* Lipsky: PRIMER NOTE. *Molecular Ecology Notes*, *3* (1), 76–78. https://doi.org/10.1046/j.1471-8286.2003.00355.x

Petit, R. J., Deguilloux, M.-F., Chat, J., Grivet, D., Garnier-Géré, P. & Vendramin, G. G. (2005). Standardizing for microsatellite length in comparisons of genetic diversity. *Molecular Ecology*, *14* (3), 885–890. https://doi.org/10.1111/j.1365-294X.2005.02446.x

Pidek, I. A., Svitavská-Svobodová, H., van der Knaap, W. O., Noryśkiewicz, A. M., Filbrandt-Czaja, A., Noryśkiewicz, B. et al. (2010). Variation in annual pollen accumulation rates of *Fagus* along a N–S transect in Europe based on pollen traps. *Vegetation History and Archaeobotany*, *19* (4), 259–270. https://doi.org/10.1007/s00334-010-0248-0

Pritchard, J., Stephens, M. & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.

Reif, A., Aas, G. & Essl, F. (2011). Braucht der Wald in Zeiten der Klimaveränderung neue, nicht heimische Baumarten? *Natur und Landschaft*, (6), 256–260. https://doi.org/10.17433/6.2011.50153103.256-260

Ricciardi, A. & Simberloff, D. (2009). Assisted colonization: good intentions and dubious risk assessment. *Trends in Ecology & Evolution*, *24* (9), 476–477. https://doi.org/10.1016/j.tree.2009.05.005

Richardson, D. M. & Rejmánek, M. (2011). Trees and shrubs as invasive alien species - a global review: Global review of invasive trees & shrubs. *Diversity and Distributions*, *17* (5), 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Roloff, A., Weisgerber, H., Lang, U. & Stimm, B. (2010). *Bäume Mitteleuropas: von Aspe bis Zirbel-Kiefer ; mit den Porträts aller Bäume des Jahres von 1989 bis 2010* (Sachbuch) (1. Aufl.). Weinheim: Wiley-VCH.

Sarewitz, D. (2011). Does climate change knowledge really matter? *Wiley Interdisciplinary Reviews: Climate Change*, *2* (4), 475–481. https://doi.org/10.1002/wcc.126

Schierenbeck, K. A. & Ellstrand, N. C. (2009). Hybridization and the evolution of invasiveness in plants and other organisms. *Biological Invasions*, *11* (5), 1093–1105. https://doi.org/10.1007/s10530-008-9388-x

Schmiedinger, A., Bachmann, M., Kölling, C. & Schirmer, R. (2010). Gastbaumarten für Bayern gesucht: Forstwissenschaftler entwickelten ein Verfahren zur Auswahl klimagerechter Baumarten für Anbauversuche. *Wald-Wissenschaft-Praxis*.

Streiff, R., Ducousso, A., Lexer, C., Steinkellner, H., Gloessl, J. & Kremer, A. (1999). Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. *Molecular Ecology*, *8* (5), 831–841. https://doi.org/10.1046/j.1365-294X.1999.00637.x

Summers, K. & Amos, W. (1997). Behavioral, ecological, and molecular genetic analyses of reproductive strategies in the Amazonian dart-poison frog, *Dendrobates ventrimaculatus*. *Behavioral Ecology*, *8* (3), 260–267. https://doi.org/10.1093/beheco/8.3.260

ThurGIS, Kartenportal Kanton Thurgau (2018) *Hauptbaumart*. Retrieved on 6.11.2018 from https://map.geo.tg.ch/apps/mf-geoadmin3/?lang=de&topic=ech&bgLayer=basemap_farbig&layers=forstliche_bestandeskarte-hauptbaumart&X=1277410.00&Y=2724790.00&zoom=3.

Tomiuk, J. & Loeschcke, V. (2017). *Grundlagen der Evolutionsbiologie und Formalen Genetik*. Berlin Heidelberg: Springer Spektrum.

Tutin, T. G., Burges, N. A., Chater, A. O., Edmondson, J. R., Heywood, V. H., Moore, D. M. et al. (1964). *Flora Europaea*. Cambridge: University Press, London; New York; Ibadan.

