Norwegian University of Life Sciences
Faculty of Landscape and Society

Philosophiae Doctor (PhD)
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Kompleksiteten ved introduserte planter som kulturarv

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Photo on previous page: Self-portrait of the author sitting next to an old *Abies alba* Mill. (European silver fir) in Elsterparken, Trondheim. The tree is possibly a remain of the plantings in the period from 1871 to 96. Photo taken on 30 October 2015.

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"A tree is a grand object in itself; its bold perpendicular elevation, and its commanding attitude, render it sublime; and this expression is greatly heightened by our knowledge of its age, stability, and duration".[1]

[1] J. C. Loudon. 1838. *Arboretum et Fruticetum Britannicum* (London: J. C. Loudon), Introduction, p. 2.

LIST OF PAPERS

This thesis is based on the following papers, referred to in the text by their roman numerals:

I **Ridbäck, U., Dietze-Schirdewahn, A.** (2017). Once in demand, now unwanted: reflections on changed attitudes towards plants introduced to Norway 1750–1900. *Landscape Research*, 42 (5): 471–481.

II **Ridbäck, U., Vike, E.**, **Dietze-Schirdewahn, A.** A battle of values: a case study of an invasive heritage tree represented by European silver fir *Abies alba* Mill. in a protected landscape in Norway. *Arboricultural Journal*, manuscript accepted with major revision.

III **Ridbäck, U., Kovi, M. R., Kent, M. P., Hansen, H. H., Rognli, O. A., Dietze-Schirdewahn, A.** Past anthropogenic dispersal of introduced European silver fir *Abies alba* Mill. in Norway was revealed by reduced representation sequencing. *Submitted manuscript.*

All papers were written by the first author with contributions and suggestions from the co-authors[2]. Papers I is reproduced with permission from the publisher.

[2] Literary data collection and analyses for paper I was performed in collaboration with ADS. Data collecting for paper II was performed in collaboration with EV, and analyses were performed in collaboration with EV and ADS. Literary studies for paper III were carried out with major inputs from ADS, laboratory work was performed by UR and HHH, and analyses were performed by and in collaboration with MRK, MPK, OAR and ADS.

ABSTRACT

As the independent nation of Norway was at its infancy in 1814, so was also an important change in Norwegian garden culture. Norway was about to experience a significant boom of plant introductions for ornamental use, which slowly began as early as in the mid-1700s. A naturalistic garden design used to dominate, which involved particularly imported plants. As a contrast to this passion for introduced plants in the past, these plants are at present increasingly approached as problematic objects. All plants introduced in the year 1800 or later are since 2012 categorised as alien species. Considering that plants can represent both cultural heritage and alien species, which potentially can harm Norwegian nature and biodiversity, it is a matter that concerns different disciplines and management interests.

This thesis is a three-disciplinary work, involving methods from the disciplines history, botany and genetics. The aim was to approach plants introduced in the 1800s by combining methods from these different fields. *Abies alba* Mill., commonly known as European silver fir, was selected as a case species to represent this category of introduced plants and, in particular, of blacklisted plant species in Norway.

Paper I examines how introduced plants were described and reflected on in Norwegian literature from 1750 to 1900. Historical literary sources were accessed from archives and historical library collections in Oslo, Ås and London (UK). The texts were analysed with emphasis on middleclass people's (i.e. academics, civil servants, merchants and the clergy) perception of introduced plants and how their attitudes changed from 1750 to 1900. Positive attitudes towards introduced plants increased significantly in the investigated period. After the century turn 1800, the middleclass played an important role regarding the use of ornamental plants. As the establishment of plant nurseries increased in the mid-1800s, new plant assortments became more accessible for the general public. This led to a garden culture marked by a diversity of exciting and new plants, which also illustrates the predominantly positive views on introduced plants after the 1850s. Regarding the term exotic plants, such plants appeared as something positive when used to describe rare, unusual and exciting plants, often new to science. In contrast, introduced plants that are presently addressed as alien plants in Norway are associated with something negative, which seemingly contributes to negative attitudes towards introduced plants in general.

With *Abies alba* as a case species, **paper II** deals with the management of a blacklisted heritage tree in a protected landscape. This was approached by combining literary studies and fieldwork in Austråttlunden, a protected landscape situated in central coastal Norway. The literary approach involved studies about Austråttlunden's history, the introduction of *Abies alba*, its management during the past 40 years and people's experience of and relation to the area. Fieldwork, with a focus on invasiveness, involved an inventory of *Abies alba* seedlings with GPS along transects to map its spreading in the area and the recording of some ecological parameters and growing conditions. As an introduced and blacklisted plant species, *Abies alba* constitutes both cultural heritage and a threat to ecological values, represented by native plants species and sensitive habitats. The study shows that *Abies alba* spreads relatively slowly and that most seedlings establish within 30 m of the parent in half-shade positions. Continued maintenance such as vegetation clearing and grazing prevents and limits the spread of *Abies alba*. This kind of maintenance is also required to conserve a protected landscape with a certain cultural historical character. *Abies alba* has received more attention as an invasive species, although it is part of the area's cultural historical identity. At present, the management is mainly the responsibility of ecological conservationists, which is why natural values have been prioritised. To equally address natural, cultural and historical values, collaborations between professionals from different disciplines are required. This would allow to safeguard not only native plants species and habitats dependent on the cultural landscape, but also a blacklisted heritage tree.

The scope of **paper III** was to generate new knowledge about plant introduction history by involving genetics. With *Abies alba* as a case species, this issue was approached through a combination of historical literary studies, fieldwork and laboratory work. Literary sources provided information about the introduction of *Abies alba* in the late 1800s and indicated that the same people had been involved in some planting projects in central coastal Norway. In cases where historical sources were lacking, the goal was to use genetic data as a complement to fill knowledge gaps. This study included seven localities in central coastal Norway and one locality in southern Norway. The DNA was extracted from fresh *Abies alba* needles collected in the field. High-molecular weight DNA samples were prepared for sequencing by following the ddRAD protocol by Peterson et al. (2012). The full genomic sequenced data were processed using STACKS v1.18 to detect SNPs. Relatedness and population structure were analysed using the STRUCTURE software version 2.3.4. For the phylogenetic analysis, we used BIONJ, and principal coordinate analysis was performed with the software package GenAlEx version 6.5. The genetic relatedness supported historical

sources regarding the connexion between three of the localities. The results also enabled predictions of how people might have accessed and shared *Abies alba* between the other localities. The study has shown that genetics, in combination with historical sources, is a valuable tool to uncover new pieces of the whole process of plant introduction.

The issue of introduced plants is a complex research object as it concerns many different fields. By looking back on the period from 1750 to 1900, the primary step involved history in order to learn about the background of plant introduction in this period and how the new plants were perceived. Further, the attention was drawn towards the challenge this category of introduced plants constitutes in a management context, with *Abies alba* as an example. With introduction history as a leading thread, genetics was involved as a third discipline to help generate new knowledge about the introduction and distribution of *Abies alba*. *Abies alba* functioned as a bridge between the past and the present and connected the three disciplines history, botany and genetics.

The thesis particularly contributes to the societal debate on the management of introduced species and is a step forward to equally address natural and cultural values. Overall, this work contributes to initiate dialogues and interdisciplinary collaborations between professionals.

OPPSUMMERING

Mange prydplanter i Norge har en introduksjonshistorie som startet samtidig som den norske grunnloven ble etablert i 1814. På denne tiden startet også en ny epoke i norsk hagekultur. En ny trend og hunger etter nye planteslag begynte sakte allerede i midten av det attende århundre, der import og bruk av planter var en betydelig del. Den gangen hadde norske hager en naturalistisk stil med innslag fra Europa. Nye planteslag fra utlandet kunne tilby mer variasjon og mangfold enn det som fantes i norsk natur. Som en kontrast til etterspørselen på introduserte planter i det attende og nittende århundrene, er disse plantene mottatt annerledes i dag. Alle plantearter introdusert år 1800 eller senere er siden 2012 kategorisert som fremmede arter. Dette berører ulike disipliner, og forvaltningsinteressen ettersom disse plantene representerer både kulturarv og fremmede arter, med potensiell evne for å bidra til skade på natur og biologisk mangfold i Norge.

Denne avhandling er et empirisk bidrag til tverrfaglig forskning på innførte planter. Målet er å se nærmere på planter introdusert i Norge på 1800-tallet ved å kombinere metoder fra disiplinene historie, botanikk, og genetikk. *Abies alba* Mill. (vanlig edelgran) ble valgt ut som case-plante, for å representere planter introdusert på 1800-tallet, i tillegg til svartlistede planter.

Artikkel I undersøker hvordan planter ble sett på og beskrevet i norsk litteratur 1750–1900. Denne problemstillingen ble besvart gjennom analyse av historisk kildemateriale fra arkiver og historiske litterære samlinger i Oslo, Ås, og London (Storbritannia). De litterære kildene ble analysert med tyngde på middelklassens (akademikere, presteskap, rådmenn og handelsmenn) syn på introduserte planter, og hvordan holdningene forandret seg 1750–1900. Resultatene fra **artikkel I** viser at holdninger til introduserte planter forandret seg i den undersøkte tidsperioden. Den norske middelklassen, som i stor grad besto av akademikere, rådmenn, handelsmenn og presteskap, spilte en viktig rolle for etterspørselen på introduserte planter. Ved midten av 1800-tallet var plantehandelen påvirket av landets gode økonomi. Antallet planteskoler økte, og snart kunne hvem som helst få tilgang til nye planter på markedet. Hagekulturen var da preget av et mangfold av eksotiske planter. Dette illustrerer at positive holdninger til plantene dominerte og økte mot slutten av 1800-tallet. Begrepet 'eksotiske planter' fremstår som noe positivt og rettet seg spesielt mot sjeldne, uvanlige og spennende planter, ofte nye for vitenskapen. I kontrast er planter som ble innført på 1800-tallet i dag kategorisert som fremmede planter i Norge, knyttet til et negativ syn på disse plantene.

Med *Abies alba* som case undersøker **artikkel II** hvordan et svartlistet arvstre vurderes i et vernet landskap. Dette ble undersøkt gjennom en kombinasjon av litterære studier og feltarbeid i Austråttlunden, et vernet natur- og kulturområde i Sør-Trøndelag. Den litterære delen omfattet Austråttlundens historie, introduksjon av *Abies alba,* forvaltning og skjøtsel av området de siste 40 år, og hvordan mennesker relaterer til og opplever landskapet. Spredning av *Abies alba* ble kartlagt med GPS langs linjer. I tillegg ble også økologiske forhold registrert. Som en introdusert og svartlistet planteart er *Abies alba* både et botanisk kulturarv og en trussel mot naturverdier, representert av innfødte plantearter og habitat. Resultatet fra studiet viser en moderat spredning av *Abies alba.* De fleste småplantene var etablert innen 30 meter fra modertreet, i halvskyggete områder. Fortsatt vedlikehold som rydding av vegetasjon og beiting forhindrer og begrenser spredning av *Abies alba.* Denne formen av vedlikehold er også viktig for å bevare landskapets unike kulturhistoriske karakter. *Abies alba* har fått mest oppmerksomhet som en invasiv art, selv om den er en del av Austråttlundens kulturhistoriske identitet. Nåværende forvaltning er hovedsakelig i hendene på naturforvalter, og naturverdier har derfor blitt prioritet. For å gi natur, kultur, og historiske verdier like mye oppmerksomhet trengs tverrfaglig samarbeid mellom fagfolk. Dette kunne gjøre det mulig å bevare ikke bare artsrikdom og habitat knyttet til kulturlandskapet, men også et svartelistet arvstre.

Målet med **artikkel III** var å undersøke hvordan genetikk kan bidra til nye kunnskaper om planters introduksjonshistorie, med *Abies alba* som case. Analyse av historiske litterære kilder ble kombinert med genetisk metode, det vil si feltarbeid og labarbeid. Historiske kilder ga indikasjoner på at ulike grupper mennesker i Sør-Trøndelag samarbeidet for å plante *Abies alba* på slutten av 1800-tallet. Genetisk data var tenkt å brukes som supplement i de tilfellene historiske kilder mangler. Åtte steder ble inkludert i denne studien, hvorav syv i Sør-Trøndelag og et i Akershus (Ås). Nåler ble samlet og siden bearbeidet i genetisk analyse for å studere slektskap mellom treene. Ekstrahert DNA-prøver ble forberedt til sekvensering med ddRAD-protokoll av Peterson et al. (2012). De sekvenserte dataene ble videre prosessert i STACKS v1.18 for å oppdage SNPs (Single nuclear proteins). Slektskap og populasjonsstruktur ble analysert med STRUCTURE software version 2.3.4., fylogenetisk slekskapsanalyse med BIONJ, og Hovedkoordinatanalyse (Principal coordinate analysis) med GenAlEx software version 6.5. Gjennom å sammenligne informasjon fra litterære kilder med genetisk data åpnet resultatene for nye tolkninger av hvordan *Abies alba* ble distribuert av mennesker på slutten av 1800-tallet. Nære slektskap mellom trær på tre av lokalene støttet funn i historiske kilder når det gjelder

introduksjon av *Abies alba*. Resultatene åpnet for tolkning av hvordan mennesker fikk tilgang til og spredt plantemateriale mellom øvrige områder som var en del av studiet, der det ikke fantes støtte fra historiske kilder. Dette studiet vis at kombinasjonen av historiske kilder og genetiske undersøkelser er verdifull for å forstå ulike deler av prosessen i planteintroduksjon. Som genetisk metode har ddRAD blitt sparsomt brukt før i slik studier, og vist seg å være et godt alternativ til andre veletablerte metoder, med tanke på kostnad og tidsbruk.

Introduserte planter er et komplekst forskningsfelt som berører flere ulike disipliner og aktører. Avhandlingens bidrag i sin helhet er et forsøk å integrere disiplinenes historie, botanikk og genetikk for å undersøke introduserte planter fra ulike innfallsvinkler. Gjennom et historisk tilbakeblikk på perioden 1750–1900 var det første steget å forstå hvordan nye planteslag ble mottatt i Norge. Neste steg var å rette oppmerksomheten mot introduserte planter som en utfordring i forvaltningssammenheng, med *Abies alba* som eksempel. Med planteintroduksjon som rød tråd ble genetikk involvert som en tredje disiplin for å generere ny kunnskap med *Abies alba* som eksempel. *Abies alba* fungerte som en bro mellom fortid, nåtid, og de tre ulike disiplinene.

Avhandlingen er et særskilt bidrag til den generelle samfunnsdebatten om bruk, forvaltning og forekomst av introduserte arter i Norge, og er et skritt fremover skape mer dialog, og forenkle kommunikasjonen og samarbeid mellom aktører som har ulike forvaltningsinteresser.

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PREFACE AND ACKNOWLEDGEMENTS

My earliest experience with an introduced plant species was in my grandparent's garden in northern Sweden. It was a Larch tree, probably *Larix decidua* Mill., growing on the border between the grandparent's and their neighbour's gardens. I remember that for me, as a child back then, it was indeed an exciting tree. Its appearance reminded me of a high and thin spruce tree, but the conspicuously soft needles changed colour and fell off in autumn, just as the leaves of a deciduous tree species. Since that early memorable experience, my curiosity about the origin and geographical distribution of plants, both wild and introduced, has grown.

I feel that the foundation of this thesis started long before I took the position as a doctoral student. After many years of studies and work as a botanist, I had obtained a very good view over the broad field of plant science. This started with eight semesters of basic training in biology, including writing a Bachelor thesis and a Master´s thesis in botany and ecology. Looking back at this time, I would like to take this opportunity to thank my student fellows at Ekologiprogrammet and GoNat, and particularly Bertil Ståhl for introducing me to Ecuador and encouraging me to continue in the field of botany. Further, I got to work at different projects as herbarium assistant and plant taxonomist. I wish to thank my colleagues who inspired and helped me during these time-limited projects at the Swedish Museum of Natural History in Stockholm, the Department of Biological and Environmental Sciences in Gothenburg and the Protección del Medio Ambiente in Tarija (Bolivia).

Time flies and 10 years after I had started my basic training as a biologist, I was offered the PhD scholar position titled 'Plants and cultural landscapes' at the Norwegian University of Life Sciences in Ås. With my botanic background and interest in botanic cultural history, it felt as if it was meant for me. Another advanced climb was about to begin, requiring new advanced tools, methods, theoretical insights and guidance for a challenging and long research expedition. Anyone who has climbed a mountain to reach the summit knows that often, when one thinks the goal is straight ahead, we reach it just to realise it was only another crest. Even with a good plan, there is more climbing ahead than it was expected. This expedition has been about trying again and again while sweating under heavy time pressure and looking for new motivation every time things did not turn out as one wanted them to. And in between, I have experienced those amazing days I made new tracks to a place where nobody or few have been before.

To reach the final goal of this long and challenging journey in writing this doctoral thesis, I am grateful to many people who have helped me and contributed to my wellbeing along the way. Above all, I wish to thank my supervisors Annegreth Dietze-Schirdewahn and Eva Vike for keeping me on track, giving me feedback, untiringly correcting and improving my papers and this thesis and supporting me when the headwind was hard. As my main supervisor, Annegreth has been the constructive 'gardener', knowing when and how to prevent my branches from growing too wild and far from my research object; Eva has particularly helped me to keep my feet on the natural scientific ground.

I thank my research group colleagues Bjørn Anders Fredriksen and Lei Gao for helpful comments on my first paper and for their valuable friendship and social lunch/coffee breaks.

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Warm thanks also to all the friendly staff at the Department of Landscape Architecture and Spatial Planning (ILP). I particularly thank Sheena Gilchrist Lisland for guiding me in all practical administration regarding the progress of a research education, Tim Richardson for helping me outlining the research problem and thesis disposition, Valborg Lippestad for helping me with any documents or certificates and explaining any economic issue to me, Ole Andreas Langemyr for helping me to solve any IT-related problems and Tove Rømo Grande for proofreading and editing my Norwegian title and abstract of the thesis.

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I particularly wish to thank Sylvia Sagen Johnsen for indispensable guidance in the lab at CIGENE. I also thank Beatrice Misaka Langwa, Aregawi Eatay Tesfa and Alye Tefera Haile for their collaboration, help and social talk in the lab.

Further, I would like to thank all friendly and helpful people in Sør-Trøndelag, who guided me when I got lost along the road, searching for localities with old European silver firs.

Ruth Vatvedt Fjeld at UiO – thank you for your reflections on the linguistic history of the word 'exotic' in Norwegian and the term's use in the context of plants.

Warm thanks to Eva Thesen and Ole-Jacob Skipperud who made me feel at home in Drøbak.

Meeting new people is always inspiring, and new friendships are like sunshine on the rainiest days. Having no family in Norway, I am especially grateful to new friends that have contributed to a pleasurable time as a PhD student in Ås and Drøbak. I wish to thank my PhD fellows at ILP, in particular[3] Gordana Marjanovic, Katinka Horgen Evensen, Sebastian Peters and Therese Andersson.

Among the acquaintances through SoDoC[4] (former FODOS[4]), I particularly thank[3] Luz Munoz, Ursula Brandes and Viktorija Viciunaite.

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My dear friends[3] Julia Stigenberg, Patricia Amaya, Sanna Siitonen and Tove Rosenberg, thank you for always having time for a chat, for sharing good advices and for wonderful occasions together when we meet!

Closest to my heart, I wish to thank my family: my mother and my siblings with families, for calling me, believing in me, supporting and comforting me whenever life is hard and for our nice social gatherings. In memorial: thanks to my father, who intensely encouraged me to study further after primary school.

Drøbak, October 2017
Ulrika Ridbäck

[3] In alphabetical order.
[4] Society of Doctoral students at Norwegian University of Life Sciences (former Forum for Doctoral Students).

1. INTRODUCTION

This thesis is the result of my doctoral studies at the Norwegian University of Life Sciences, School of Landscape Architecture, in Ås. It is a multidisciplinary work and includes three papers with methods from both social and natural scientific fields, i.e. history, botany and genetics. Introduced plants are the focus of this work, with emphasis on plants brought to Norway and used as ornamental plants in the 1800s, here represented by *Abies alba* Mill. (European silver fir) as a case plant.

The decision to investigate the issue of introduced plants in a multidisciplinary way has developed successively. With the theme 'Plants and cultural landscapes' as a starting point, my research was connected to the research group 'History and Botanic Heritage' at the Department of Landscape Architecture and Spatial Planning (present School of Landscape Architecture). As I was not familiar with Norwegian garden history, initially, I started my doctoral studies with an extensive literature review, with emphasis on the use of ornamental plants. I found the 19th century particularly interesting, as the year 1800 has been set as a delimitation in time to define alien species in Norway (Gederaas et al. 2012, 12). It soon occurred to me that, in literature from the concerned period (see e.g. Hammer 1773; Fasting 1781; Fasting 1791a; Fasting 1791b; Wilse 1777; Wilse 1790; Schübeler 1862a), introduced plants appeared differently seen upon compared to present public documents such as the *Norwegian Black List 2012* (Gederaas et al. 2012; Artsdatabanken 2012) and a new legislation to regulate the use of introduced plants (Lovdata. no 2015; Miljødirektoratet 2015). In addition, some terms were particularly used to address the plants, without regarding the terms origin and meaning. From this, my research took on a historical approach, mainly based on published and printed works in libraries and archives. When I attended the PhD course *Applied theory in historical research* in Uppsala in spring 2014, I was exposed to different theoretical approaches and inspired by the different ways one can approach a research object that partly belongs in the past, in this case, plants introduced in the 1800s.

Against my background as a botanist, I regarded plants as a phenomenon traditionally belonging into natural sciences. However, by being used by humans, plants have become a social scientific object. During the course *Restoration, conservation and development – Garden, park or cultural landscape* in Ås, which also was part of my doctoral studies, I performed fieldwork in a protected landscape (*Austråttlunden*, central coastal Norway) containing both introduced and native (naturally occurring) plants. It occurred to me that some of the introduced trees represent cultural

and historical values in an area dominated by natural values. I observed a conflict in the conservation of these values, and it became relevant to explore this issue by involving *Abies alba* as a case plant. In addition to history, botany became the second discipline in my methodical approach. The focus was on the spread of *Abies alba* in a protected landscape, where the case plant constitutes both cultural heritage and a potential invasive plant species.

The presence of *Abies alba* in Austråttlunden made me curious about its introduction history. Literary sources showed that the tree was planted in the late 1800s. As there were several other *Abies alba* trees contemporarily introduced in the same region, I found it interesting to study their genetic relatedness as a way to explore a possible distribution scenario. At this stage, genetics was involved as a third discipline to approach *Abies alba*, to generate new information to complement the findings in historical literary sources.

With a focus on plant introduction, the discipline history was present throughout all papers (**I–III**) presented in this thesis. Botany was the complementary discipline in **paper II,** while genetics was that of **paper III**. The main objective was to show how these disciplines can interplay to generate new knowledge.

Background

"If wild plants are said to follow those animals to which they supply food, cultivated plants are the followers of a man in a state of civilisation" (Loudon 1838, Chap. II., 31). Since ancient times, plant introduction has been an activity of man. One of the oldest known records is from Mesopotamia about 2500 B.C., describing how King Sargon brought plants from Asia Minor to his own land (Ryerson 1933, 110). Whenever people have been moving, there has been a variety of reasons to bring plants with them to new places (Borowy 2011, 155). Initially, plants were an important source of food (Raven et al. 2003, 823); depending on the human needs, this involved the introduction of plants to geographic places where they did not originally occur (Lundquist 2000, 43).

This section will give a brief introduction to the history of plant introductions in Europe after 1492. For the purpose of this thesis, the use of plants is highlighted, with emphasis on plant science and garden culture in the 19th century. Further, I will shed light on the situation in Norway; the development of plant introductions from the mid-19th century until the century turn in 1900. I also

look at the development of invasion biology as a field that evolved from challenges and problems that people face with introduced species worldwide.

Plant introduction in Europe after 1492

The European history of exploring the planet and transportation technology are closely linked to plant introduction (Binggeli 2011, 202). This literally took off after Cristobal Colón made the existence of the Americas known to Europe in 1492. Contemporary seafarers started to explore new ways by sea and brought back new exotic discoveries from all over the world. This was a significant start of a new era of plant introductions to Europe (Rotherham 2011, 236). One can sense that there was a competitive concern among scientists to provide Europe with the latest natural historical news. One example is Charles de l'Ecluse (1526–1609, also known as Carolus Clusius) and his *Rariorum Plantarum Historia* (1601), which illustrates the scholar's persistent desire for documenting the newest plant discoveries in the 16th century (Mason 2009, 148).

With botanists in the 16th and 17th centuries as predecessors, plant science literally experienced a revolution in the mid-18th century, when Carl von Linné (1707–1778, earlier Carolus Linnaeus) introduced his systematics and binomial naming of species in the botanic world. As his pupils brought back new plant specimens from all over the world, this opened the door for scientific descriptions of newly discovered plant species as well as new plant introductions (Lundquist 2000, 50). Explorations and colonial expansion also played an important role in the new global dispersal of introduced plants (Borowy 2011, 155). North America supplied Europe with new trees and shrubs, which in turn contributed to a growing plant demand, with increasing naturalistic approaches in current garden designs (Dietze 2007, 103–104).

The 1800s were a central part of a 'golden age of plant introductions' (Rotherham 2011, 239). The increasing interest in particularly botanic rarities was reflected in science as well as in the design of European parks, where introduced trees contributed to a diversity of forms and areas of use (Nolin 1999, 113). Another important force behind plant introductions in this century was the acclimatisation of plants, which became a new scientific discipline that engaged scientists and laymen in active experiments to investigate which plant species could best adapt to new conditions (Borowy 2011, 155). Colonial ambitions, along with nationalistic movements, contributed to the transfer of European crops to non-European environments, such as colonies in Australia, New Zealand and North Africa. The other way around, plant species native to the new environments were adopted into the Europeans' agricultural traditions (Borowy 2011, 156). Also related to the

acclimatisation of plants, from an economic perspective, was the establishing of Botanic gardens, which were also developed in European colonies (Binggeli 2011, 205). Acclimatisation societies, which were established throughout Europe in the 1800s, contributed to promote introductions of new plant species, a process that carried on well into the following century (Rotherham 2011, 236–237).

Turning point in Norwegian garden culture

Located in the very northwest, comparable to the periphery of Europe, Norway is particularly interesting in terms of the use of introduced plants. Compared to other European regions in the 1700s, one might expect that introductions of exotic plants to pleasure gardens and forestry arrived later in Norway, a country were the climate, in most parts, is anything but suitable for the cultivation of foreign plants. First belonging to Denmark (1380–1814) and later to Sweden (1814–1905), Norway was no great power, neither economically nor politically (Dietze 2007, 25, 27). The small population grew rapidly, along with increased urbanisation in the 1800s. Compared to Copenhagen and Stockholm, Christiania (present Oslo) was the fastest growing large-sized town in Europe. This led to an outstanding position based on the number of inhabitants and the development of communication and the economy (Helle et al. 2006, 249).

Affected by movements in Europe, Norwegian garden culture started to change in the 18th century. Towards the end of the century, new garden influences seemed well perceived by the generally Europe-orientated middleclass in Norway (Bruun 1987, 187; Dietze 2007, 45–46). Exposed to a mixture of different influences, a central part was the use of plants that were literally from newly discovered lands faraway. Plants became important elements of garden design through the effects one could create with them (Bruun 1987, 183; Hobhouse 1992, 204).

Norway hence reached a turning point in the late 1700s. Contemporary news in garden art and botany reached Norway earlier than they had ever done before. Wealthy garden owners kept pace with leading nations in Europe on gardening and plant science (Bruun 1987, 187). Norwegian merchants developed their own naturalistic garden style based on experiences from, among others, Britain, Denmark, France, Germany, Italy and Sweden (Dietze 2007, 31, 51). With a presumed reference to the English landscape style, the naturalistic approach particularly involved imported plants (Dietze 2007, 155). The plants, especially exotic species, were even more important than the actual garden design (Dietze 2007, 128).

As individual plants became the centrepieces of Norwegian landscape gardens, they also played a crucial role in the demonstration of economic and botanical success of the garden owners (Dietze 2007, 107, 132). At the start of the 19th century, plants still appeared as luxury goods and as such contributed to a scientific and academic enlightenment in botany (Dietze 2007, 135). Plant import at this time was, in general, the business of wealthy merchants, and there were hardly any imported plants available for the public at the ordinary markets (Skard 1963, 108; Ridbäck and Dietze-Schirdewahn 2017, 471).

After 1850, the Norwegian garden culture reached a new phase of its development. New species that were suitable for specific aims could raise economic interests, which in turn led to an increased number of local plant nurseries. Soon, any garden owner had the opportunity to acquire exciting new plants (Skard 1963, 222–224, 238–239), and local nurseries became more and more specialised. Fruit-bearing and ornamental woody plants appeared to be of particular interest, and the assortment considerably increased from 1850 to 1880 (Bjerke 2002, 32).

Picturesque sceneries seemed to influence the design of middleclass villa gardens as they increased in numbers and decreased in size. The planting of rare and eccentric plants continued to catch people's interest, and many gardens were established with the aim to create picturesque and spatial effects on smaller scales (Bruun 2007, 295, 303). With a diversity of plants as dominating garden features, this probably contributed to the increased demand for introduced plants.

Evergreen trees and shrubs were a good supplement to deciduous plants. Particularly conifers were excellent elements when planted in the background or as solitary trees in gardens designed according to the 'English style'. The Norwegian gardener Nøvik (1891, 83) expressed that "in each garden, large or small, conifers should not be missing" ("*I enhver have, stor eller liden, bør nåletræer ikke savnes*"). Loudon (1838, 5) stated that trees and shrubs were "greatly superior to herbaceous plants". He argued that, when properly planted, woody plants require little care in relation to herbal plants. For 'landscape-gardening', he particularly recommended trees as picturesque and decorative ornaments (Loudon 1838, 6; (Chap. IV) 227).

Depending on the area in which new plant species were introduced in Norway, a limited number of these species could survive in the harsh climate. However, some species appeared so well adapted that they soon managed to naturalise and spread on their own, 'escaping' the localities where they once were intentionally planted. This was something that the enthusiasts in botany, gardening and experimental planting had not taken into account back in the 1800s, when the great wave of new plant introductions accelerated in Norway.

Introduced plants as an international concern

As people travelled all over the globe in search of exotic species to exhibit, this contributed to increased collections and the dispersal of introduced species (Rotherham 2011, 236). In the 1600s, a series of debates rose in Europe regarding the desire to distinguish 'exotic' and 'indigenous' plants from one another. At this time, the spreading of introduced plants did not appear as the main concern, but the focus was rather on the harm of new 'exotic' natural substances when used in food and medicine (Cooper 2003, 51–52). Learned physicians argued that Europeans, "in their rush for new and glamorous *exotica*, had violated the basic order of nature" (Cooper 2003, 53). Suspicious views on 'exotic plants', supported by physicians that appealed renewed studies of 'indigenous' floras, contributed to the publications of the earliest floras of given areas in the European nature. The development of the environmental sciences was considerably affected by the eager debate regarding 'exotic' and 'indigenous' species (Cooper 2003, 53).

In an economical context, the acclimatisation of plants was both an agricultural and garden cultural business that launched introduced species. Along with interests in creating new landscapes developed the idea by William Robinson (1838–1935) of 'naturalising' introduced plants instead of planting them to achieve particular effects in the landscape design. Relatively early, some of the naturalised species could be recognised as invaders (Rotherham 2011, 237–238). Even Charles Darwin (1809–1882) noted the invasion of alien newcomers in their new native grounds. To test his theories on natural selection, Darwin studied the invasiveness of introduced plants and how they interacted with plants native to particular geographical areas (Darwin 1859, 64–65, 69).

By the turn of the 19th century, there was an increased categorising of introduced species as an unwanted threat to native species. This new concern slowly started in Britain with early biologists as predecessors, including Darwin. These biologists mainly studied recently introduced species, more precisely addressed as alien species (Qvenild 2013, 39–40). However, the potential damage caused by introduced species did not appear as an urgent problem back then.

Charles Elton (1900–1991) is often perceived as the founder of 'invasion biology' as a discipline on its own. He discussed the 'spreading of species' in his book *Ecological Succession* (1927) and used the word 'invasion', albeit not to distinguish between different kinds of spreading (Davis et al. 2001, 98). In 1958, Elton was possibly affected by wartimes and characterised invasions as something unique. In his book released in the same year, he introduced invading species as 'ecological explosions.' He distinguished species invasion from the colonisation of new habitats

and stated that invading species constituted a distinct group of organisms. Elton pointed out that if the barriers to the movement of a distinct group of species were removed, this could disrupt the ecological balance (Davis et al. 2001, 98– 99).

Apparently, studies of biological invasions escalated after a new release of Elton's book *The Ecology of Invasions by Animals and Plants* (1958) in the 1980s (Borowy 2011, 153; Qvenild 2013, 40). The issue of introduced species soon obtained international significance as ecologists and conservation biologists observed and communicated threats by introduced plant species to ecosystem functions and native species existence (Simberloff 2011, 124).

The distinction between native and alien plants as well as the species' geographical origins have dominated nature conservation and restoration initiatives in North America, Australia and New Zealand over a long period (Qvenild 2013, 42). Although a few plant species have been observed to cause problems for some time in Scandinavia and northern Europe, targeting alien species is rather a very recent issue (Tyler et al. 2015, 300). The Convention on Biological Diversity (CBD) was entered into force on 29 December 1993 and has since had a seemingly strong impact on national policies on alien species.

In Norway, the concern regarding the spreading of introduced plants has risen merely over the past two decades. Norway has been a party of the CBD since 1993 (Convention on Biological Diversity 2016). Since the Global Invasive Species Programme (GISP) was established in 1996 at the Norway/UN Conference on alien species, this has become a global priority issue for environmental policy-makers (Qvenild 2013, 43). The following year, 1997, the first law to regulate species introduction in Norway was established. Qvenild (2013, 39) argues that by this law, the protection of native species became a national duty. By the millennium turn, politicians and scientists had established the concept of alien species as something rather negative, due to the potential threats to native biodiversity (Qvenild 2013, 43). This is also reflected in research with emphasis on economic and ecological damage on both human prosperity and biodiversity and on characteristics that can reveal a species´ invasive potential (Borowy 2011, 153).

It was not until 2007 that the first Black List was published in Norway (Gederaas et al. 2007, 3–4). An updated version of the Black List was published in 2012, in which the year 1800 was selected as a delimitation in time to categorise what is an alien species in Norway (Gederaas et al. 2012, 12). Categorisations of plants as alien and native are increasingly contested due to their capacities to be both useful and harmful (Qvenild 2013, 23). The most recent document that has

attracted considerable public attention is the new legislation to regulate the use of introduced species (Lovdata. no 2015).

Natural immigration and dispersal of species from the south to Scandinavia are still in process. In Norway, for instance, many invasive species are possibly a part of a natural development that started after the last ice age, which is rather recent. A counterview regarding the case plant *Abies alba* is that it was, or could have been, naturally moving towards Norway in the Subboreal period about 5000 years ago. By then, *Abies alba* co-occurred with *Picea abies* (L.) H. Karst. in the eastern Alps and had completed its colonisation of the central European mountains. In some places, it even surpassed its present natural distribution (Sauer 1988, 153). In the same period, Neolithic pastoral and agricultural people started to arrive in northern Europe, which probably affected and delimited the further northward migration of *Abies alba* (Sauer 1988, 155). Anthropogenic plant introduction may hence contribute to a species´ colonisation of areas where it could have occurred naturally. This view challenges the categorisation of *Abies alba* as an alien plant species, and this may also be the case for many other introduced plant species in Norway.

Neighbouring research, knowledge status and gap

With an emphasis on introduced plants, this section gives an overview of closely related research in Norway and internationally. For this purpose, different disciplines in social sciences, humanities and natural science were approached, with a focus on garden history, nature management and invasion biology. Starting with a literary retrospective of plant introduction in Norway, this reflects the rising interest for botany and garden art and the people's relation to these areas from the mid-1700s onward. Further, national and international contributions related to the use and perception of introduced plants are discussed, including the use of multidisciplinary approaches.

Literary retrospective

A historical view on plant introductions between 1750 and 1900 in Norway reveals that there are a few pioneers in Norwegian literature that have reflected on the meaning of introduced plants and their contribution to humankind. Starting in the late 18th century, Christoffer Hammer (1720–1804) was among the earliest authors in Norway dedicated to botany and gardening and published several works in these two fields. He involved both native and introduced plants in his writings about how

to cultivate plants for household and ornamental uses; his descriptions also involved curiosa about the plants' origins and economic importance (see e.g. Hammer 1773; Hammer 1794).

Contemporary with Hammer was Claus Fasting (1746–1791), who wrote about cultivated plants and their cultural history (see e.g. Fasting 1781; Fasting 1791a; Fasting 1791b). Other contemporaries were Jacob Nicolaj Wilse (1735–1801) and Niels Knag Jæger (1706–1780). Wilse, with a botanic interest, had strong opinions concerning the use of introduced plant materials (see e.g. Wilse 1777; Wilse 1790), and Jæger contributed with a pamphlet in 1778, where he distinguished the wild growing native from the introduced trees in the Bergen region, southwest Norway (see e.g. Moe 2004).

In the 19th century, several works about introduced plants were written and published by the botany professor Fredrik Christian Schübeler (1815–1892). He was interested in gardening and the people's ability to provide themselves with food from kitchen gardens (see e.g. Schübeler 1850; Schübeler 1856; Schübeler 1865). With an extensive account of all plants that occur in Norway, his plant descriptions involved natural distributions, time of introduction and where each plant species occurs in the wild and as cultivated. His studies included orographic observations of the arrival of migrating birds and flowering seasons (see e.g. Schübeler 1886; Schübeler 1888). In addition to the scientific descriptions, his publications gave accounts of the climatic zones in Norway. All parts of the country are described thoroughly, including geographical and meteorological observations, complemented by descriptions of his planting experiments using cultivated plants (see e.g. Schübeler 1857; Schübeler 1862a; Schübeler 1862b; Schübeler 1875; Schübeler 1879).

The art historian Carl W. Schnitler (1879–1926) was the first in Norway to publish an extensive book series about garden art history and the design of Norwegian gardens, which included descriptions of ornamental plants and their importance in different garden designs (see e.g. Schnitler 1916a; Schnitler 1916b). Schnitler also described how some people expressed themselves regarding their experience with new plants, but he did not analyse this further.

Another important contributor to Norwegian garden history is Torfinn Skard (1891–1970). He gave an extensive insight into the development of gardening, garden art, plant import and the plant market in Norway, covering the time from the 9th century to the 1950s (see e.g. Skard 1963). Skard placed particular emphasis on the plant material and touched the importance of introduced plants in society, regarding culture and economy. Even though he reflected on the growing interest in introduced plants, he did not analyse people's perceptions nor how they expressed themselves regarding the use of plants.

Introduced plants as common denominators

When it comes to research with focus on introduced plants in Norway, the use of plants in the past has been approached in different contexts for different time epochs. The first part of this literary review is based on other historical studies related to the use of introduced plants. In regard to the 19th century, it appears that several studies have particularly highlighted the plants' functions as design elements, but sparsely reflected on different methodical approaches.

With garden art history in Norway as a starting point, the function of introduced plants as ornaments has been repeatedly reflected on as something people wanted, i.e. exotic elements in 1800s parks and gardens, and the garden and park design has been the central focus (see e.g. Bruun 1987; Bjerke 2002; Bruun 2007; Fredriksen 2012). With light on gardens in southeast Norway, Saxhaug (1989) reflected on the assortment of plants that were used as ornaments in gardens and available for sale from 1870 to 1920. Bjerke (2002) explored which conditions and ideals in society marked and contributed to the development of farm gardens from the 18th to the 20th century. In these studies on the practical use of plants as a part of a specific design, the approaches has in general been limited to one discipline.