Vitt, P., Havens, K., Kramer, A. T., Sollenberger, D. & Yates, E. (2010). Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation*, *143* (1), 18–27. https://doi.org/10.1016/j.biocon.2009.08.015

Vornam, B., Decarli, N. & Gailing, O. (2004). Spatial Distribution of Genetic Variation in a Natural Beech Stand (*Fagus sylvatica* L.) Based on Microsatellite Markers. *Conservation Genetics*, *5* (4), 561–570. https://doi.org/10.1023/B:COGE.0000041025.82917.ac

Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R. D. & Sagheb-Talebi, K. (2010). Beech regeneration research: From ecological to silvicultural aspects. *Forest Ecology and Management*, *259* (11), 2172–2182. https://doi.org/10.1016/j.foreco.2010.02.029

Wang, J. & Shete, S. (2012). Testing Departure from Hardy–Weinberg Proportions. In R.C. Elston, J.M. Satagopan & S. Sun (Hrsg.), *Statistical Human Genetics* (Band 850, S. 77–102). Totowa, NJ: Humana Press. https://doi.org/10.1007/978-1-61779-555-8_6

Weir, B. S. & Cockerham, C. C. (1984). Estimating F-Statistics for the Analysis of Population Structure. *Evolution*, *38* (6), 1358. https://doi.org/10.2307/2408641

Williams, M. I. & Dumroese, R. K. (2013). Preparing for Climate Change: Forestry and Assisted Migration. *Journal of Forestry*, *111* (4), 287–297. https://doi.org/10.5849/jof.13-016

Willner, W., Jiménez-Alfaro, B., Agrillo, E., Biurrun, I., Campos, J. A., Čarni, A. et al. (2017). Classification of European beech forests: a Gordian Knot? (A. Schwabe-Kratochwil, Hrsg.) *Applied Vegetation Science*, *20* (3), 494–512. https://doi.org/10.1111/avsc.12299

Windatlas (2018) Windgeschwindigkeit: Windrose und Weibull-Verteilung. Retrieved on 28.10.2019 from https://wind-data.ch/windkarte/.

Wittenberg, R. (2006). *Gebietsfremde Arten in der Schweiz. Eine Übersicht über gebietsfremde Arten und ihre Bedrohung für die biologische Vielfalt und die Wirtschaft in der Schweiz.* No. 0629. (S. 154). Bundesamt für Umwelt BAFU, Bern.

Zimmermann, N., Schmatz, D. & Psomas, A. (2013). Future ranges in European tree species. *Adapting to climate change in European forests - results of the MOTIVE project* (S. 9–14). Sofia: Pensoft Publishers.

List of figures

List of tables

List of appendices

Appendix A: HWE P-values for adult *F. sylvatica*, adult *F. orientalis* and saplings/young tree populations

Marker names	*F. orientalis (P)*	*F. sylvatica (P)*	Saplings/Young trees (P)
csolfagus_06	0.90	0.17	0.49
csolfagus_09	0.41	1.00	0.45
csolfagus_31	1.00	0.87	0.49
csolfagus_19	0.05	0.20	0.00
sfc_0036	1.00	0.73	0.84
sfc_1143	0.75	0.06	0.01
csolfagus_05	0.36	0.23	0.30
DUKCT	1.00	0.89	0.27
EEU75	1.00	0.46	0.92
ERHBI	0.02	0.24	0.42
DE576	0.16	0.07	0.19
concat14	0.92	0.19	0.41
EMILY	0.46	0.26	0.04
DZ447	0.16	0.27	0.07
EJV8T	0.73	0.05	0.41

Appendix B: Expected and observed heterozygosity in adult *F. sylvatica*, adult *F. orientalis* and saplings/young tree populations