With plant import as a focal point, Dietze (2007) investigated the Norwegian bourgeoisie's (middleclass) relation to garden art in the period from 1750 to 1850. Similar to previous studies, Dietze reflected on the importance of exotic plants, but she also further discussed the attitude change towards the use of introduced exotics in the concerned time epoch. She reflected on movements in society as a driving force behind plant introduction and how this was expressed through the use of plants. This was partly illustrated by presenting different perceptions of gardens with exotic plants, but she left it to future research to further explore the terms that addressed these plants.

By exploring the modern functionalistic garden design in the 1930s, Apall-Olsen (2007) shed light on how the design reflected the garden architects' ideologies of that time and mentioned that different opinions occurred regarding the use of introduced plants.

Regarding the connection between people and garden plants, Marstein (2008) explored what plants mean for people, involving plant species and cultivars that were common as ornaments before 1960, which include many species introduced in the 1800s. Based on interviews, Marstein discusses the values connected to the plant material and reflects on how some of the plants once represented the modern, exotic and new enlightenment.

The following part of this chapter reviews and discusses studies more related to current situations with introduced plants. Starting with a contribution from social science regarding terms and how these are applied on plants, Qvenild (2013) researched how plants are perceived presently and categorised as alien, invasive and native, respectively, at individual, professional and political levels. She demonstrates how private gardeners, professionals and politicians perceive and express alienness, invasiveness and nativeness. In a Norwegian context, regarding plants as being alien and native, she stresses that research on human perceptions, experiences and encounters is largely missing and that nobody had previously dealt with peoples' perceiving and categorising of plants in Norway (see e.g. Qvenild 2013, 30).

Considering the time of the plant introductions, the approach of introduced species as a research field is a relatively recent global phenomenon. It appears that the interest in issues concerning introduced species has lately grown in almost all related disciplines. The historian Borowy (2011, 153–154) argued that in studies of introduced species, the involvement of human agency and people's perceptions have seemingly not been of equal importance as the understanding of a species' behaviour, adaptation and ability to establish in new environments and the negative effects this may have.

Regarding the use of plants, movements in society related to plant introduction have recently started to attract more attention. With reflections from historical and present events and challenges, new contributions are made by both natural and social scientists regarding research on introduced plants. One attempt is to explore people's confused understanding of non-indigenous species and the harm they cause (see e.g. Lodge & Shrader-Frechette 2003).

The emerging concepts of alien and non-native species as something negative has recently become a more diligently debated issue. In studies of introduced plants that have spread from gardens in Norway, Handeland (1990) involved reflections on emotions that made people introduce certain plants and highlighted the actions that fuelled plantings in some areas of Norway. Regarding the values connected to plants, Handeland's study is interesting as it reflects how plants brought from abroad have become a problem and require adequate management. Since the late 1990s, introduced plants have become more frequently approached as problematic alien species in terms of their introduction, naturalising and spreading in Norwegian natural environments (see e.g. Fremstad and Elven 1997; Ouren 2008; Sandvik et al. 2013).

With arguments that the rise and development of the concept of alien species is a modern idea, Smout (2011) has researched this issue in Britain from a historical perspective (see. e.g. Smout

2011). Further, by investigating people's perceptions of introduced plants, Selge et al. (2011) have revealed how non-nativeness is understood in various ways by the general public and by professional ecologists (see e.g. Selge et al. 2011). Similar studies have been performed on the public perception of species invasiveness in Mediterranean Europe (see. e.g. Gherardi 2011) and of people's concern regarding invasive plants in tropical Africa (see e.g. Binggeli 2011). Studies in the United States have reflected on events that led to the rise of modern invasion biology, which in turn has contributed to negative attitudes towards introduced species, depending on their ecological roles (see e.g. Simberloff 2011).

Even terms that are used to address introduced plants have been questioned. Rotherham and Lambert (2011, 4) reflect on the use of terms such as exotic, alien and invasive plants and how the lack of precise definitions challenges people's understanding and interpretations of native and non-native species and their occurrence.

In addition to people's perceptions of introduced plants, some studies have reflected on the actual behaviour that caused the plant introductions and the problems that followed. With Britain as example, Rotherham (2011, 233–247) shed light on the cultural role of humans in the spreading of introduced plants. This social science approach involved reflections on how positive and negative perceptions have had ecological, economic and social consequences from the early 1800s until present. Another related historical study focused on the importance of European acclimatisation associations in the 19th century and how this contributed to an increased use of introduced plants (see e.g. Borowy 2011).

Regarding the demand for introduced plants in the 19th century and how the plant use came to affect society, Rotherham's (2011) approach slightly relates to the central time epoch researched in this thesis. With emphasis on the use of ornamental plants in Sweden, the peoples' relation to introduced plants has been reflected on as an important part of the public park design in the 1800s (see e.g. Nolin 1999). Another related attempt involved the public perception of a Swedish manor and its plant contents and forces that fuelled the actions which contributed to create the manor's park and gardens in the period from 1820 to 1925 (see e.g. Tandre 2008).

The management of introduced plants and their invasiveness are further issues generally approached in natural science. Here, it is worth mentioning Lundberg (2010), who highlighted the problematic differences between nature managers' judgment of invasive species by focusing on conflicts between their perception of alien species and these species' actual roles and long-term behaviour (see e.g. Lundberg 2010). Another relevant study focused on strategies to manage

introduced plants that are both economically important and harmful to biodiversity, exemplified with *Acacia* in South Africa (see e.g. van Wilgen et al. 2011).

The need for a multidisciplinary approach

Even though research on introduced plants is not a new field, the emphasis has mostly put on the problems caused by introduced plant species (Borowy 2011, 153–154). With a focus on the nature of introduced species and their spreading behaviour, research has, in the context of environmental management, largely been dominated by natural science (Sharp et al. 2011, 2098; Qvenild 2013, 29). Turning the focus on the use of plants introduced by humans, contributions from social sciences and humanities are required. As reflected on above, the use of introduced plants is largely a cultural historical matter. Research related to the use of plants has usually involved the two disciplines history and botany; where history represents the people's behaviour and cultural relations to the plants, whereas botany is the discipline directly linked to the plant material, involving its natural origin, ecology and scientific descriptions. One Norwegian example using this two-disciplinary approach is provided by Marstein (2008, 13) when exploring common plants that occur in old gardens. Driven by the plants´ introduction history, her approach was a way to investigate which sources reveal knowledge about the history of old garden plants in Norway. According to her, it can be challenging to find sources about plants that no longer exist as living specimens (Marstein 2008, 5, 93). This relates to my research as it also involves history and how methods from more than one research discipline may help me to generate new knowledge when historical sources are limited, hard to access or even completely lacking.

On the interplay between natural and social sciences and humanities, genetics is increasingly involved in research on organisms dispersed both naturally and by humans. It is an evolving source to estimate the genetic relatedness between individuals of unknown origin (Kalinowksi et al. 2006, 576), and to identify species introduced in the past (Witcher 2013, 20). As genetic relationships between plants can be linked to the anthropogenic dispersal of them, genetic data can indicate, with documentations of possible relationships between people and localities, where plants were introduced.

With emphasis on research on people's involvement in plant introduction, working with multiple disciplines is not a new way to generate knowledge. In garden art history, which is related to plant introduction, multidisciplinary approaches are necessary. In the last 20 years, this has involved methods and techniques that generally appear in natural sciences (Moe et al. 2006, 221).

To research a historical park, for instance, the four disciplines history, archaeology, botany and construction engineering are combined to obtain an overall picture and to include all values connected to such cultural heritage (Dietze-Schirdewahn 2013, 5). Another example of a multidisciplinary study on plants combines history, botany and geography to carry out a study on the establishment and spread of alien plant species in Poland (see e.g. Tokarska-Guzik 2005).

The involvement of new research techniques has provided significant amounts of new data (van Etten and Hijmans 2010, 1). Combining DNA analysis and historical sources in research on the distribution of introduced plants is a well-established method. In Norway, Salvesen and Kanz (2009) and Salvesen et al. (2009) combined history, botany and genetics in studies of historical cultivars of Boxwood (*Buxus sempervirens* L. and *Buxus microphylla* var. *japonica* (Müll. Arg.) Rehder & E.H. Wilson) in historic gardens. Another study in the context of plant introduction was carried out by Besnard et al. (2007), who combined historical records and molecular genetic data to investigate the origins and mutual relationships of invasive introduced olive populations.

Even though not relevant for the scope of my study, another multidisciplinary example interplaying between natural and social sciences and the humanities is classical archaeology, regarding the involvement of DNA and pollen analysis. The latter, as an important contribution to define the former vegetation, age and spreading of plant species, depends on the representation of the produced pollen spectra (Grüger 2013, 361, 385).

As a case plant, the main plant material represented in this thesis is *Abies alba*, which is well represented in research on genetic diversity and variation (see e.g. Lewandowski et al. 2001; Sagnard et al. 2002; Korshikov et al. 2004; Dering et al. 2014; Masternak et al. 2015), population genetics (see e.g. Ballian et al. 2012), conservation genetics (see e.g. Piovani et al. 2010), the genetic exchange between divergent lineages (see e.g. Gömöry et al. 2011) and seed dispersal (see e.g. Cremer et al. 2012). These studies focus on wild and naturalised trees, and *Abies alba* appears less researched when representing individual introduced trees, such as park trees. However, multidisciplinary methods are more represented. For example in a study of tree-migration rates of *Abies alba*, Cheddadi et al. (2014) used a multidisciplinary approach by involving genetics, geography and pollen analysis techniques.

To summarise the research status regarding the use of introduced plants, it emerges that multidisciplinary approaches are sparsely represented in Norway. Former studies on introduced plants have, in general, been approached as either a natural or social scientific research target. Until recently, few studies have involved more than two disciplines from both social and natural sciences.

Here, social science and the humanities are represented through the use of introduced plants, past and present, and natural science is represented through the plants' natural origin, ecology, adaptation to and dispersal in new environments. Among a wide range of studies, either history and botany or history and genetics were combined. However, it is crucial to involve all three disciplines to explore methods which have been seldom combined before; such an approach would generate new knowledge about plant introduction history and provide new insights into the management of introduced plants as cultural heritage.

Elaboration of the research theme

Aim and research topic

When introduced by humans, plants become parts of ecosystems and habitats dependent on human impact and can, over time, function as historical objects. In cases when cultivated plants manage to spread and establish on their own in nature, their presence can turn into an issue that attracts interest in both cultural history and nature management. This challenges the methodical approach to investigate the values that introduced plants represent. This multidisciplinary approach enables me to also reflect on the actual combination of different methods in the research on introduced plants in general. The aim of this thesis is to approach introduced plants as cultural heritage by combining methods from history, botany and genetics.

The selection of the research topic was originally inspired by the time delimitation (year 1800) that defined which plant species are treated as alien in Norway. In the context of the *Norwegian Black List 2012* and the new legislation established in 2015 to regulate the use of introduced plants, the thesis touches the perception of plants in society by focusing on the period from 1750 to 1900 in Norway (**paper I**), which was a period when several blacklisted and regulated plant species were introduced into the country.

Botany is involved through a study of how an introduced tree species is valued as a heritage tree in a protected landscape, with special focus on invasiveness, cultural values and management (**paper II**). As presented above, *Abies alba* was selected as an appropriate case plant, which will be explained further in Chapter 3. Secondly, the same case plant inspired me to reflect upon its introduction and distribution history in the 1800s, which also relates to the development in Norwegian society regarding the use of introduced plants. To study introduction history, I wanted to try methods related to studies of genetic relatedness and to combine such a methodical approach in genetics with information from historical literary sources (**paper III**).

Research questions

Based on the research topic presented above, this thesis seeks to frame the following three issues:

1. How were introduced plants described and reflected on in Norwegian literature from 1750 to 1900?

2. How should we deal with the management of a blacklisted heritage tree in a protected landscape, with *Abies alba* as a case species?

3. How can genetics help to generate new knowledge about plant introduction history, using *Abies alba* as a case species?

Based on these research questions, the issues addressed in the papers emerged and developed into three different studies, all approaching introduced plants from different disciplinary angles.

In **paper I**, the purpose was to investigate "how attitudes have changed towards plants introduced in the years 1750–1900" (Ridbäck and Dietze-Schirdewahn 2017, 472). The attitudes were addressed in this study by focusing on garden owners as customers at the plant market, plant nurseries as the suppliers of plant materials and gardening professionals represented by middleclass authors that practiced gardening in addition to writing. The author's experiences were analysed from published books on the topic, which constituted the main literary and historical sources. Also, terms addressing introduced plants were analysed.

With *Abies alba* as a case species, the aim of **paper II** was "to investigate how such an introduced tree is valued as a heritage tree in a protected biocultural landscape, with focus on its cultural historical background, ability to invade and management of the area" (Ridbäck et al. manuscript (a), 2). The study addresses a blacklisted heritage tree that constitutes both cultural heritage and a potential threat to natural values, i.e. plant diversity and unique sensitive habitats. The interesting challenge is how to give historical, cultural and natural values equal attention in a management strategy that involves introduced trees.

In **paper III**, the aim was to "determine the genetic relatedness between old specimens of *Abies alba* to provide new insights on the anthropogenic distribution routes of this species" (Ridbäck et al. manuscript (b), 4). With a focus on the use and distribution of *Abies alba* introduced in the late 1800s, the approach was to combine historical records and genetic data to obtain better and more informative results.

Limitations

A broad multidisciplinary approach limits how deep one can dive into each discipline. Here, time is an important and major limitation. Initially, at the start of such a project, considerable time is required to become familiar with the concerned disciplines and the research methods one aims to

apply (Pooley et al. 2014, 25). Another challenge is represented by mismatching timescales and time constraints, as each discipline requires its particular time for literary reviews and data collection (Drew and Henne 2006, 2). It is hence hard to know in advance how much time is needed for each methodical approach, and it is challenging to find a balance between a broad approach and a narrowed research theme.

Information based on historical records is limited to published and printed material in libraries and archives. In the part where I reflect upon the perception of plants in society (**paper I**), the intention was to provide an overall insight from a selected part of society, i.e. the role of the middleclass regarding the development of plant introduction and the demand for introduced plants in Norway. In this context, the middleclass is represented by academics, civil servants, the clergy and merchants in the period from 1750 to 1900.

In the parts where *Abies alba* is used as a case species, the research in **paper II** was limited to one protected landscape, in which the spreading of *Abies alba* was investigated through a field inventory. The selected study area was particularly interesting as there is only one mature specimen of *Abies alba* left in the whole area, i.e. an old individual tree planted in the late 1800s, which allowed an overall analysis of the spreading of this species in an area that is under continuous maintenance. By limiting the extent of this part to a single study area, it also functioned as a pilot study to explore how professionals from different disciplines can be involved in a management context that involves introduced plants.

The fieldwork for **paper III** allowed me to involve more localities, represented by five areas in central coastal Norway in and near Trondheim. One locality in southeast Norway, outside Ås, was also included in the study. Pivotal for the selection of the localities was the occurrence of old *Abies alba* specimens planted in the late 1800s. Old plantings of *Abies alba* as ornamental and forestry trees are particularly represented in Trondheim and the surrounding countryside, which is why this region was an important area for the purpose of this study. Laboratory work was another challenging and time-consuming part of the working process, where full genomic DNA of the sampled trees was extracted and analysed. Due to complications with the DNA extractions, the number of sampled *Abies alba* was reduced to eight.

Initially, I had planned to involve more introduced tree species in the case studies of this thesis. However, by narrowing the number down to one, it was possible to go deeper into the introduction history of *Abies alba* and its different values when represented as single heritage trees and an invasive species.

Thesis structure

The following chapters describe the theoretical and methodical approaches applied in this thesis. Further, the results of the papers are presented, followed by a discussion of the thesis results and contribution. Chapter 1 has introduced the aim and research theme, presented a background of this research field, the knowledge status and gap, and elaborated the research topic and limitations. Chapter 2 introduces the theoretical framework, while Chapter 3 describes the research design and the methodical approaches. Chapter 4 presents the results based on the respective papers, followed by discussions in Chapter 5. The findings and contributions of this thesis are summarised in Chapter 6, followed by the final conclusions of this work.

2. THEORETICAL APPROACH

The definition of a multidisciplinary project is that it "involves different academic disciplines researching a single problem or theme, but working in parallel without integration" (Pooley et al. 2014, 23). 'Introduced plants' as a research theme connects the different disciplines in this thesis to a common ground. Even though each discipline generally approaches a problem and deals with it through theory and methods that are well-rooted and specific for each field, this thesis tries to integrate the disciplines through a multi-methodical approach. An interdisciplinary approach differs from a multidisciplinary by integrating the involved disciplines, making them to 'cross disciplinary boundaries' (Pooley et al. 2014, 23).

The present occurrence of introduced plants in Norwegian society is a result of events that took place in the past, depending on how people perceived plants and interacted with them. The first paper addresses the way in which the attitudes shifted towards introduced plants in the society of 1750–1900, which required a theoretical approach related to phenomena which caused this attitude change. For this reason, in the analysis of attitude change, the social impact theory by Bibb Latané (1981) was applied. Emphasis was placed on how middleclass authors (i.e. academics, civil servants, merchants and the clergy) perceived introduced plants, based on their personal narratives and essays in published sources. From a theoretical perspective of social impact, this chapter explains how to define and recognise attitudes.

As this thesis involves the analysis of historical literary sources, I found that hermeneutics was another appropriate analytical approach. This was particularly relevant for the first paper, when interpreting authors regarding their perception of introduced plants. Further in this chapter, I will describe what hermeneutics is and how it is applied.

In brief, this chapter of the thesis outlines the theoretical insights that have been of importance for the research design. First, terms and concepts that are relevant for this purpose and appear in the text are presented. Subsequently, the two following sections will describe the social impact theory and philosophical hermeneutics, respectively, which I have briefly introduced.

Terms and concepts

Concepts are tools we use when we think. By learning how people use their concepts, one may be able to understand why people think and act as they do. As concepts and their applications are in constant change, so is the research on them (Oostra 2006, 6). In this thesis, concepts are reflected upon as terms used to express or describe different categories of plants. This section is an introduction to all terms appearing in the text, primarily regarding introduced plants. Some descriptions include reflections on the term's linguistic origin and meaning in this context.

Introduced plants

Generally, the term 'introduced' is associated with "deliberate actions", regarding species introduced intentionally for a purpose (Gederaas et al. 2012, 11). Also referred to as 'foreign' or 'alien species', "introduced species are species that have spread to new areas because of human activity and that are able to get established in the new areas" (Hjermann 2009, snl.no). 'Introduced plants' was seemingly used in preference to other terms to address new plants brought to Norway in the 1800s (see e.g. Schübeler 1886, 587).

In this thesis, I selected the term 'Introduced plants' as a neutral term to represent any introduced plant species.

Exotic plants

The term 'exotic plants' is widely used among authors. However, in some contexts, this term means something slightly different than just any foreign plant species.

Over time, foreign words acquire their own meanings and unique associations. When it comes to the term 'exotic', in modern Norwegian, there is a particular association with southern latitudes, "belonging to warmer, especially tropical parts of the Earth" (*Norsk riksmålsordbok* 1937–1957). The Swedish *Nationalencyklopedin* also confirms that exotic "has to do with far away (tropical) countries" (NE 2014), while the *Oxford English Dictionary* (2015) defines exotic nouns as "objects considered interesting because they are out of the ordinary, especially because they originated in a distant foreign country".