Marker names	Exp. Heterozygosity (*F. orientalis*)	Obs. Heterozygosity (*F. orientalis*)	Exp. Heterozygosity (*F. sylvatica)*	Obs. Heterozygosity (*F. sylvatica*)	Exp. Heterozygosity (Saplings/young trees)	Obs. Heterozygosity (Saplings/young trees)
csolfagus_06	0.83	0.88	0.82	0.74	0.86	0.90
csolfagus_09	0.54	0.63	0.36	0.38	0.70	0.73
csolfagus_31	0.50	0.50	0.79	0.81	0.80	0.86
csolfagus_19	0.81	0.75	0.83	0.87	0.83	0.87
sfc_0036	0.76	0.86	0.67	0.73	0.83	0.81
sfc_1143	0.81	0.88	0.79	0.72	0.86	0.87
csolfagus_05	0.82	1.00	0.67	0.68	0.80	0.80
DUKCT	0.62	0.63	0.62	0.77	0.76	0.80
EEU75	0.84	0.88	0.75	0.74	0.82	0.84
ERHBI	0.73	0.38	0.67	0.55	0.84	0.87
DE576	0.44	0.25	0.74	0.97	0.73	0.75
concat14	0.73	0.88	0.48	0.37	0.73	0.78
EMILY	0.80	1.00	0.81	0.81	0.85	0.74
DZ447	0.81	0.75	0.72	0.68	0.83	0.78
EJV8T	0.87	0.75	0.68	0.45	0.82	0.87
Average	0.73	0.73	0.69	0.68	0.80	0.82

Appendix C: Number of alleles and private alleles in total and in adult populations (*F. sylvatica* and *F. orientalis*)

Marker names	No. of alleles	No. of alleles (*F. orientalis)*	No. of alleles (*F. sylvatica)*	No. of private alleles (*F. orientalis*)	No. of private alleles *(F. sylvatica*)	Size of private alleles *(F. orientalis*)	Size of private alleles (*F. sylvatica*)
csolfagus_06	11	6	10	1	5	224	203, 205, 209, 211, 212
csolfagus_09	5	3	3	2	2	134, 136	132, 140
csolfagus_31	11	2	10	1	9	94	108, 110, 114, 116, 118, 119, 125, 127, 129
csolfagus_19	11	5	11	0	6		167, 169, 175, 181, 183, 185
sfc_0036	10	7	7	3	3	111, 113, 115	105, 107, 97
sfc_1143	13	8	8	5	5	105, 109, 115, 123, 99	121, 127, 131, 133, 135
csolfagus_05	8	6	7	1	2	158	162, 164
Mean Kit1	9.86						
DUKCT	7	4	6	1	3	81	77, 87, 91
EEU75	13	7	10	3	6	87, 91, 93	101, 105, 113, 117, 95, 97
ERHBI	7	6	5	2	1	169, 175	161
DE576	7	4	5	2	3	223, 232	211, 217, 229
concat14	7	6	4	3	1	201, 203, 211	177
EMILY	8	5	6	2	3	136, 140	148, 150, 152
DZ447	7	5	5	2	2	183, 185	191, 192
EJV8T	7	6	5	2	1	145, 149	154
Mean Kit2	7.88						
Total both Kits	132	80	102	30	52		

Appendix D: AMOVA locus by locus for adult populations (*F. sylvatica* and *F. orientalis*)

AMOVA Locus by Locus	% variation
csolfagus_09	56.2
DE576	32.6
DUKCT	32.2
csolfagus_31	31.7
concat14	29.8
ERHBI	27.4
sfc_0036	23.5
EEU75	18.5
DZ447	17.0
sfc_1143	15.4
EJV8T	14.9
EMILY	12.4
csolfagus_06	11.7
FS1_15	11.2
csolfagus_19	7.7
csolfagus_05	6.0