In the 18th century, when Norway still belonged to Denmark, Danish was generally the main language used by Norwegian researchers and scientists. Little by little, the term 'exotic' started to appear in Danish literature. Though probably lent from English, the term appeared more as a Latin

word in written Danish, i.e. "*Plantae exotica"* (Hammer 1773, 150). In a dictionary from 1851, 'exotic' was particularly related to plants and shortly explained as "foreign" ("*udenlandsk*"; Hansen, 1851, 106). About 30 years later, the German word *Exotisch* was translated to "exotic, foreign" in a German–Danish–Norwegian dictionary (*"exotisk, udenlandsk"*; Kaper, 1885, 194). It seems that the relation between exotic plants and the Tropics was established towards the end of the 19th century, when 'exotic' was defined as "foreign, from warmer countries" ("*udenlandsk, fra varme land*") in the 1891 book *Norwegian Pocket-conversations* (*Norsk lomme-konversations lexicon*, Konow, 1891, 260).

However, in the Great dictionary of Danish language (*Ordbog over det Danske Sprog*, 1918-1956), with the most extensive descriptions in older Danish, one finds neither *exotic* nor *exotica*. It seems that it was not until a latter supplementary volume (1992–2005) that the term 'exotic' appeared again, matching tropical associations as described above.

In this thesis, the term 'exotic plants' is sparsely used. When appearing in the text, it refers to introduced plants that, in addition to being recently discovered species from abroad, were something out of the ordinary, as exciting and curious rarities worth admiring and showing.

Alien plants

Based on the criteria by Gederaas et al. (2012), in Norway, 1,719 vascular plant species are categorised as alien and constitute the largest group of alien organisms in the country (Gederaas et al. 2012, 85). Regulations on the use of 'alien plants' and the definition of them in documents such as the Norwegian blacklist are national discussions, as some plant species are blacklisted only in Norway and not in other countries.

"The more recently the species has been introduced, the more recognisable that species is as alien" (Gherardi 2011, 195). 'Alien plants' (*fremmede planter*) is as a rather modern term, at least for Norway. *Alien* in its own context might appear strange as an adjective for an introduced plant species and might turn one's thoughts to the outer space. In the *Encyclopædia Britannica*, an alien organism is defined as an 'extraterrestrial being' and relates to 'life that may exist or may have existed in the universe outside of Earth' (Encyclopædia Britannica 2017, academic.eb.com). The etymology of alien as an adjective on its own originates in the Latin terms *alienus* and *alienum*, the former a noun that meant 'foreigner, outsider, stranger to the family' and the latter referring to another's property/land/possessions (Whitaker 2007, archives.nd.edu). This seems related to the noun *alius*, which also meant 'a stranger, foreigner' and relates to the adverb *alias*, which refers to

'another, other and different'. As early as in the mid-15th century, the term 'alien' was used to describe something "residing in a country not of one's birth". The modern meaning that relates to 'extraterrestrial' was first recorded 1920 as "not of this Earth" (Harper 2017, etymonline.com). Even though it expresses a similar meaning as the term 'exotic plant', the term 'alien' seems a little more direct when addressing plants as not belonging to a particular area.

The term 'alien species' was presented in the *2007 Norwegian Black List – Ecological Risk Analysis of Alien Species* (Gederaas et al. 2007, 3, 16), while 'alien organisms' was mentioned in the *Nature Diversity Act 2009* (Government.no 2009, Section 3e). In *Alien species in Norway – with the Norwegian Black List 2012*, alien species are defined in accordance with the International Union for the Conservation of Nature (IUCN; Invasive Species Specialist Group 2000, 5–6[5]):

> "Alien species" (non-native, non-indigenous, foreign, exotic) means a species, subspecies, or lower taxon occurring outside of its natural range (past or present) and dispersal potential (i.e. outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans) and includes any part, gametes or propagule of such species that might survive and subsequently reproduce".

An additional criterion set by Gederaas et al. (2012, 12) is that an alien plant is a plant brought to Norway after the year 1800 or a plant not considered to have naturalised and established reproductive populations until after 1800.

The new legislation from 2015 defines an alien organism as "an organism that does not belong to any species or population which occurs naturally at the locality" ("*fremmed organisme*: en organisme som ikke hører til noen art eller bestand som forekommer naturlig på stedet", Lovdata.no 2015, § 4.c).

In this thesis, which is mainly focused on plants that were brought to Norway by purpose, the term 'alien plants' is avoided. However, when the term 'alien species' occurs in the text, it is in accordance with the definition by Gederaas et al. (2012, 12), including the time delimitation year 1800.

[5] Invasive Species Specialist Group. (2000). *IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species.* The 51ST meeting of the IUCN council, Gland, Switzerland. Accessed 1 August 2016 from https://portals.iucn.org/library/sites/library/files/documents/Rep-2000-052.pdf

Native plants

Gederaas et al. (2012, 12) stated that "all species with established populations in Norway before 1800 are considered as being native". In other words, the opposite of non-native, non-indigenous, foreign, exotic or alien plants.

In the 18th century, it seems as native plants where the ones occurring naturally in Norway, well adapted to the Norwegian climate and natural conditions. In works written by Norwegian authors, it appears as plants were either native (*indenlandske*) or foreign (*udenlandske*), in lack of other descriptive or categorising terms (see e.g. Hammer 1773, 132, 144; Wilse 1790, 230; Fasting 1791a, 84; Schübeler 1888, 551). Its synonym 'indigenous plants' appeared as a common literary term as early as in the 1600s (Cooper 2003, 52).

In this thesis, the terms 'native plants' refers to species that are not established as a result of human activities.

Blacklisted plants

The term 'blacklisted species' in Norway was seemingly established in 2007, aiming at alien species that constitute "the highest ecological impact" (SE/severe impact and HI/high impact) towards native species diversity and habitats (Gederaas et al. 2012, 16).

The present *Norwegian Black List* contains 135 introduced plant species which constitute a high or severe risk for native plants and habitats (Artsdatabanken 2012, 2). The assessments in which species are 'blacklisted' put significant emphasis on the negative ecological impacts on native species and habitats (Gederaas et al. 2012, 16). Hence, the authors did not take into account whether the plants appear in an area under frequent maintenance (such as gardens, parks or other green areas) or in areas under less management and control. Because of the differences in the climate and growing conditions between different parts of Norway, some professionals suggest that there should be regional blacklists of a higher significance than the one covering the entire nation (Marschhäuser 2016, 02 June).

Thirty blacklisted plant species are completely forbidden to import, sell and plant in Norway (Lovdata.no 2015 appendix I). In addition, there is a limited number of blacklisted plant species that require a permission from the Norwegian Environment Agency to be planted (Lovdata.no 2015, § 10). These restrictions, however, mainly concern professionals and not private people and their gardens (Lovdata.no 2015, § 11b).

The term ‘blacklisted plants’ is used in this thesis in accordance with the above-mentioned criteria for blacklisted species.

Heritage trees

Blicharska and Mikusinski (2014, 1561) claim that “trees in general are valuable as objects with symbolic meaning”. Some trees that have occurred for a long time at the same place and reached an honourable age have also become a part of people’s perception of a particular landscape. An old tree’s aesthetical value in the landscape can be reflected in local people’s emotional perceptions, as some people can become ‘personally attached’ to specific trees. Heritage trees are hence trees that are important to people by housing cultural values, as for instance childhood memories or a “sense of place” (Blicharska and Mikusinski 2014, 1561). Any initiative to protect heritage trees aim to “maintain the cultural heritage they embody” (Blicharska and Mikusinski 2014, 1563).

In this thesis, the term ‘heritage trees’ refers to old trees that fulfil a monumental function. A heritage tree can be any old tree, for instance in a forest, on a field or as an ornament in a garden, as long as local people have a relation to or a certain attitude to it.

Nature

Basically, ‘nature’ as a concept appears as something natural and untouched. As described in the encyclopaedia *Store norske leksikon*, nature is the opposite of culture, “in the broadest sense of reality not processed by human, but through organic development” (“*i videste forstand den del av virkeligheten som ikke er bearbeidet av mennesket, men fremkommet ved organisk utvikling*”, Store norske leksikon 2011). How well does this match the explanations in public documents such as the *Norwegian Black List*? The *Nature Diversity Act* frames the background for all regulations of red and black lists and the management and protection issues (Lovdata. no 2009). The definition there includes all “biological, geological and landscape diversity … that is not largely a result of human influence”.

Halvorsen et al. (2009, 1) approach nature as a phenomenon they define as a sort of nature type (*naturtype*). Their definition is in accordance with the *Nature Diversity Act*, i.e. “a homogeneous environment, including all plant and animal life and environmental factors that operate there, or special types of natural features such as ponds, habitat islands in fields or the like, and special types of geological features” (Lovdata.no 2009; Government.no 2009, § 3, j). “

Gederaas et al. (2012, 10) used "Norwegian nature" as a specific term to basically cover all nature in Norway. However, this only involved a selected part of nature, which they defined in accordance with Halvorsen et al. (2009), i.e. nature types. The *Norwegian Red List* used the same definition of nature (Henriksen and Hilmo 2015, 9). Understanding nature types as generally ecological units organically developed, this is close to the encyclopaedic definition above, but also confusing, as the nature types involve areas processed or semi-processed by humans.

In the 18th century, as many new plants started to cross Norwegian borders, some authors reflected on the concept of nature. Regarding gardeners from abroad and plant materials they brought with them to Norway, Wilse (1777, 106) stated: "here they work against nature". This can be interpreted in different ways. One interpretation is that Wilse meant it was unnatural to introduce plants that did not occur naturally in Norway, while he could have also thought that the gardeners literally were faced with challenges when introducing plants in a new environment and climate.

It seems that Wilse's view and understanding of 'nature' was as something that exists on its own, without human impact. This partly matches the present definitions of nature types as being little or not affected at all by human actions. Gederaas et al. (2012, 10) based their impact assessments regarding the effects of alien species entirely upon the ecological impact, which they meant "should not deal with the effects of humans and our activities". Therefore, they excluded areas that are "used specifically for food production or other business ventures such as grain fields, vegetable fields, orchards and coniferous plantations" (Gederaas et al. 2012, 10). This supports a definition of nature as areas occurring without human impact, i.e. not represented by man-made artificial structures.

In this thesis, the term 'nature' represents an environment where plants and animals exist without human management and settle in accordance with their own needs and adaptations.

Cultural landscape

The concept of a 'cultural landscape' started to appear in geographical literature in the late 1800s (Jones and Daugstad 1997, 267). One of the most classic definitions was established by the geographer Carl Sauer in 1925: "The cultural landscape is fashioned from a natural landscape by a culture group. Culture is the agent, the natural arena the medium, the cultural landscape the result" (Sauer (1925) cited in Fowler 2002, 17).

Cultural landscapes are 'part of our collective identity' (UNESCO 2017, whc.unesco.org). In brief, cultural landscapes can be defined as "landscapes that have been affected, influenced or

shaped by human involvement" (The Cultural Landscape Foundation 2016, tclf.org). The most classical or stereotyping cultural landscapes appear to be pastoral and agricultural landscapes (Jones and Daugstad 1997, 270).

A cultural landscape can represent both a historical site and any landscape that is still under the impact of humans, even if the activities that originally formed the landscape have ceased. Fowler (2013, 4) presents three different categories of cultural landscapes from a World Heritage perspective, of which the second category, 'organically evolved landscape', is defined as follows:

> (a.) a relict (or fossil) landscape "in which an evolutionary process came to an end at some time in the past, either abruptly or over a period. Its significant distinguishing features are, however, still visible in material form".
>
> (b.) a continuing landscape "which retains an active social role in contemporary society closely associated with the traditional way of life, and in which the evolutionary process is still in progress. At the same time, it exhibits significant material evidence of its evolution over time".

These definitions can be exemplified with the cultural landscape (Austråttlunden) approached in this thesis, where certain activities that affected and shaped the landscape in the past have stopped and now need to be continued in order to manage and conserve a unique historical landscape character. The present cultural use is also represented by the people's relation to and perceiving of the landscape, in addition to their concrete use of the area.

In this thesis, the term 'cultural landscape' represents a landscape that has been marked by human activity over a long time and is still impacted by such activities. This also includes the meaning of the landscape, in its present condition, for the cultural identity of the local people.

Cultural history

As a term, 'history' on its own refers to the discipline characterised by the generating of dependable knowledge about the past. Leopold von Ranke (1790–1886) is a person closely associated with modern historiographic work and played a significant role in the establishment of history as a discipline on its own (Moses & Knutsen 2012, 121). 'Cultural history' originates in Germany as *Kulturgeschichte* in the late 18th century, when it was applied in historical studies of human culture (Burke 2008, 6). It was not until the 1960s that cultural history started to appear in the academic world as a discipline separated from general history, leaning towards anthropology to particularly study human cultural development (Burke 2008, 40–43)

When addressed in this thesis, 'cultural history' *and* 'cultural historical' emphasise actions, objects and values that depend on people's behaviours, ideas and emotions in the past.

Social impact theory

"One can usefully think of social impact as being the result of social forces" (Latané 1981, 343). Individuals and groups that hold a particular attitude can influence others directly and indirectly through communication and hence affect people to develop new attitudes (Gordon 2016, academic.eb.com). Bibb Latané (1937–) offers a general theory of social impact and uses the term 'social impact' when referring to effects by which individuals may affect one another in different ways. "We are influenced by the actions of others, entertained by their performances, and sometimes persuaded by their arguments … we are also comforted by the support of others" (Latané 1981, 343). Nowak et al. (1990, 363) define social impact as "any influence on individual feelings, thoughts, or behaviour that is exerted by the real, implied, or imagined presence or actions of others". Individuals are targets exposed to social sources that influence them. The intensity of which a source impacts a target is determined by, among others, its socioeconomic status and its relationship with the target (Latané 1981, 344). One can associate this to the social networks of the middleclass in the late 18th century, where the botanical interest in exotic plants, and particularly the achievement of a certain status, knowledge and affluence, seemed to fuel positive attitudes regarding the use of introduced plants (Dietze 2007, 132.).

What is an attitude?

In the *Encyclopædia Britannica* (2016, academic.eb.com) it is stated that an 'attitude' is a cognition, "often with some degree of aversion [negative] or attraction (emotional valence) [positive], that reflects the classification and evaluation of objects and events". This is a social psychological description, related to the behaviour of individuals. Nowak et al. (1990, 365) argued that "this attribute can be used to classify the population into two subgroups holding different opinions". When an individual holds an attitudinal position or opinion, the person is either for or against something (Nowak et al. 1990, 365). Logically, attitudes are hypothetical constructs and not objectively observable. One can judge the quality of attitudes by observing and assessing the value of responses to something (Encyclopædia Britannica 2016, academic.eb.com).

Philosophical hermeneutics

According to Wilhelm Dilthey (1833–1911), one applies hermeneutics to understand an author better than the author understands himself (Ricœur 1999, 144). Dilthey expressed that "to understand an action or an argument, it is necessary to put oneself in the agent's (or author's) shoes, relive her experiences and image oneself in her social location as if were" (quoted in Moses & Knutsen 2012, 187). To understand how people understood their own time and expressed themselves, one needs to know the selected sources, their situations and time period, in this case, the late 1700s and the 1800s.

The analytical process when applying hermeneutics[6] is commonly described as 'the hermeneutic circle', which refers to the pending between a source and one's interpretation of the information (Moses & Knutsen 2012, 188). A challenge that Ricœur (1999, 59) reflects upon is how to understand a text from the author's original intension. To understand a text´s point of view, as well as the particular time it was written, a historical event demands to be seen in a certain context (Moses & Knutsen 2012, 187). To relive the particular historical events that one's research concerns, one must seek to be free from own ideas, conceptions and one´s own time period. Reading a text is an experience, and a text comes to life when it rises questions to the reader's knowledge in advance (Wind 1987, 17). A researcher's own prejudices may be distracted from having an objective approach. The hermeneutic philosopher Hans Georg Gadamer (1900–2002) helped me understand my own and other's theories and to recognise my own prejudices. With Dilthey as predecessor, Gadamer sought understanding, meaning and truth from particular contexts and situations and argued that "it is part of our historical finitude that we are aware that others after us will understand in a different way" (Gadamer, quoted in Østnor 2004, 40).

Another challenging part is the language in which authors express themselves (Wind 1987, 80). Language is also part of a historical epoch and a particular tradition. The meaning of a sentence or a word might have had a slightly different meaning then, in a particular historical time, than it

[6] Hermeneutics has its origin in the Greek word *hermeneuein*, meaning to read, interpret and understand (Wind 1987, 6). Historically, theologians were the earliest interpreters to apply hermeneutics in their work. They mastered the privileged art of reading messages from God. The art, labelled 'hermeneutics', literally referred to Hermes, who carried God's messages (Moses & Knutsen 2012, 187). Hermes was a Greek god and the gods' messenger (Wind 1987, 6).

has today. One cannot understand an individual part without understanding the whole context, which in turn means that one can only understand a text through its individual propositions and relations (Moses & Knutsen 2012, 188–189).

3. RESEARCH DESIGN AND METHODS

Research questions	Knowledge gap	Theoretical field	Methods
How were introduced plants described and reflected on in Norwegian literature 1750–1900?	Lack of knowledge of people's perceptions of introduced plants in the 1800s in relation to present attitudes in public documents.	***History:*** - Plant introduction - Social impact theory	• Literature review • Archival printed sources • Analytical approach: philosophical hermeneutics
How to deal with the management of a blacklisted heritage tree in a protected landscape, using *Abies alba* as a case species?	Lack of research on colliding management interests involving blacklisted heritage trees and high ecological values.	***History:*** Plant introduction ***Botany:*** Naturalistic approach from an ontological perspective	• Case study • Literature review: - Management plans - Investigations and reports of biodiversity, flora and vegetation - Public documents on management • Communication with supervisory manager • Fieldwork involving data collection and analysis of invasiveness
How can genetics help to generate new knowledge about plant introduction history, using *Abies alba* as a case species?	Lack of sources on the introduction and distribution of introduced plants in the 1800s.	***History:*** Plant introduction ***Genetics:*** Naturalistic approach from an ontological perspective	• Case study • Literature review of historical printed sources • Fieldwork: genetic study involving the collection of plant material, laboratory work and data analysis

Table 1. Methodologic approach including research questions, knowledge gap and theoretical fields.

The methodology of this thesis involves the three disciplines history, botany and genetics (**Table 1**). As the first research question (**paper I**) involves a historical literature review, I selected a method suitable for historical research, involving collecting and analysing historical literary information. In contrast, the second and third research questions (**paper II** and **paper III**) are the main multidisciplinary challenges, involving both historical literary studies and data collection through

fieldwork in botany and genetics. A strategy to bring through this part of the study needed to be worked out, and the main challenge was to combine historical findings with botanical and genetic studies on introduced plants. I decided to use a case study and to select a 'case plant species' to represent plants introduced in the 1800s. Methodical approaches that are briefly introduced here are explained further in this chapter.

Case study

Moses and Knutsen (2012, 133) define case studies as 'histories with a point', as these are 'cases of something', relevant to solve a specific research problem. This fits the aims of the cases of **papers II** and **III**.

In **paper II**, the case was to investigate how an invasive historical tree, represented by *Abies alba*, is valued in a protected landscape. The case in **paper III** investigates possible distribution routes of *Abies alba* by involving genetic data. *Abies alba* functions as a 'case plant' in both cases.

As a large number of plants were introduced into Norway after 1800, I needed to select a plant species that could represent this plant category. Trees are durable plants; one can find specimens still growing on the same spot several 100 years after they were planted. The most accessible trees in Norway are evergreens, which can contribute with fresh plant material all year round. The final choice was *Abies alba*, which, in addition to being categorised as an alien species, appears on the *Norwegian Black List*. *Abies alba* has the potential to naturalise and invade new areas, albeit with minor ecological impact (Gederaas et al. 2012, 98).

Abies alba represents the link between the historical, botanical and genetic parts of this thesis, as it incorporates the category of introduced plants. It also served as a case plant in **paper II** and **III**; both studies were based on empirical findings through data collecting, which also involved literary and primary sources and fieldwork (including laboratory work). This will be explained further in the sections Botany and Genetics.

Commonly known as European silver fir, *Abies alba*[7] Mill[8]. is a member of the plant family *Pinaceae*, naturally occurring in central European mountainous areas. *Abies alba* had the potential to spread naturally to Scandinavia after the last ice age (Sauer 1988, 153). The most northern natural *Abies alba* forests are presently found in Germany and Poland (Farjon 2014, iucnredlist.org). The species spreads by winged seeds, which are distributed from upright oblong cones at the top of the tree. As a conspicuous morphological characteristic, the needles grow in two directions, i.e. branches with a distinct upper and lower side. On the lower surface of the needles, two white stripes are visible; the needle tips have notches. The needles can be unequal in length (**Fig. 1**).

[7] According to Miller (1759, 29*), the name *Abies* is derived from Greek [*abeo*], meaning 'to extend or advance', which refers to the splitting bark which falls off or can easily be teared off. Another explanation is offered by the Greek words *aei*, which means 'always', and *bios*, which means 'life'. Hence, meaning 'always green' as for evergreen (Anderberg and Anderberg 1999**), and the species epithet *alba* means white (Anderberg and Anderberg 2004***).

[8] There are professionals in botany that consider Linnaeus (L.) as the correct author of *Abies alba* as a species name. When addressing *Abies alba* in this thesis, I refer to the scientific name as published by Miller (Mill.) to avoid confusion. However, I agree that Linnaeus is the author of the genus *Abies* (in accordance with Linnæi, C. 1737, 277, *Flora Lapponica*. Amstelaedami: Apud Salomonem Schouten. Accessed 21 May 2015 at Kew Library, London).

* Miller, P. (1759). *The Gardeners Dictionary*, seventh edition. Available at the British Library (34.i.9.)

**Anderberg, A. and Anderberg, A.-L. (1999). *Abies* Mill.

***Anderberg, A. and Anderberg, A.-L. (2004). Silvergran. Available at *Den virtuella floran*: http://linnaeus.nrm.se/flora/welcome.html

Figure 1. Needles of *Abies alba* Mill. collected in Austråttlunden, Ørland, Sør-Trøndelag, Norway. The needles grow in two directions. Note the white stripes on the lower surface and that each tip has a notch (Photo: Ulrika Ridbäck 2014).

Introduction notes on Abies alba

Among the *Abies* species that represent the genus in Europe[9], *Abies alba* is the most widespread one (Cheddadi et al. 2014, 115). *Abies alba* has been a popular timber tree over the centuries (Farjon 2014, iucnredlist.org) and was one of the earliest introduced tree species for small-scale plantings in Norway (Dahl Kjær et al. 2014, 325). Elieson (1881, 39) expressed that this fir species fulfilled the criteria as a promising forestry tree by being fast-growing and providing excellent wood.

Schübeler (1862, 60) had, through correspondence with the forester Mejdell, learnt that some of the oldest specimens of *Abies alba* had been planted 'the last century' [in the 1700s] outside

[9] In *Species Plantarum* 1753, Carl von Linné merged *Abies* with three other coniferous genera (*Pinus*, *Cedrus* and *Larix*), as he considered them all belonging to one genus and selected *Pinus* as the genus name. This, however, caused confusion among people involved with garden plants. When writing *The Gardeners Dictionary*, Miller therefore decided to keep the genera *Abies* separate under the name it first received by Linné (Miller 1759, 29).

Kongsberg in southeast Norway. This is also confirmed by Elieson (1881, 39), who had observed the oldest specimens of *Abies alba* himself and stated that these had been planted at least 'over 100 years ago', i.e. in the late 1700s. Krag (1880, 31) indicates that *Abies alba* was brought to Norway as early as in the 1730s by the brothers Johann Georg (1699–1776) and Franz Phillip von Langen (1709–1751). The brothers von Langen, who moved to Norway via Denmark, were the ones who founded the old Forestry institute (*Forstvæsenet*) in Kongsberg, southern Norway (Elieson 1881, 36–44). As they were involved in forestry and the introduction of forestry trees, they had introduced *Abies alba* to Denmark already in the early 1700s. It is therefore possible that *Abies alba* specimens were planted shortly afterwards in Kongsberg, which then was an important town for the mining industry and the forestry sector. Johann Georg von Langen was recruited to Norway in 1736, together with his brother Franz Phillip and a company of forestry people from Germany (Westrin 1911, 1139). If the first specimens of *Abies alba* would have been planted in Kongsberg in 1740, those trees would have been able to give rise to several reproductive generations before 1800, dependent on the growing conditions, the number of mature trees and the survival of the seedlings. It should be noted, however, that *Abies alba* is not reproductive until about 20 years of age (Holm Nygaard 2012, 1).

In the late 1700s, influences from the English Landscape style probably contributed to the use of *Abies alba* as exotic garden ornaments. A plant catalogue printed in 1874 is currently the earliest proof of *Abies alba*[10] for sale as an ornamental tree in Norway (Aas Høiere Landbrugsskole 1874, 6). The following year, it was particularly recommended to be used as 'living fence' (*'levende hegn'*), i.e. as hedge around properties, gardens etc. (Aas Høiere Landbrugsskole 1875, 6). *Abies alba* appeared particularly suitable for planting in central western Norway, where Schübeler (1862, 60) observed that it was commonly used as an ornamental plant.

Abies alba has recently been among the most concerning tree species in mountain forest conservation in Europe, as it is a keystone species of many mountain forest ecosystems. Because of intense forestry, over-browsing, drought and poor regeneration, the species is currently threatened at many locations where it naturally occurs, and a further decline of abundance is

[10] In Norway, *Abies alba* has been known under different names, both in binomial Latin and in Norwegian common names. When reading literary sources, this was challenging until the use of former names was figured out. Schübeler (1886, 433) used the Latin name *Abies pectinata* (Lam.) DC., which had replaced the former name *Abies alba* established by Miller (1759, 29). The binomial name *Abies pectinata* remained in Norway until 1928, when *Abies alba* Mill. replaced it permanently (Norges Landbrukshøiskole 1928, 13. *Sorts- og prisliste fra Planteskolen og veksthusene ved Norges Landbrukshøiskole Høsten 1928 og Våren 1929*. Ås Lantbrugshøyskole, Ås).

expected (Ficko et al. 2011, 853). Compared to other coniferous species, *Abies alba* is less tolerant to climatic changes, such as shifting temperature and drought (Postolache et al. 2014, 750–751). While there are efforts to limit the distribution of *Abies alba* in Norway, there are also extensive efforts to conserve forests associated with *Abies alba* in some central European countries, where it is an economically important local species (Ficko et al. 2011, 845).

Historical approach

How people have understood, perceived and interacted with plants in the past is a cultural historical matter. As a discipline, history is located in social sciences and the humanities, separated from the natural historians' studies of the physical or natural world (Pooley et al. 2014, 23). The initial method to answer the first research question was a literature review (**Table 1**), which mainly provides the basis for **paper I**.

'We who write about the past were not there. We can never be certain that we have recaptured it as it really was' (Tuchman 1981, 18). From evidence one can select essential pieces of information. As presented in the previous chapter, hermeneutics was the main analytical tool when interpreting evidence collected from historical and literary sources and helped me to understand and imagine events that occurred in the past.

Information based on literary studies was primarily searched for in the Norwegian National Library (Nasjonalbiblioteket), national archives (Arkivverket) and historic library collections at the Norwegian University of Life sciences. Visits to the British Library and the Kew Library in London were also included. Accessible primary sources were plant catalogues, essays, published works, unpublished manuscripts, newspapers, illustrations and photographs. The historical sources also involved original publications of the first descriptions of the genus *Abies*, fir trees, by Carl von Linné, and later Philip Miller's description and definition of the species[11].

[11] Philip Miller (Mill.) is at present the officially accepted author of the binomial scientific name of *Abies alba**. Gardeners did, according to Miller, find the taxonomic and systematic changes confusing when including or excluding Latin species names in the same or another genus name. When recognising and describing species in garden contexts in the 1700s, several gardeners followed their own method and ignored Linnaeus' new classification. "As they have always been distinguished by all writers in botany by the order of their leaves, and these distinctions are now universally known to all gardeners, we shall choose to continue this method of arranging them under their former genera to avoid confusion" (Miller 1759, 29).
*The Plant List (2013). *Abies alba* Mill. Accessed 25 November 2016 from http://www.theplantlist.org/tpl1.1/record/kew-2609691

The literary sources have contributed with references of primary sources and with general information on the field. To become familiar with the 1800s' garden culture in Norway, it was appropriate to visit a selection of historical gardens and parks, preferably where *Abies alba* was represented. The visual experience also contributed to my understanding of the importance of introduced plants in those recreation areas.

Natural scientific approach

Botany and genetics are traditionally rooted in biology and natural sciences. In a theoretical perspective, the fields of natural sciences are generally a matter of selecting the right methodology to test a hypothesis or a theory. The classical question related to this is "how do we know?", based on the ideology of *Naturalism*, which is traditionally connected to natural sciences as a methodological approach that "seeks to discover and explain patterns that are assumed to exist in nature" (Moses and Knutsen 2012, 7–8). Naturalists rely on observation and direct experience; "something is true when somebody has seen it to be true (and recorded it as such)" (Moses and Knutsen 2012, 8). From an ontological[12] perspective, plants are physical elements contributing to what I experience is the real world. One's observations confirm the existence of plants.

In order to answer a question, theoretical approaches are hence mainly hypotheses to be either validated or falsified. In this section, I will present how each discipline has been approached and applied in this thesis.

[12] Ontology means "the study of being/the basic building blocks of existence" (Moses and Knutsen 2012, 4) and represents the naturalistic idea that the real world exists irrespective of whether humans observe it or not (Moses and Knutsen 2012, 48–49).

Figure 2. The author observing the silver-grey stem of the old *Abies alba* tree in Austråttlunden (Ørland), central coastal Norway (self-portrait by Ulrika Ridbäck 2014).

Botany

The case plant *Abies alba*, here representing plants that were introduced mainly as exotic ornaments in the 19th century, constitutes the main botanic part of this thesis. The second research question (**paper II**), which treats a problematic management issue that involves a blacklisted heritage tree in a protected landscape, was approached by combining literary studies and botanic fieldwork.

In the protected landscape Austråttlunden in central coastal Norway, one could sense a conflict in the conservation of different values. *Abies alba* was selected as a case tree that represents both botanic cultural heritage and a potential invasive plant species (**Fig. 2**). Only one old specimen of *Abies alba* remains in whole Austråttlunden. The botanic approach mainly focused on the management and spreading of *Abies alba*. For this, it was relevant to collect information regarding the management of the protected landscape, with emphasis on practical maintenance actions.

Situated on the peninsula Ørland in the province Sør-Trøndelag, Austråttlunden has been a protected landscape since 1975 and houses several cultural historical objects; it has a high botanic diversity and unique habitats (Holten 2010, 10). The area has been used as recreation area since the 17th century, when a pleasure park with beautiful tree plantings and animals was established there. It was the first park of this kind in Norway (Bruun 2007, 44). Regarding the keeping of animals, the area presumably functioned as a hunting park. In the late 1700s, the historian Schøning (1774, 302) confirmed that it was still a beautiful forest with a diverse tree growth and with the remains of a former animal park.

Austråttlunden is connected to Austrått Manor, about 1 km away, which is an old castle originally built in the 17th century. The area offers interesting insights into the biology of introduced plants and their interaction with and impact on the environment. Presently, there is a diversity of both introduced and native trees. *Abies alba* seemingly occurs as remains from former planting experiments at the Austrått Manor garden and Austråttlunden (Njøs 1963, 28–29). Other introduced coniferous trees in this area are European larch *Larix decidua* Mill. and Norway spruce *Picea abies* (L.) Karst (Gangås 1988, 5).

The literary approach involved studies about Austråttlunden's history and the introduction of *Abies alba*. Historical information was gathered from published sources. Public maps and old photographs were used to a limited extent to locate past and present occurrences of vegetation and *Abies alba*.

Management plans, reports and published inventories were reviewed to obtain an overview of Austråttlunden's management history. The supervisory manager of the area was an oral source regarding the present management situation, and a local representative of the Ørland municipality and Cultural Centre was an oral source regarding the area's cultural history and development.

The fieldwork mainly involved an inventory of *Abies alba* seedlings to map the spreading of this species in the area. The limited sampling was based on the fact that only one mature *Abies alba* tree remained in the area. The documentation of the spreading of *Abies alba* was performed with GPS along transects. The height of all recorded individuals of *Abies alba* (except the parent tree) was measured, and ecological parameters such as distance to the closest tree (any species), estimated light conditions and dominant vegetation were also recorded for each individual of *Abies alba*. The light conditions were recorded in a scale from 1 (very dark) to 5 (very light). The data was then processed in ArcMap 10.3.1. to obtain an overview of the present spreading situation. The invasion ability of *Abies alba* was reflected on in relation to the maintenance run in the area.

Figure 3. Overview of the sampling sites. **A:** Austråttlunden (sample 1); Reins Kloster (sample 2); Rotvoll (sample 3); Elsterparken (sample 4); Skånes (samples 5–7); **B:** Fougnerhaugen (sample 8). The localities are fully described in the thesis appendix (full-length version paper III).

Genetics

As a research discipline, genetics involves the study of heredity and variation of genes (Raven et al. 2003, 184, 242) and explores the relatedness between organisms of the same or of different species. In research on introduced plants, the involvement of genetics is a useful method to track the origin and distribution of a particular species (Raven et al. 2003, 256).

The third research question (**paper III**), which asks how the involvement of genetics can help to generate new knowledge about plant introduction history, was approached through a combination of historical literary studies, fieldwork and laboratory work.

In sources that provide information about the introduction of *Abies alba*, there were indications that the same people had been involved in some of the plantings in central coastal Norway. By involving genetics, I wanted to test if a selection of old trees was closely related, using *Abies alba* as a case species.

Genetics constituted a mayor part of the study to either support or falsify the hypothesis that there were collaborations between landowners to distribute *Abies alba*. The study involved six different localities where *Abies alba* was introduced in the late 1800s and the early 1900s; five localities in Trondheim with surroundings in central coastal Norway and one locality in Ås, southeastern Norway (**Fig. 3**).

Schübeler (1862, 60) indicates that *Abies alba* was planted at many localities in and near Trondheim. A large planting experiment with *Abies alba* took place 1871–1896 in an area called Bymarken, just outside Trondheim (Jansen and Svendsen 1954, 372–373). As this illustrates a demand for particularly *Abies alba* in this period, it makes central coastal Norway an interesting part of the country to study introduction history.

The genetic part involved fieldwork to collect plant material, laboratory work and data analysis. Fresh needles were collected in the field, directly dried in silica gel and then freeze-dried. I also measured tree height and stem circumference. For extraction of the full genomic DNA, all samples of *Abies alba* were ground[13] with a pestle in liquid nitrogen and DNA was extracted using a DNeasy® Plant Mini Kit (Qiagen), following the manufacturer's instructions with minor variations.

In studies of genetic relatedness among plants, a major effort is to deduce accurate and comprehensible relationships among taxa (species). Polymerase chain reaction (PCR) emerged in the early 1990s (Chase et al. 1993) and has since been a frequently used tool to analyse polymorphic loci[14] for phylogenetic plant analysis. However, this method is relatively expensive and time-consuming. Miller et al. (2007) have therefore developed a high-throughput, low-cost method to identify and type numerous RAD (restriction-site associated DNA) markers on microarray genotyping resources.

In the last 10 years, RADseq (restriction-site associated DNA sequencing) has emerged as a cost-effective genotyping method based on sequencing (Ree and Hipp 2015, 196; Andrews et al. 2016, 81). A modification of the RADseq approach, called ddRAD (double-digest RAD; Peterson et al. 2012, e37135), has become widely used for the discovery and genotyping of SNPs (Single

[13] The plant material was processed into smallest possible pieces in order to perform successful DNA extraction. If not well ground, the plant cells will not lyse properly, i.e. break down the cell walls to release the DNA. Needles contain considerable amounts of starch, which challenges this part of the extraction process.
[14] The position of a particular gene or allele in a chromosome.

Nucleotide Polymorphisms[15]) and allow investigators to find and score SNPs dispersed randomly across a target genome (Baird et al. 2008, e3376; Davey and Blaxter 2011, 416–417).

After the extractions, the DNA purity of each *Abies alba* sample was determined by agarose gel electrophoresis (**Fig. 6**, Appendix) and UV absorbance (NanoDrop, Thermo Scientific). The DNA concentration was quantified using fluorescence measurement (Qubit®, Invitrogen, Thermo Fisher) (**Table 4**, Appendix).

The high-molecular weight DNA samples were prepared for sequencing in accordance with the ddRAD protocol by Peterson et al. (2012) and sequenced using a MiSeq Sequencer (Illumina) and a 600-Cycle MiSeq Reagent Kit. The final ddRAD library was validated by quantification, using a Qubit® 2.0 Fluorometer and the Qubit® dsDNA BR Assay Kit (Invitrogen™, Thermo Fisher).

The genomic sequence data were then processed using STACKS v1.18 (Catchen et al. 2013) to detect SNPs. Analysis of relatedness and population structure was performed with STRUCTURE software version 2.3.4 (Pritchard et al. 2000; **Figs. 7**, **8** and **9**, Appendix), as described by Kovi et al. (2015, 929). The final SNP genotype data obtained from STACKS was used to derive a genetic distance matrix using GenAlEx software version 6.5 (Peakall and Smouse 2012). Based on the genetic distance matrix, a phylogenetic tree was calculated using BIONJ (Gascuel 1997). For differentiation in trees by the GenAlEx, principal coordinate analysis (PCoA) was performed based on a dissimilarity matrix.

Further, ARLEQUIN software version 3.5.1.3 (Excoffier and Lischer 2010) was applied to perform analysis of molecular variance (AMOVA) to estimate the variance among genotypes between the sampled trees and to calculate expected heterozygosity (H_e).

[15] Single nucleotide polymorphisms (frequently called SNPs, pronounced “snips”) are the most abundant class of markers in genomic DNA (Jehan and Lakhanpaul 2006, 437*). In brief, each SNP represents a difference in a DNA building block called nucleotide (also known as one of the four different nitrogenous bases (T, C, A, G) that make up the DNA. A SNP marker is hence a variation where a nitrogenous base is replaced by another in a certain stretch of DNA.

*Jehan, T. and Lakhanpaul, S. (2006). Single nucleotide polymorphism (SNP)–Methods and applications in plant genetics: A review. *Indian Journal of Biotechnology*, 5 (4): 435–459.

4. Results and Presentation of Papers

This chapter presents the research findings of the respective papers.

Paper I

Ridbäck, U., Dietze-Schirdewahn, A. (2017). Once in demand, now unwanted: reflections on changed attitudes towards plants introduced to Norway 1750–1900. *Landscape Research* 42 (5): 471–481.

Aim

The aim of this paper is to show how attitudes have changed towards plants introduced to Norway in the years 1750–1900.

Methods

This study was based on historical literature related to gardens and gardening in Norway and on archival printed sources such as personal essays and plant catalogues. In the literature, one can find attitudes expressed through the use of terms regarding introduced plant materials. In plant catalogues, the assortment of plants for sale indicate a demand for plants, which relates to the customers´ attitudes towards plants. In this study, garden owners represented the customers, while plant nurseries represented the suppliers of plants. Gardening professionals dealing with plants were represented by authors that published works based on their gardening experiences and on new species from abroad. By exploring how they perceived and described introduced plants, it might be possible to sense the development of terms as well as the shift in their views upon the plants.

Results

Positive attitudes towards introduced plants were seemingly dominating throughout the 1800s, but there were apparently mixed emotions about introduced plants in the late 18th century. One out of three authors (gardeners) was sceptical. But as time proceeded, even the most sceptic one expressed that there was an entertaining side of having rare and odd introduced plants. This can be interpreted

as a positive change, which increased after the century turn. There were no descriptive terms directly expressing anything negative, but rather intending to illustrate the plants´ origin and appearances.