Appendix E: Allele frequencies per locus for both adult populations (*F. sylvatica* and *F. orientalis*)

csolfagus_06

Allele size	*F. orientalis*	*F. sylvatica*
203	0.00	0.03
205	0.00	0.05
209	0.00	0.02
211	0.00	0.03
212	0.00	0.21
214	0.06	0.16
216	0.06	0.32
218	0.25	0.08
220	0.13	0.08
222	0.19	0.02
224	0.31	0.00

csolfagus_09

Allele size	*F. orientalis*	*F. sylvatica*
132	0.00	0.08
134	0.63	0.00
136	0.31	0.00
138	0.06	0.79
140	0.00	0.13

csolfagus_05

Allele size	*F. orientalis*	*F. sylvatica*
158	0.06	0.00
162	0.00	0.02
164	0.00	0.16
166	0.25	0.48
168	0.31	0.27
170	0.25	0.02
172	0.06	0.02
174	0.06	0.03

sfc_0036

Allele size	*F. orientalis*	*F. sylvatica*
97	0.00	0.52
99	0.06	0.05
101	0.44	0.08
103	0.06	0.16
105	0.00	0.03
107	0.00	0.02
109	0.13	0.11
111	0.06	0.00
113	0.06	0.00

csolfagus_31

Allele size	*F. orientalis*	*F. sylvatica*
94	0.38	0.00
108	0.00	0.03
110	0.00	0.02
112	0.63	0.02
114	0.00	0.05
116	0.00	0.35
118	0.00	0.06
119	0.00	0.18
125	0.00	0.24
127	0.00	0.02
129	0.00	0.03

sfc_1143

Allele size	*F. orientalis*	*F. sylvatica*
99	0.06	0.00
105	0.13	0.00
109	0.44	0.00
115	0.06	0.00
117	0.06	0.06
119	0.06	0.10
121	0.00	0.03
123	0.06	0.00
127	0.00	0.10
129	0.13	0.34
131	0.00	0.23
133	0.00	0.06
135	0.00	0.02

csolfagus_19

Allele size	*F. orientalis*	*F. sylvatica*
165	0.38	0.03
167	0.00	0.11
169	0.00	0.06
171	0.13	0.13
173	0.19	0.35
175	0.00	0.10
177	0.19	0.08
179	0.13	0.02
181	0.00	0.02
183	0.00	0.08
185	0.00	0.02

115	0.06	0.00

DUKCT

Allele size	*F. orientalis*	*F. sylvatica*
77	0	0.07
81	0.56	0
87	0	0.15
89	0.06	0.58
91	0	0.03
94	0.31	0.15
96	0.06	0.03

EEU75

Allele size	*F. orientalis*	*F. sylvatica*
87	0.06	0.00
91	0.31	0.00
93	0.19	0.00
95	0.00	0.11
97	0.00	0.45
99	0.25	0.08
101	0.00	0.03
105	0.00	0.05
107	0.06	0.02
109	0.06	0.02
111	0.06	0.19
113	0.00	0.03
117	0.00	0.02

ERHBI

Allele size	*F. orientalis*	*F. sylvatica*
159	0.06	0.31
161	0.00	0.45
163	0.06	0.19
165	0.06	0.02
167	0.19	0.03
169	0.50	0.00
175	0.13	0.00

DE576

Allele size	*F. orientalis*	*F. sylvatica*
211	0.00	0.34
217	0.00	0.23
220	0.75	0.05
223	0.06	0.00
226	0.13	0.32
229	0.00	0.06
232	0.06	0.00

concat14

Allele size	*F. orientalis*	*F. sylvatica*
177	0.00	0.05
195	0.19	0.68
197	0.50	0.06
199	0.06	0.18
201	0.13	0.00
203	0.06	0.00
211	0.06	0.00

EMILY

Allele size	*F. orientalis*	*F. sylvatica*
136	0.38	0.00
140	0.19	0.00
142	0.19	0.21
144	0.06	0.11
146	0.19	0.19
148	0.00	0.31
150	0.00	0.13
152	0.00	0.05

DZ447

Allele size	*F. orientalis*	*F. sylvatica*
183	0.25	0.00
185	0.25	0.00
190	0.06	0.15
191	0.00	0.11
192	0.00	0.45
194	0.13	0.08
195	0.31	0.21

EJV8T

Allele size	*F. orientalis*	*F. sylvatica*
145	0.13	0.00
146	0.06	0.42
149	0.25	0.00
150	0.19	0.35
152	0.19	0.02
154	0.00	0.16
156	0.19	0.05