Back then, the cultivation of introduced plants was challenging. In spite of difficult growing conditions, this challenge was, however, worth taking on. Garden owners achieved status when succeeding in growing their novelties. Another positive perception was based on the fact that plants could help demonstrate the wealth and knowledge of the garden owners. An increased demand for new plants reflected positive attitudes among garden owners. As the assortment increased in plant catalogues towards the end of the 19th century, this reflects how the salesmen tried to meet the growing demand for new plants and particularly to arrange the available plant categories in new ways to help customers find what they were looking for.

An 'exotic plant' was not necessarily simply any plant brought to Norway from abroad, but in particular a rare, unusual and exciting specimen, new to science and often requiring specific care. Most needed to be kept in a greenhouse or a winter garden to survive the Norwegian climate. As a contrast, plants that were introduced during the flowering epoch of the 1800s are at present categorised as 'alien plants'. As a large number of the concerned plant species are also blacklisted, they are commonly regarded as something negative, which seemingly contributes to a negative perception of introduced plants in general.

Discussion

Since policymakers selected the year 1800 as a delimitation in time, to categorise which introduced plants are alien, the consequences may be that an important era of plant importation is in danger of being wiped away. As the results revealed, the attitudes towards introduced plants have certainly experienced a change, reflected in term use and trade. Positive views dominated and increased particularly after 1850, as plant import was no longer limited to private merchants, but also accessible for common people. The term 'exotic plants' had seemingly another meaning in the 18th and 19th centuries than it has today, as it is currently used synonymously with 'alien plants'. As introduced plants are addressed as alien plants in present public documents, there appears to be an increased negative rhetoric use of terms. This in turn may affect the public's perception of introduced plants in a negative way. With respect to the variations in climate and ecology, more research is needed for each introduced species to recognise the actual impact, which is dependent on their ability to spread and survive in different parts of Norway.

Paper II

Ridbäck, U., Vike, E., Dietze-Schirdewahn, A. A battle of values: a case study of a blacklisted heritage tree represented by European silver fir *Abies alba* Mill. in a protected landscape in Norway. *Arboricultural Journal*, manuscript accepted with major revision.

Aim

The aim of this study was to investigate how a blacklisted heritage tree is valued in a protected biocultural landscape, with *Abies alba* as a case species. This involved the cultural historical background and invasiveness of *Abies alba* and the management of the protected area.

Methods

This study was performed in the protected landscape Austråttlunden in central coastal Norway. The area houses a diversity of natural, historical and cultural values. Only one old individual of *Abies alba* remains in the area, as a remnant of a planting experiment in the late 1800s. The study initially applied an ecological approach with focus on the invasiveness *and* management of *Abies alba*. A historical literary approach was applied to include cultural values, landscape history and introduction history of *Abies alba*. Information about the management strategy in Austråttlunden was collected from management plans, reports based on biodiversity mapping and vegetation investigations in Austråttlunden. Present management strategies were identified through personal communication with the supervisory manager. Emphasis was placed on maintenance such as clearing of vegetation and grazing by cattle and sheep. The invasion of *Abies alba* was documented through an inventory of offspring, which were recorded with GPS along 18 transects in a north–south direction. In addition, ecological parameters that affect the survival of seedlings were recorded.

Results

Since 1975, the management of the transect area has primarily focused on protecting nature values such as botanic species richness and to preserve the cultural landscape on which these values depend. Maintenance actions have involved the clearing of vegetation and grazing in the years from 1976 to 1998. Cattle were kept in the area from 1977 to 1987 and were then replaced by sheep in 1988. In the late 1990s, specimens of particularly introduced trees were cleared, including a grove

of *Abies alba*. However, one individual of *Abies alba* was kept in accordance with the recommendations specified in the last management plan.

At present, there is no new management plan for Austråttlunden; the last one has expired in 1998. With directives from the Department of Environmental Protection, there has since been continued keeping of sheep and the clearing of invasive introduced trees, primarily *Abies alba*, Sitka spruce *Picea sitchensis* (Bong) Carrière and Norway maple *Acer platanoides* L. Work on a new management plan was initiated in 2011 by the Department of Environmental Protection, but was paused in 2013 by the municipality.

In an area constituting approximately 13,600 m^2 (2% of Austråttlunden), 114 individuals of *Abies alba* were recorded, including the old parent tree. The majority of the recorded individuals (88%) were less than 15 cm tall. None except the parent tree had reached the reproductive age. Most individuals, irrespective of height, were found within 30 m of the parent tree in half-shade to shady positions. The surrounding forested parts were dominated by downy birch *Betula pubescens* Ehrh., hazel *Corylus avellana* L., Norway spruce *Picea abies* (L.) H. Karst., Scots pine *Pinus sylvestris* L. and great wood-rush *Luzula sylvatica* (Huds.) Gaudin.

Discussion

In spite of having a variety of characteristics that enable successful spreading, such as small windborne seeds, a short juvenile period and short intervals between large seed crops, *Abies alba* appears less invasive compared to many other conifer species. The seedlings are sensitive in the first years and generally, only a small number survive. Grazing pressure, high light conditions, a thick ground cover of organic litter and the clearing of vegetation are different factors that limit the survival of *Abies alba* seedlings. It appears that *Abies alba* is an extremely shade-tolerant species, which can survive even when light is reduced by 80–95%. As an invasive tree species, *Abies alba* has less impact when represented by single trees in an open landscape with continued maintenance.

Compared to natural values, historical and cultural values have received less attention in the management of Austråttlunden. The people´s perception of the landscape and the historical trees therein is part of their cultural identity, which has been largely overlooked in management programs. Such an approach would require the use of interdisciplinary methods with the involvement of professionals in different disciplines to safeguard the diversity of natural, historical and cultural values.

Paper III

Ridbäck, U., Kovi, M. R., Hansen, H. H., Rognli, O. A., Dietze-Schirdewahn, A. Past anthropogenic dispersal of introduced European silver fir *Abies alba* Mill. in Norway was revealed by reduced representation sequencing. *Submitted manuscript.*

Aim

The aim was to test a hypothetical distribution route of *Abies alba* in central coastal Norway by combining findings in historical literary records with genetic data.

Methods

This study involved eight individual trees distributed at six localities, of which five were located in central coastal Norway and one in southern Norway. For the DNA analysis, needles of *Abies alba* were collected and dried in silica gel immediately after collection. Additional data included measurements of stem circumference and estimated height of each individual (see also Chapter 3).

In central coastal Norway, all localities where in and near Trondheim. The first area, Austråttlunden (sample 1), is a recreation area situated on the peninsula Ørland. The second area, Reins Kloster (sample 2), is a recreation site located on the remains of a former monastery. The third area, Elsterparken (sample 4), is a forested park situated in the western part of Trondheim. The fourth area, Fjæraskogen (sample 3), is a former park or arboretum situated in the eastern part of Trondheim. The fifth area, Skånes (samples 5–7), is a recreation area in Levanger municipality, northeast of Trondheim. In southern Norway, the sixth locality was Fougnerhaugen (sample 8), an old arboretum located in the southeast of the Ås municipality (see **Fig. 3**).

Information on the cultural history of the selected areas was gathered through literary sources and other printed historical sources. Total genomic DNA (gDNA) was isolated from needles of each of the eight samples, using the DNeasy® Plant Mini Kit (Qiagen), following the manufacturer's instructions with minor variations in order to recover a sufficient amount of genomic DNA. The high-molecular weight DNA samples were prepared for sequencing according to the ddRAD protocol described by Peterson et al. (2012). Sequencing was performed using a MiSeq Sequencer (Illumina) and a 600-Cycle MiSeq Reagent Kit v3. The software STRUCTURE (version 2.3.4 by Pritchard et al. 2000), as described by Kovi et al. (2015, 929), was applied to analyse genetic relatedness and population structure. A genetic distance matrix was derived of the genotype data

using GenAlEx software (version 6.5 by Peakall and Smouse 2012). The package BIONJ (Gascuel 1997) was used to establish a phylogenetic tree based on the genetic distance matrix. A principal coordinate analysis (PCoA) was performed based on a dissimilarity matrix. Analysis of Molecular Variance (AMOVA) was performed with ARLEQUIN software version 3.5.1.3 (Excoffier and Lischer 2010) to estimate the variance among genotypes between the sampled trees and to calculate the expected heterozygosity (H_e).

Results

With respect to stem circumference, height and literary sources, the *Abies alba* individuals 1, 3, 4 and 8 were most likely planted in the late 1800s, whereas individuals 2, 5, 6 and 7 were probably planted later at the turn of the century or in the early 1900s. Findings in historical sources indicate connections between plantings of *Abies alba* in Elsterparken (4), Reins Kloster (2) and Austråttlunden (1). The STRUCTURE (ΔK value = 3) and PCoA analysis sorted the samples into three groups, i.e. 1, 2, 4 and 8; 3 and 6; 5 and 7. Phylogenetic analysis also partitioned the samples into three groups, where 8 was closer related to samples 5 and 7. The STRUCTURE analysis (ΔK value = 4 and higher) also showed other probable relatedness, where 8 appeared unique and distantly related to all the other samples. Population structure was estimated based on 642 SNP markers. When the eight samples were categorised into three populations (i.e. Pop 1 samples 1, 2 and 4, Pop2 samples 3 and 6, and Pop 3 samples 5, 7 and 8), the level of heterozygosity was high, which indicates a high level of outbreeding. The genetic variation was higher between the individuals than between the three groups.

Discussion

Due to the limited time, the historical records were mainly based on printed archival and literary sources. Apart from the localities Elsterparken (4), Reins Kloster (2) and Austråttlunden (1), there were no records regarding plantings at the other localities involved in this study. Both historical sources and the genetic relatedness support that Elsterparken functioned as a distributor of *Abies alba* to Reins Kloster and Austråttlunden. The genetic relatedness between samples from Fjæraskogen (3) and Skånes (6) can help predict how people accessed and shared the plant material in the late 1800s. Fjæraskogen is a former arboretum, and material might have been distributed from there to other localities such as Skånes, where samples 5, 6 and 7 were collected. This hypothesis is slightly supported by the relatedness between samples 3 and 6. Sample 8 from Fougnerhaugen

(southeast Norway) was not expected to be closely related to any sample collected in central coastal Norway. This was also supported by the results, with the exception for the phylogenetic analysis, where samples 5 and 7 were most closely related to sample 8. The distant relationship between the sampled trees does not exclude collaborations between landowners, but rather suggests that the specimens stem from different origins, such as different plant nurseries in Norway or abroad.

The overall aim of this study was twofold: to provide new knowledge about *Abies alba*'s introduction history and to test a new combination of methods. Few other studies in Norway have had a similar approach by combining historical archival findings and genetics. A method similar to ddRAD is the AFLP fingerprinting, which was applied by Salvesen et al. (2009) to study the genetic relatedness between historical cultivars of Boxwood (*Buxus sempervirens* L.).

Phylogenetic studies that concentrate on a particular gene may be more accurate to study genetic relatedness. The RADseq data sets are particularly useful in resolving extensive phylogenetic relationships. Eaton et al. (2016, 27) claimed that an increased sequencing coverage, as obtained with ddRAD, may increase the phylogenetic utility. This makes ddRAD a good substitute to study genetic relatedness on a phylogenetic level.

In spite of the small number of samples, this study functions as a basis for further investigation. Using this kind of multidisciplinary approach is both valuable and challenging, compared to studies based on only historical records or genetic data. The combination of genetics and historical records would benefit from further research in archives and a larger number of samples.

5. THESIS STATEMENT AND DISCUSSION

The aim of this thesis is to approach introduced plants by combining methods from the disciplines history, botany and genetics. This contributed to a threefold approach shedding light on plant introduction history and cultural meaning. The discipline history is present throughout all papers. Term use and attitudes towards introduced plants are approached in **paper I**; values and management of an introduced tree species in a protected landscape is dealt with in **paper II**; and the anthropogenic dispersal of an introduced tree species is investigated in **paper III**. *Abies alba* functioned as a case plant to represent plants introduced as ornaments in the 1800s (**papers II** and **III**).

I. Literary reflections on plants introduced as ornaments in the 1800s

Norwegian garden culture in the 1800s followed the development in society. With a focus on middleclass authors (i.e. academics, civil servants and the clergy), the findings in **paper I** revealed that positive views generally dominated regarding the use of introduced plants from 1750 to 1900. In the 18th century, middleclass social networks played an important role in the perception of introduced plants (Dietze 2007, 44, 54). Some middleclass authors were particularly eager to describe their social manor visits and the new introduced plants they encountered there (see e.g. Wilse 1790, 229–230; Hammer 1794, 11–12).

There were also those who held negative and sceptical ideas regarding the use of introduced plants. This, however, changed over time as people became convinced by the entertaining pleasure in having rare and extraordinary plants (Ridbäck and Dietze-Schirdewahn 2017, 475). As Latané (1981, 343) discusses, people are 'influenced by the actions of others'. If a group of people is entertained by the performances of others, this can have a persuading effect on them. One can see that positive experiences with introduced plants had an impact on sceptics. Literature appears as an important channel that distributed information about introduced plants and probably affected people´s opinions.

After the century turn 1800, introduced plants started to become more accessible for the public. There was a significant breakthrough for the Norwegian plant trade and the establishment

of plant nurseries in the 1850s. As a result of industrialization, the national economy started to flourish, and a growing number of employment opportunities followed (Skard 1963, 223–224). As the number of inhabitants increased, so did the number of suburban middleclass villas. Attached to the villas were small gardens, which were marked by a design that depended on a high diversity of exciting and new plants (Bruun 1987, 192). Increasing plant assortments in local plant nurseries reflected an increasing demand for introduced plants (Ridbäck and Dietze-Schirdewahn 2017, 478). Reflected on in contemporary plant catalogues, the plant assortment became even more diverse towards to end of the century (see e.g. Aas Høiere Landbrugsskole 1875; Aas Høiere Landbrugsskole 1887; Norges Landbrugshøiskole 1899; Norges Landbrugshøiskole 1903).

Just as picturesque became a term for gardens marked by romanticism (Bruun 1987, 181), the term 'exotic plants' was synonymously used for numerous plants introduced in the 18th and 19th centuries. These plants were generally perceived as rare and unique, something positive and out of the ordinary to have and to show (Ridbäck and Dietze-Schirdewahn 2017, 478–479).

Paper I revealed that 'exotic plants' (*eksotiske planter*) was a sparsely used term in Norwegian garden literature in the 1700s and 1800s (**Table 2**, Appendix). The term started to appear more often in literature published after the century turn 1900 (Ridbäck and Dietze-Schirdewahn 2017, 476). Authors writing about the design and use of introduced plants seem to prefer the term 'exotic plants' rather than 'alien plants' (*fremmede planter*) (see e.g. Bjerke 2002; Bruun 1987; Bruun 2007; Dietze 2007; Marstein 2008; Fredriksen 2012), whereas environmental policymakers mainly use the term 'alien plants' to address the same plant category in a different context (see e.g. Gederaas et al. 2012; Artsdatabanken 2012; Lovdata.no 2015, §1c).

Plants that were introduced in the 1800s represent a botanic cultural heritage, which was a major element in the development of Norwegian garden culture. Further, many new plants were often recent scientific discoveries (**Table 3**, Appendix). These days, such plants constitute the cultural heritage in old gardens from this time and are an inherent part of people's cultural identity (Marstein 2008, 92, 97; Ridbäck and Dietze-Schirdewahn 2017, 471).

The new legislation that regulates use of introduced plants mainly affects professionals that use and handle plants on a daily basis. Even though a limited number of plant species are blacklisted and regulated, the selection of plant materials requires thorough attention from professionals. The evaluations behind the risks that have placed some alien species on the Norwegian Black List do not take into consideration different geographic locations or actions that may facilitate the invasion of introduced species (see e.g. Gederaas et al 2012, 10, 12). Plants that may cause damage in the

southern parts of the country may not do any harm in the northern parts. According to interviews with Marschhäuser (2016, Aftenposten 2 June), some professionals have suggested to develop regional blacklists, taking into account the differences in climate and growing conditions between different geographical parts of Norway. This illustrates that the views on plants introduced from 1800 onwards are still shifting and differ between professionals and authorities. This is supported by Qvenild (2013, 93), as she debates that the perceptions and categorisations of private gardeners and professionals do not always correspond to the judgement by environmental authorities.

A new updated edition of the Norwegian Black List is about to be published in 2018. The forthcoming evaluation of alien species and their impacts on Norwegian nature will be open for the public in autumn 2017 (Artsdatabanken.no 2017). Perhaps opinions of the general public and professionals, as well as regional differences in climate, will be taken into account at public hearings.

2. Dealing with introduced trees as cultural heritage in protected landscapes

The management challenge approached in **paper II** involves *Abies alba* as an introduced blacklisted plant species. *Abies alba* as a case plant is represented by an old tree, the only specimen remaining in a protected landscape. Here, *Abies alba* functions as a cultural historical monument of experimental planting in the late 1800s and is part of the area´s cultural and historical identity. At the same time, *Abies alba* represents a problematic plant species with a good ability to spread and can potentially harm native plant species and their sensitive habitats.

Paper II illustrates the complexity of introduced plants as a phenomenon that concerns professionals in different disciplines. To equally consider the natural, historical and cultural values in the management discussion in **paper II**, it appeared necessary to contribute with approaches from both social science and humanities (i.e. history and the cultural use of the protected landscape) and natural science (i.e. the spreading of *Abies alba*). While the concern of environmental managers is focused on the preservation of ecological values, local people might be more concerned about the loss of values that mean something to them on a cultural level (Rotherham 2015, 3410).

The protected landscape (Austråttlunden) presented in **paper II** has been the object for several plant introductions during the last five centuries (Ridbäck et al. manuscript (a), 5). Other authors have highlighted that the area is a former 1600s' Hunting park ('*dyrepark*', see e.g. Bruun 2007,

44), whereas the experimental plantings in the 1800s are less described. In **paper II,** it appears that the protection of historical and cultural values is generally less prioritised than that of natural values, i.e. native plant species and habitats sensitive to disturbance. Natural values are well mapped and protected in accordance with the Norwegian Nature Diversity Act (*Naturmangfoldloven*, Lovdata.no 2009). Two historical trees are protected from clearing in the area (*Quercus robur* L. and *Tilia cordata* Mill.), as they contribute with unique habitats. However, the only cultural historical objects presently protected by law, i.e. by the Norwegian Cultural Heritage Act (*Kulturminneloven*, Lovdata.no 1979), are the archaeological cultural heritage and the Austrått manor (Skjoldager 2012, 46).

Cultural heritage contributes to people's understanding of past events, and this is particularly relevant in cultural landscapes. With a claim that "conservation is about people as much as it is about species and ecosystems", Mascia et al. (2003) raise the question of how we can integrate social science and the humanities into conservation and management. Worldwide, society generally turns to natural sciences to obtain information for policymakers and practitioners. As the identification and protection of rare and endangered species and habitats are prioritised issues, the theoretical and analytical tools can be found in the field of biology (Mascia et al. 2003, 649). In Austråttlunden, the evaluation of the area's nature values is well documented in former management plants, inventories and reports on species richness and habitats (**paper II**). However, when it comes to the origin and the present condition of cultural historical values, observations and investigations appear to be limited. By approaching both the spreading of *Abies alba* and its cultural values, one takes a step towards an integration between conservation and management interests in different disciplines.

Antrop (2005, 31) claims that the "management of landscapes begins with land use planning". To conserve a historical-cultural landscape, one must keep an eye on the area's functionality in relation to how or whether the spatial context is changing (Antrop 2005, 31). Maintenance is hence a key to keep a particular landscape and the elements in it. Consequently, the loss or preservation of values depends on the maintenance (Skjoldager 2012, 47). To cover all different maintenance interests of Austråttlunden, the concerned disciplines must be involved in the development of a new management plan at an early stage.

Several scholars in environmental research have proposed interdisciplinary collaboration between natural sciences, social sciences and the humanities (Head et al. 2005, 253). As indicated above, the management of considerably invasive introduced plants is generally approached as a

natural scientific matter (Lundberg 2010, 323). The academic community has a responsibility to integrate conservation practices from different scientific disciplines. It is challenging for academics and practitioners in different conservation disciplines to find a common ground, and this requires communication and collaboration between professionals in different working traditions and research cultures. To work across disciplines and share knowledge areas, the people involved must be willing to learn and try new approaches. The presence of professionals from social sciences and the humanities in a project team would then be as given as that of the biologists (Mascia et al. 2003, 650).

Traditional cultural landscapes have evolved slowly over long time periods and are, in many places, rich in biodiversity. However, their dependence on continued land use is a challenging issue. With light on landscape management and bio-cultural values, abandoned land use may result in a landscape change with "spontaneous ecological successions" (Rotherham 2015, 3410). To preserve biodiversity that have been formed by long-time cultural impacts, as in Austråttlunden, it is necessary to continue with such traditions. For this reason, it is important to understand the origin of a specific tradition and how it has contributed to the development of a particular landscape. This requires knowledge about a landscape's historic periods, occupancy and development, which in turn can facilitate and progress management (Birnbaum 1994, nps.gov/tps; Antrop 2005, 21).

Individual reserves need specific management plans designed for the particular situations in the areas (Pyšek et al. 2013, 220). As Lundberg (2010, 334) argues, it is not a plant's status as alien or native that is a problem, but a species´ ecological behaviour in a specific region at a specific time. *Abies alba* exemplifies an introduced species that threatens a particular kind of landscape, where species and habitats depend on continued cultural impact.

Paper II shows that *Abies alba* has the ability to spread, but the situation appears to be under control with present maintenance attempts (Ridbäck et al. Manuscript (a) (Fig. 2), 11–12). However, the absence of a new management plan clearly challenges the maintenance. A recent aerial photo shows that Austråttlunden is rather overgrown, mainly by other native vegetation. When compared to a historical photo, the area where the old *Abies alba* specimen grows appeared sparsely cleared of vegetation in the 1960's, i.e. one decennium before the area became a protected landscape (**Fig. 5**, Appendix). The vegetation, however, appears rather young, suggesting that grazing had been abandoned some ten years before the historical photo was taken. In recent years, a priority has been to clear particularly invasive introduced species, including *Abies alba*, but it appears that the dominating vegetation is not particularly composed of introduced species.

3. Involvement of genetics to generate new knowledge

The genetic approach in **paper III** was inspired by findings in historical literary sources, which indicate that there had been connections between landowners regarding the introduction and dispersal of *Abies alba* in central coastal Norway. One of the two aims with this approach was to contribute with new knowledge about *Abies alba*'s introduction history in the 1800s. The second aim was to test the combination of different methods in order to generate new knowledge (Ridbäck et al. Manuscript (b), 4).

When applying genetics, the high costs and the time consumption are a challenge. Therefore, RADseq data are widely used in studies of genetic relatedness, as such an approach provides a large amount of information at relatively low costs (Ree and Hipp 2015, 196–197; Eaton et al. 2016, 22, 28). Compared to phylogenetic studies that involve polymerase chain reaction (PCR), restriction-site associated DNA sequencing (RADseq) is a more cost-effective genotyping method (Ree and Hipp. 2015, 196; Andrews et al. 2016, 81). The increased sequencing coverage of RADseq data sets may increase the phylogenetic applicability (Eaton et al. 2016, 27). In this thesis, a modification of the RADseq approach, called "ddRAD" (double-digest RAD; Peterson et al. 2012), was applied. The ddRADseq method can be applied at a lower cost and requires less time and genomic sample material than the RADseq approaches (Peterson et al. 2012, 10).

A small number of studies with a similar purpose, also using a multidisciplinary approach, have been carried out in Norway. Among them, Salvesen et al. (2009) applied AFLP fingerprinting (which is similar to ddRAD) to investigate the genetic relatedness between introduced plants. Their purpose was to establish unique markers for different cultivated and cloned specimens of *Buxus* L. (Boxwood) in historical gardens as a way to further trace distributions of *Buxus* across Europe (Salvesen et al. 2009, 135). The RADseq loci have an advantage over other semi-anonymous markers, such as AFLPs, in that they can be mapped back to a reference genetic resource such as an assembled genome (Ree and Hipp 2015, 194). Quite a few phylogenetic studies involving RADseq have been published recently worldwide (Ree and Hipp 2015, 813), among them, the identification of SNPs in plants (see e.g. Barchi et al. 2011; Wang et al. 2013; Hipp et al. 2014).

Even with a small number of samples, the involvement of genetics can help to plot a possible dispersal scenario of an introduced plant species. One of the localities where the case plant *Abies alba* was sampled (Elsterparken, **paper III**) is a former area for a planting project. The plantings took place from 1871 to 1896 and ended three years before the first plant nursery providing forestry trees was established in the region (Ridbäck et al. Manuscript (b), 6). The close relatedness between trees from Elsterparken and two other localities in the same region suggests that this project was an important source for the dispersal of *Abies alba*. In cases where the genetic relatedness between samples is low, collaboration in plantings cannot be excluded, but this indicates that the plant material was obtained from different origins, either cultivated in Norway or abroad (Ridbäck et al. Manuscript (b), 16).

Whilst genetic analysis is able to establish lineages and spatial distributions, it cannot independently date these patterns with any precision. Therefore, geneticists must, for instance, turn to archaeological and textual evidence (Witcher 2013, 21). The main objective of **paper III** was to explore and illustrate how to combine and compare genetic data with findings in historical sources. This methodical approach contributes to new interpretations of how people might have accessed and shared introduced plants. In spite of a small number of trees, this approach functions as a basis and inspiration for further studies on the dispersal of introduced plant species by involving ddRAD (Ridbäck et al. Manuscript (b), 17).

Abies alba as a genetic source

The advantage of working with conifers is that they are evergreen and can always supply fresh plant material, irrespective of the season. However, as in the needles contain high amounts of starch, conifers are generally challenging material in botanic genetics (Bashalkhanov and Rajora 2008, 1). It can therefore be a time-consuming process to achieve satisfactory concentrations of DNA. In this study, the DNA concentration was too low for the majority of the samples, and the original number was therefore reduced to eight samples.

When extracting the DNA of *Picea rubens* Sarg. (red spruce), Bashalkhanov and Rajora (2008, 5) found that the CTAB method (buffer containing 2% cetyltrimethylammonium bromide (CTAB) resulted in higher DNA yields. Compared to other methods, including the use of the DNeasy® Plant Mini Kit, Bashalkhanov and Rajora (2008, 5) indicated that CTAB was the best method when extracting DNA from conifers. Based on their results, CTAB was applied in the

analysis of some of the *Abies alba* samples. Due to limited time and funding, it was not possible to use the protocol for the extraction of all samples.

In other genetic studies of particularly *Abies alba*, other methods have been designated and applied for specific purposes (see e.g. Lewandowski et al. 2001; Sagnard et al. 2002; Ballian et al. 2012; Masternak et al. 2015), including the extraction of chloroplast and mitochondrial genomes (see e.g. Piovani et al. 2010; Dering et al. 2014).

The multidisciplinary approach – challenges, advantages, insights

Multidisciplinary research has both challenges and advantages. To many researchers, it appears as an impractical ideal, "more akin to the mythical chimera: an ungainly (and impossible) conglomerate of a lion's head, a goat's body, and a serpent's tail" (Pooley et al. 2014, 23). It is both problematic not being able to enter deeper into each discipline and challenging to keep up with literature in all different fields involved. By reviewing articles that evaluate interdisciplinary research, MacMynowski (2007, 2) found no crossover between natural science journals and social science literature. This raises the question whether researchers are exposed to methodological developments in other fields (Pooley et al. 2014, 25).

The broad and multidisciplinary approach presented in this thesis has indeed been both challenging and stimulating. Primarily, it has given me, as a researcher, the opportunity to try different approaches. The practice of different methods contributed to frame my research issues and to make new data available. However, trying to integrate the different disciplines through the common link "introduced plants" was challenging (**Fig. 4**). Another challenge was to initiate a collaboration between different research fields and to adapt to well-rooted traditions. It was also a struggle to achieve a suitable research design in which the analytical work and results of the different parts would fit in and contribute to a whole framework.

Jones et al. (2005, 1870) emphasize the importance of a truly multidisciplinary approach for the outcome of research projects, involving different actors and areas. The collaboration between different disciplines benefits from sharing knowledge and experiences. Every research discipline has its intrinsic limitations in both theory and methods when applying a single disciplinary approach, but does not necessarily have to be less successful than a multidisciplinary approach (Pooley et al. 2014, 28). Applying a method used in another discipline may not only contribute to a

more fruitful outcome, but also broaden the individual as well as the institutional research competence.

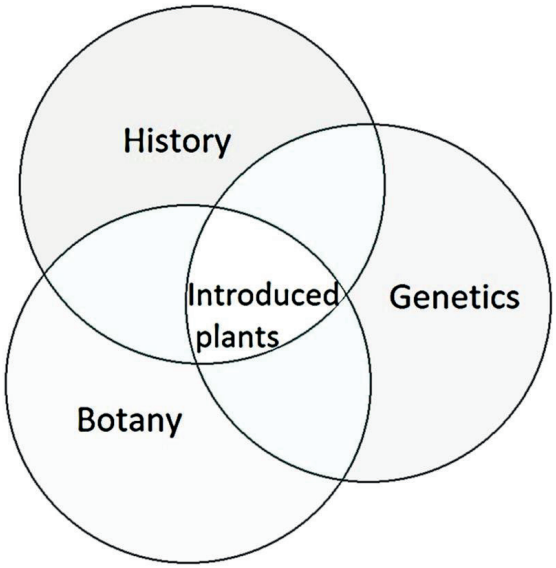

Figure 4. Introduced plants and the interplay between three disciplines. Illustration: Ulrika Ridbäck 2016.

As reflected on in the introduction of the thesis, introduced plants represent a complex research object that concerns different fields and professions. Approaching the research target through methods rooted in different disciplines has enabled me to shed light on introduced plants in more than one dimension. As a botanist, my experience was initially limited to the plant material as a natural scientific phenomenon and how it interacts with and affects its environment. I had little insight into how introduced plants concern people and the society. The historical literary approach functioned as a foundation to understand why and how the era of plant introduction has accelerated in the 1800s. The involvement of botany made it possible to approach also natural values and management problems associated with *Abies alba* as a case plant. The third approach initiated from findings in historical literary sources, which indicated that some landowners had collaborated in

plantings of *Abies alba* in the late 1800s. Combined with genetics, this research method was another way to investigate the distribution of introduced plants.

Contribution to the research field

The thesis primarily contributes to research on introduced plants. With light on ornamental plants from the 1800s, the research theme concerns fields such as the management of cultural landscapes and recreational areas, botanic cultural history and garden plant history. In recent years, the research on introduced plants was dominated by natural science, with a focus on invasiveness and impacts by alien species. The thesis, however, represents a social science contribution to the field.

Secondly, the thesis is a contribution to multidisciplinary research in general and may function as a framework for research, particularly in terms of introduced plants. The multidisciplinary approach has crossed borders of different research traditions towards an interdisciplinary collaboration and has enabled me to explore new ways of generating knowledge on the interplay of social science, the humanities and natural science. With the selection of methods, I had an ambition to highlight the advantages of integrating untraditionally combined disciplines, in this case, history, botany and genetics.

Thirdly, through the historical analysis of the situation in Norwegian society, regarding the use of introduced plants, I contribute with reflections on how important these plants were for the development of Norwegian garden culture, and hence why introduced plants constitute an important cultural heritage. As a contrast to the passion for gardening and the consumption of introduced plants in the 19th century, the same category of plants is today perceived in a very different way. This highlights the need for further studies on plant introduction and the perception of plants in general. The studies of *Abies alba* also showed that there are relatively few studies about its introduction to Norway. Especially when it comes to historical knowledge, there is more information to be researched for in archives.

Fourthly, the thesis is a contribution to the general societal debate on the management of introduced species in Norway. By investigating how a historical, but invasive, tree is valued in a protected landscape, I wish to point out the importance of a broad interdisciplinary approach in management. This also contributes to a debate about how to deal with introduced plants in general.

Fifthly, this thesis is an important step forward to increase and facilitate dialogues and collaborations between actors with different management interests or to deal with introduced plant species in new ways. The thesis highlights the importance of introduced plants as heritage as well as a problematic matter in nature conservation. This research is therefore informative for a broad range of readers and enables me to show how and why introduced plants are a complex field that concerns many disciplines.

Sixthly, *Abies alba* is a good example to illustrate the challenge in determining which plants should be accepted as 'native' or 'alien plants'. Further research is needed to assess the actual impacts of introduced plant species that tend to naturalise, spread and survive on their own in nature. It appears highly relevant to gather new knowledge on this matter, as it concerns the planning, performance and costs of the management and conservation of introduced plants. In addition, it concerns people's relation to the plants and the landscape where the plants occur. It would be of interest to see whether *Abies alba* could be accepted as a native tree species and the consequences of this acceptance.

Further archival research and genetic analyses can contribute with new knowledge about a plant's natural origin and its planting history in Norway. There are still knowledge gaps to be filled in terms of the public´s perception of and attitudes towards introduced plants in the past, and how different groups in society contributed to different parts of the cultural development related to the use of plants.

6. CONCLUSIONS

The aim of this thesis was to approach introduced plants by combining methods from the disciplines history, botany and genetics. This approach resulted in a threefold study involving a historical literary review and two field studies. *Abies alba* was selected as a case species in the field studies and represented plants introduced as ornaments in the 1800s. In addition to being an alien species, *Abies alba* appears on the Norwegian Black List.

The thesis framed three research issues based on the research theme and approach.

1. How were introduced plants described and reflected on in Norwegian literature from 1750 to 1900?

2. How should we deal with the management of a blacklisted heritage tree in a protected landscape, with *Abies alba* as a case species?

3. How can genetics help to generate new knowledge about plant introduction history, with *Abies alba* as a case species?

The first research question was answered through **paper I**, which briefly illustrates the introduced plants' journey from pleasurable garden elements to a contemporary issue. The findings showed that there was a significant shift in middleclass society regarding the perception of introduced plants from 1750 to 1900. The growing middleclass (i.e. academics, civil servants, merchants and the clergy) was an important factor, where generally positive attitudes towards new plants were dominating. They were commonly seen as an exciting challenge and a positive contribution that indicate the botanical skills and considerable success of the garden owners.

A change in terminology reflects a change in attitudes among middleclass authors. Plants described as exotic were exciting news and, in many cases, recent contributions to science, with a natural origin outside Scandinavia. The commonly used term 'exotic plants' is associated with a positive tone in the 1800s. This is a contrast to its present synonymising with 'alien plants' by nature managers, which implies a rather negative perception.

Presently, there appears to be a rather increased concern in society about the potential damage caused by introduced plants. In 2012, policymakers selected the year 1800 to delimit the use of introduced plants. By this, it seems that an important historical era of plant introductions is in danger of being cleared.

The second research question was answered through **paper II**, namely by investigating how a blacklisted heritage tree, represented by *Abies alba*, was valued in a protected landscape in Norway. In a protected landscape where *Abies alba* is both a heritage tree and a threat to botanic species richness, natural values have generally been given the highest priority and until now, the management has mainly been the responsibility of environmental conservationists. This highlights the meaning of interdisciplinary collaborations to embrace and conserve all values of interest.

The study indicated that continued maintenance, involving vegetation clearing and grazing, is required in order to conserve the cultural historical character of the protected landscape. In addition, this can prevent or limit the further spread of an unwanted introduced tree species, in this case, *Abies alba*. Further, this allows the possibility to safeguard and to equally prioritise natural, historical and cultural values.

The third and final research issue was approached in **paper III** by exploring the combination of historical and genetic methods to study the anthropogenic dispersal of an introduced tree species. With indications from historical literary sources, RADseq was employed to investigate how selected *Abies alba* specimens might have been dispersed through planting in central coastal Norway. Sources that indicated a collaboration between people who planted *Abies alba* in Elsterparken (near Trondheim) and Reins Kloster could be supported by genetic data, which also revealed that *Abies alba* in Austråttlunden seemingly originated in Elsterparken. The genetic data also showed a relatedness between the other *Abies alba* trees sampled in this study, indicating that sample 6 in Skånes originated in the old arboretum Fjæraskogen in Trondheim, i.e. is related to sample 3. Samples 5 and 7 are closely related and were seemingly planted at the same time as sample 6 in Skånes, but from another origin.

As exemplified in paper III and in similar previous studies, the involvement of genetics can complement historical sources and contribute to reveal how people accessed, shared and distributed plant materials. In studies of genetic relatedness, ddRAD has become widely used to find and score SNPs (single nucleotide polymorphisms), but has been sparsely applied in similar studies on plant introduction history.

This thesis is an empirical contribution to multidisciplinary research on introduced plants. The research approach illustrates the complexity of introduced plants as a research field, as it involves many different and connected parts of different areas. The overall contribution is the attempt to integrate different disciplines to study and solve issues concerning the addressed plants.

By looking back on the period from 1750 to 1900, the primary step was to understand the background of the introduction of new plant species to Norway in the 1800s. This provided new insights on the importance of introduced plants as a cultural heritage and their significance in Norwegian garden culture and history. Further, the attention was drawn towards the issues regarding introduced plants in a nature conservation context. From there, the involvement of natural science became a part of the approach, with light on both cultural historical values and the introduced plants´ ability to naturalise and spread, hence constituting a threat to native species diversity and habitats. With the introduction history of the plants as a leading thread, genetics was involved as another natural scientific discipline to help generate new knowledge about the plants´ introduction and spreading.

The integration between different disciplines, regarding work with and research on introduced plants, would probably benefit from starting at an early stage. Professionals that work with plants in a social science field, such as landscape architects and planners, may know too little about the plants as organisms, their reproduction ecology and spreading ability. This knowledge, however, should not be limited to natural scientists. In turn, environmental scientists may know little about the introduced plant species' cultural history and the heritage they represent in different areas and contexts. This thesis is hence a step forward to inspire further dialogues and collaborations between social science, the humanities and natural science regarding introduced plants.

Introduced plants are often dealt with separately in either social science, natural science or the humanities. Previously, there have been attempts to use multidisciplinary research approaches on topics that involve introduced plants. While it is common to select two disciplines, this thesis took a step from two to three disciplines, which has rarely been done before. This led to the privilege of opening new doors between the disciplines involved in this thesis.

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8. APPENDIX

The appendix includes additional tables and figures to complement the historic, botanic and genetic parts of the thesis and the full-length versions of the papers.

Table 2 presents the authors' use of the term 'exotic plants' (**paper I**). **Table 3** presents a survey of selected plant species approached by Norwegian authors from 1750 to 1900, including the year when and by whom each plant species was scientifically published. In addition, the plants' origin and appearance are mentioned.

Figure 5 gives an aerial overview of Austråttlunden in 1964 (11 years before it was protected as a landscape) and of its present condition (**paper II**).

Figure 6 illustrates the results when determining the quality of the extracted DNA samples with agarose gel electrophoresis. **Table 4** shows the DNA concentration when quantified with UV absorbance and fluorescence measurement (**paper III**). **Figures 7, 8** and **9** show additional graphs of the most probable relatedness between the sampled trees when analysed using the software package STRUCTURE (**paper III**).