Appendix F: Positive LOD-scores from parentage analysis with *Cervus*

Offspring ID	First candidate ID	Pair LOD score	Second candidate ID	Pair LOD score
OM2	OA7	5.35E+14		
SM1	SE2	6.37E+13		
V1H1	SA1	1.35E+15	SA33	3.68E+14
V1H10	OA1	1.03E+15		
V1H11	OA1	8.98E+14		
V1H12	OA1	1.09E+15		
V1H13	OA1	7.09E+14		
V1H14	OA1	9.07E+14		
V1H15	OA1	1.19E+15		
V1H16	OA7	1.26E+15		
V1H18	OA1	8.98E+14	SA34	1.11E+15
V1H19	OA1	1.09E+15		
V1H20	OA1	1.65E+15	OA2	1.62E+15
V1H21	OA1	1.27E+15		
V1H22	OA1	1.34E+15		
V1H23	OA1	1.15E+15		
V1H24	OA1	7.78E+14		
V1H3	OA1	8.59E+14		
V1H4	OA1	9.89E+14		
V1H6	OA1	1.25E+15		
V1H7	OA1	1.15E+15		
V1H8	SA1	1.40E+15	SA4	4.70E+13
V2H1	SE6	8.03E+14		
V2H10	SA2	1.26E+15	SA27	4.84E+13
V2H11	SA27	3.91E+14		
V2H12	SA11	3.90E+14		
V2H15	SE7	3.31E+14		
V2O4	SA2	2.62E+14		
V2O6	OA1	7.91E+13		
V2O7	SA34	1.35E+15		
V3H1	OA3	1.62E+15		
V3H2	OA3	1.22E+15		
V3H4	OA3	1.54E+15		
V3O1	OA3	5.38E+13		
V3O5	OA3	7.40E+14		
V4H1	OA4	1.00E+15		
V4H3	OA4	1.57E+15		
V4H4	OA4	1.28E+15		
V4H5	OA4	1.36E+15		
V4H6	OA4	1.74E+15		
V4H7	OA4	1.09E+15		
V4H8	OA4	1.27E+15		
V4O1	OA1	1.57E+15	OA4	1.67E+15
V4O2	OA4	1.11E+15		
V4O3	OA4	1.26E+15		
V5H4	SA27	7.14E+14	SE6	5.53E+14
V5H8	SE7	1.23E+14		
V6H1	OA1	1.12E+15		
V6O1	OA1	1.34E+15	OA2	1.87E+15
V6O2	OA1	1.32E+15	OA2	2.27E+15
V6O4	OA1	9.58E+14		

zh aw

Erklärung betreffend das selbständige Verfassen einer Bachelorarbeit im Departement Life Sciences und Facility Management

Mit der Abgabe dieser Bachelorarbeit versichert der/die Studierende, dass er/sie die Arbeit selbständig und ohne fremde Hilfe verfasst hat.

Der/die unterzeichnende Studierende erklärt, dass alle verwendeten Quellen (auch Internetseiten) im Text oder Anhang korrekt ausgewiesen sind, d.h. dass die Bachelorarbeit keine Plagiate enthält, also keine Teile, die teilweise oder vollständig aus einem fremden Text oder einer fremden Arbeit unter Vorgabe der eigenen Urheberschaft bzw. ohne Quellenangabe übernommen worden sind.

Bei Verfehlungen aller Art treten Paragraph 39 und Paragraph 40 der Rahmenprüfungsordnung für die Bachelor- und Masterstudiengänge an der Zürcher Hochschule für Angewandte Wissenschaften vom 29. Januar 2008 sowie die Bestimmungen der Disziplinarmassnahmen der Hochschulordnung in Kraft.

Ort, Datum: Unterschrift:

Wädenswil, 8.11.18 M. Kurz

Das Original dieses Formulars ist bei der ZHAW-Version aller abgegebenen Bachelorarbeiten im Anhang mit Original-Unterschriften und -Datum (keine Kopie) einzufügen.