Century	Author	Profession	Use of the term 'exotic'
20th	Magne Bruun (1932–2018)	Former Professor of landscape architecture, present Emeritus	Yes. He used 'exotic' to describe foreign plants introduced before the 20th century as ornaments. Bruun distinguished the 'exotic' ones from other introduced and cultivated plants (see e.g. Bruun 1984, 37).
	Carl Wille Schnitler (1879–1926)	Art historian, interested in garden architecture	Yes. He described foreign woody plants, such as "exotic tree growth" (see e.g. Schnitler 1915, p. 251).
19th	Frederik Christian Schübeler (1815–1892)	Professor of botany at the Tøyen Botanic garden in Christiania (present Oslo)	No. Schübeler referred to non-native plants as 'foreign', mentioning the plants' geographical origins and their 'ornamental' value.
18th	Christoffer Hammer (1720–1804)	Land surveyor and writer	Yes. He used the term 'exotic' when describing foreign trees and perennial plants, mainly recently discovered and with origins in warmer climates (see e.g. Hammer 1773, 150).
	Jacob Nicolaj Wilse (1735–1801)	Natural scientist, writer and priest	No. In addition to 'foreign', he used the terms 'strange', 'rare' and 'remarkable' when describing recently introduced plants.
	Claus Fasting (1746–1791)	Civil servant, writer and botanist	No. Concerning foreign, recently introduced plants, he presented their geographical origins and used the terms 'foreign' and 'rare'.
	Gerard Schøning (1722–1780)	Historian	No. He used the terms 'rare', 'noble', 'exquisite' and 'eminent'.

Table 2. Cited Norwegian authors and their use of 'exotic plants' or other related terms.

Plant species or genus	Author, year published[16]	Origin	Cited reference	Ecology/Appearance
Aloe sp. (Aloaceae)	Linnaeus, 1753	Africa, America and Asia	Hammer (1773, 149)	Herb with healing qualities, colourful flowers on large spikes
Bauhinia (Fabaceae)	Linnaeus, 1753	Central- and South America	Hammer (1773, 149)	Tree with large, colourful flowers
Liriodendron tulipifera (Magnoliaceae)	Linnaeus, 1753	South-West North America	Schübeler (1888, 281)	Deciduous tree with conspicuous leaves and blooming
Lupinus (Fabaceae)	Linnaeus, 1753	North America, Mexico and South America	Schübeler (1888, 535)	High growing herb with brightly coloured flowers
Asclepias syriaca (Asclepiadaceae)	Linnaeus, 1762	North America	Wilse (1792, 428)	High growing herb, pink flowers
Chamaelea tricoccos[17], (Rutaceae)	Lamarck, 1778	Europe (Mediterranean)	Hammer (1773, 149)	Low growing herb, small yellow flowers
Lepidium oleraceum (Brassicaceae)	Sparrman, 1780	New Zealand	Wilse (1792, 427)	Low growing herb with small white flowers
Saxifraga sarmentosa (Saxifragaceae)	Linnaeus, 1781	Japan	Wilse (1792, 427)	Low herb, conspicuous white flowers
Magnolia obovata (Magnoliaceae)	Thunberg, 1794	China and Japan	Schübeler (1888, 280)	Deciduous tree with large white flowers
Zinnia haageana (Asteraceae)	Regel, 1861	Mexico	Schübeler (1888, 9)	Low growing herb with conspicuously coloured flowers
Cerinthe gymnandra (Boraginaceae)	Gasparrini, 1863	Algeria	Schübeler (1888, 120)	Low growing herb, multi-coloured flowers
Lonicera ruprechtiana (Caprifoliaceae)	Regel, 1869	Siberia	Schübeler (1888, 73)	Shrub with conspicuous flowers

Table 3. Selection of 'exotic plants' mentioned by Norwegian authors 1750–1900.

[16] In this context, an Author is the person who first published a new species' name and made its existence officially known to science (after 1753, i.e. the publication Linnæi, C. (1753). *Species Plantarum ... Tomus II*. Upsal, Sveciæ, Holmiæ, Impensis Laurentii Salvii).

[17] Present accepted name is *Cneorum tricoccon* L., published 1753 (Tropicos.org 2015, *Cneorum tricoccon* L. Accessed 29 March 2017 from http://tropicos.org/Name/50002973).

Figure 5. Above: aerial photo of Austråttlunden captured on June 22, 1964, Bm. scale 1:7000 (Archival source provided by The Norwegian Mapping Authority)[18]. Below: aerial photo captured after 2014 (Norkart 2017, kart.finn.no/). *Abies alba* is marked with a white circle. The transect area in **paper II** is on the left side. It appears that the right part of Austråttlunden was more open in the 1960s and even contained a villa with a garden (centre of the photo above).

[18] The Norwegian Mapping Authority (Statens Kartverk, Norway). Aerial photo 1964, no. 01522_E18. Available at http://www.kartverket.no/en/About-The-Norwegian-Mapping-Authority/

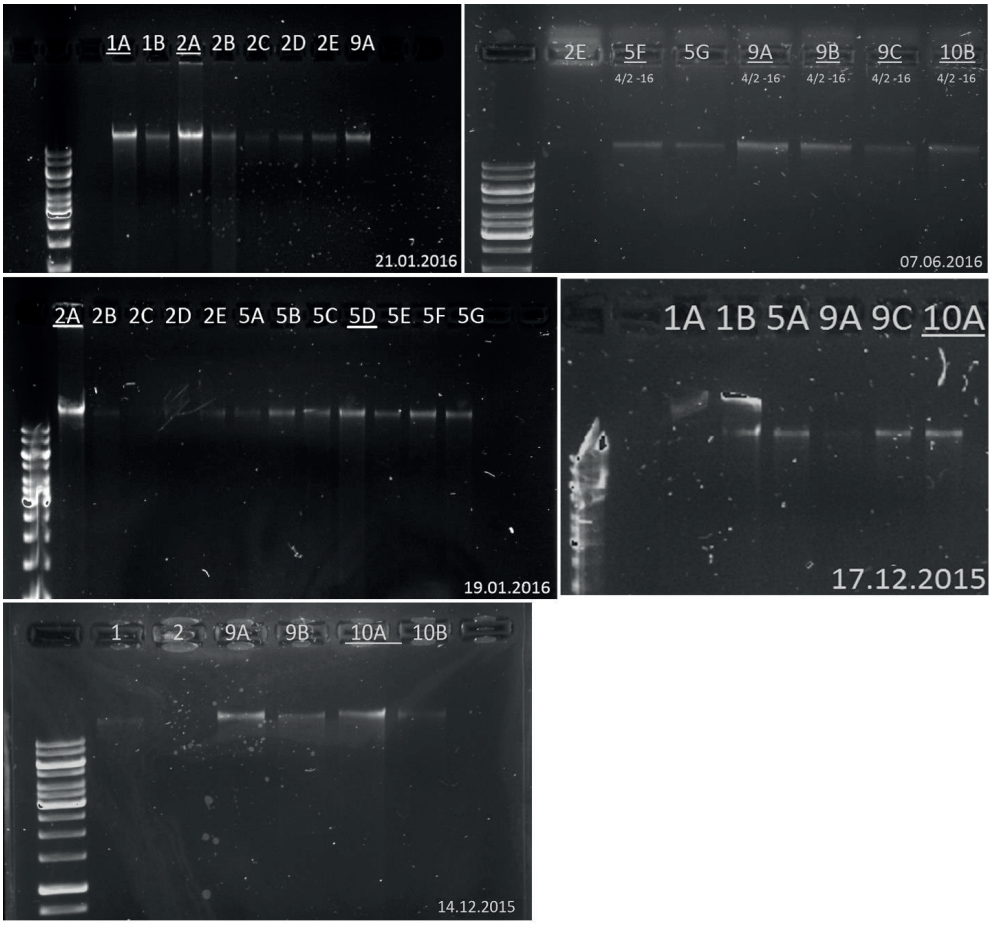

Figure 6. Results of DNA samples run in agarose gel electrophoresis (**paper III**). This also illustrates the challenge in getting sufficiently high concentrations of DNA. The brightest stripes are the samples of best quality, while many samples of poor quality were left out. The final samples selected for sequencing and further analysis were 1A, 2A, 5D, 5F, 9A, 9B, 9C and 10B (**Table 4**).

Tree individual	Sample ID no.	Date of extraction	NanoDrop Conc. (ng/µl)	NanoDrop 260/280 ratio	NanoDrop 260/230 ratio	Qubit Conc. (ng/µl)	Total volume (µl)
1	1A	15. Dec. 2015	(20.6)	(1.8)	(2.6)	(18.1)	40 x 2
2	2A	18. Jan. 2016	(29.6)	(1.8)	(2.3)	(25.9)	40 x 2
3	5D	19. Jan. 2016	(19.7)	(1.7)	(1.9)	(15.0)	40 x 2
4	5F	4. Feb. 2016	(9.5)	(1.6)	(2.4)	(12 .1)	40 x 2
5	9A	4. Feb. 2016	(16.9)	(1.7)	(1.8)	(15.0)	40 x 2
6	9B	4. Feb. 2016	(16.3)	(1.8)	(2.9)	(19.4)	40 x 2
7	9C	4. Feb. 2016	(8.7)	(1.7)	(4.4)	(15.6)	40 x 2
8	10B	4. Feb. 2016	(15.0)	(1.8)	(3.0)	(16.6)	40 x 2

Table 4. Overview illustrating the final eight samples selected for sequencing and further analysis. The selection was based on DNA concentration (ng/µl), determined with agarose gel electrophoresis and UV absorbance (NanoDrop, Thermo Scientific) and quantified using fluorescence measurement (Qubit®, Invitrogen, Thermo Fisher). The ultimate NanoDrop ratio (260/280) should be between 1.8 and 2.0 (**paper III**).

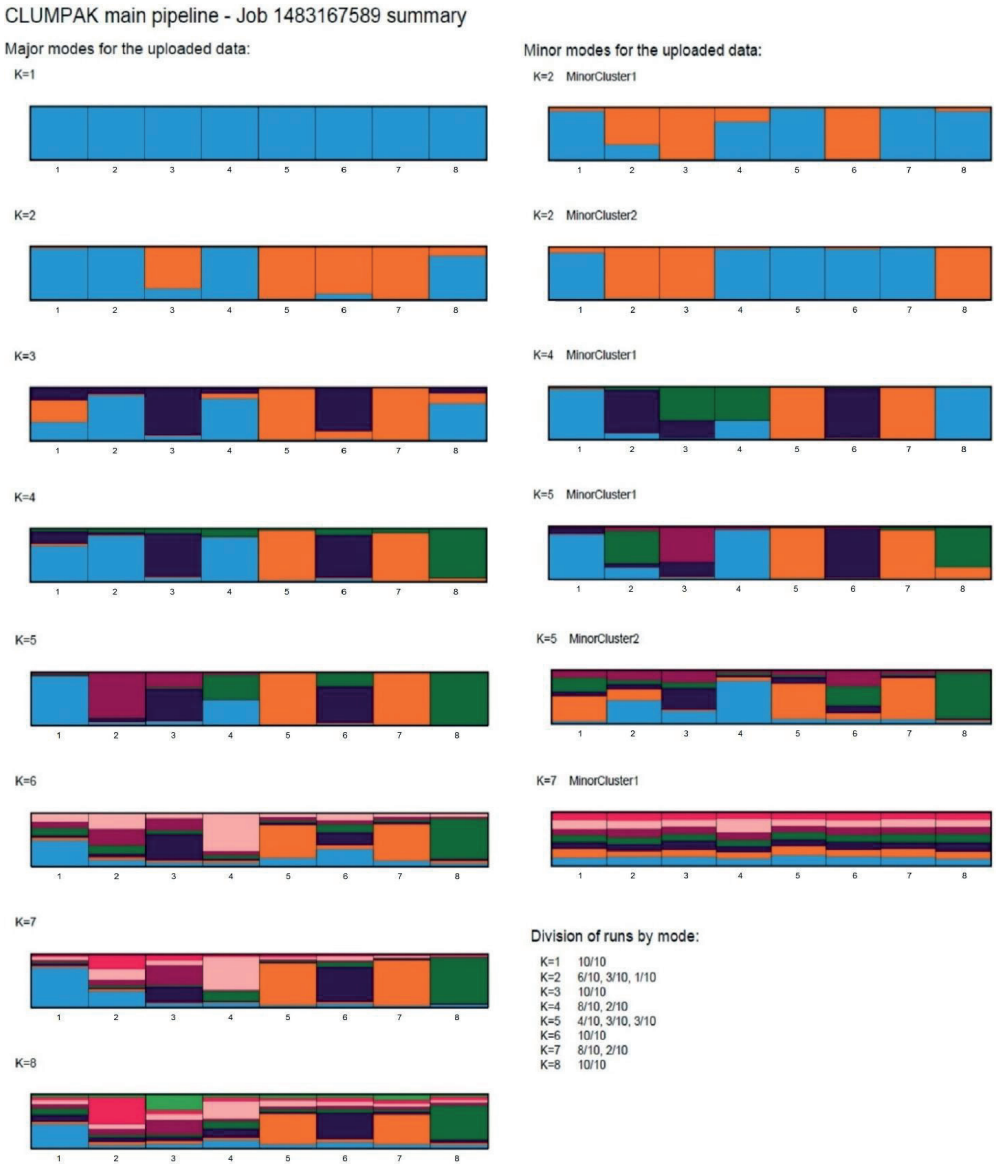

Figure 7. Graphs processed from STRUCTURE analysis, showing different K-values (most probable relatedness). Each coloured square represents a sample, 1 to 8 from left to right. K=2 and K=3 (left side, second and third from above) are the most probable clusters in accordance with the graph below. In **Figure 8**., K=4 is the second most probable K-value according to **Figure 9** below (STRUCTURE version 2.3.4 by Pritchard et al. (2000) as described by Kovi et al (2015, 929).

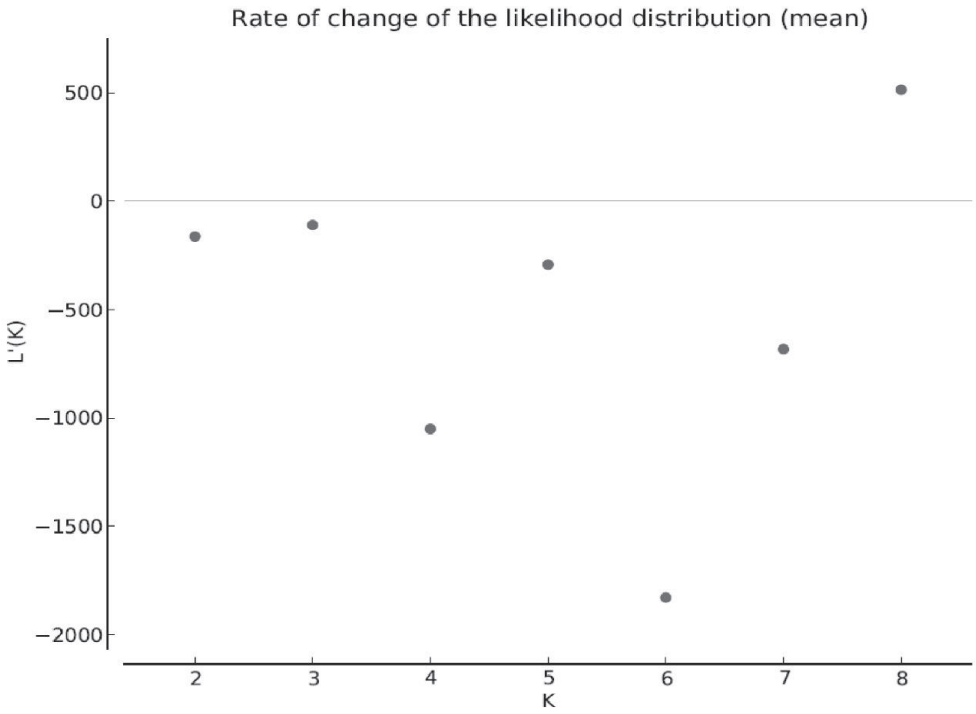

Figure 8. Most probable K-values: 2 (K=2) and 3 (K=3) closest to 0 in the L'' (K) axis (STRUCTURE).

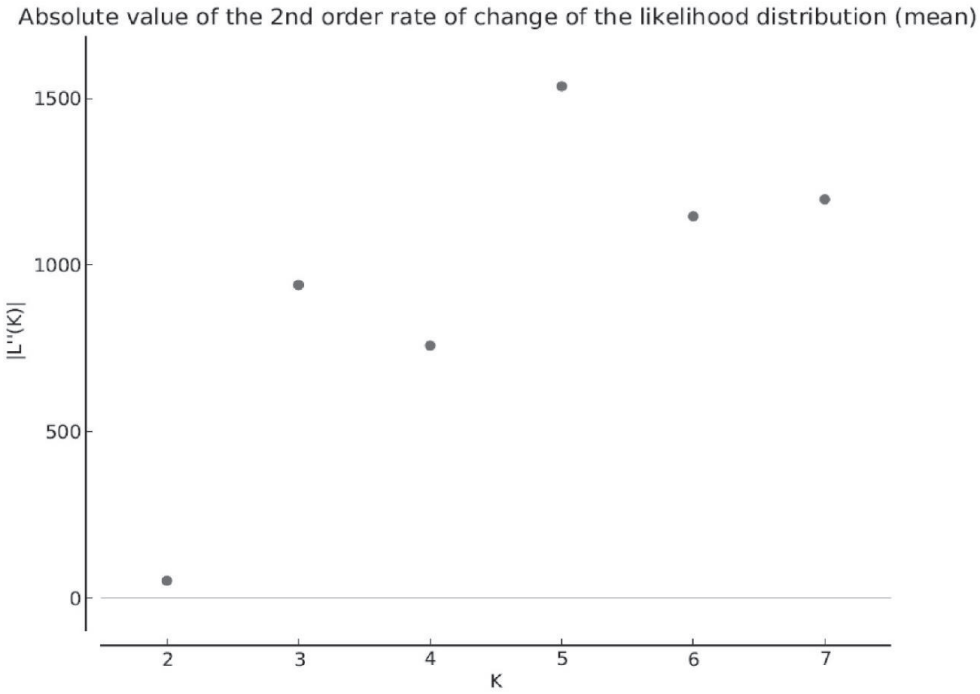

Figure 9. Most probable K-value: 2 (K=2) closest to 0 in L'' (K) axis. Here 4 (K=4) is the second most probable K-value (STRUCTURE).

FULL-LENGTH PAPERS

PAPER I

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Once in demand, now unwanted: reflections on changed attitudes towards plants introduced to Norway 1750–1900

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ABSTRACT

Among plant species introduced to Norway, several are naturalising and spreading in the landscape in an aggressive way. There is an ongoing debate between professionals in nature management and cultural heritage. Policy-makers have selected the year 1800 as a time delimitation: the use of plant species introduced later is to be regulated or even forbidden. Looking back in history, the perception of the introduction of plants between 1750 and 1900 differs from present attitudes. Introduced plants were once regarded as positive contributions that could be used to demonstrate botanic skills and wealth, as well as garden owners' skills in cultivating them. At present, many of the plant species that were once desirable are now regarded as threatening 'aliens'. This article examines changed attitudes towards introduced plants, with an emphasis on the period 1750–1900, when the majority of new plants arrived.

KEYWORDS

Introduced plants; Norway; exotic; alien; nineteenth century; garden culture; botany

Introduction

Professionals in nature management and cultural heritage are in debate about how to limit the use of plants introduced to Norway. Among introduced plant species, several are showing an aggressive way of naturalising and spreading, potentially threatening what is regarded as Norwegian nature (Gederaas, Moen, Skjelseth, & Larsen, 2012). New legislation by the Norwegian Environment Agency has given rise to an ongoing discussion on this matter, as it regulates future use of foreign species introduced after the year AD 1800. This moment in time—'a historical cut-off point' (Gederaas et al., 2012, p. 12)—was selected without reference to historical documentation about these species' actual time of arrival, either unaided or brought into the country by humans.

Given 1800 as the time delimitation, the legislation embraces a large number of plant species of high cultural value, i.e. plants that were introduced in an era when the Norwegian plant market started to flourish. In the nineteenth century, Norwegian garden culture went through an important development. This was a time when introduced plants were seen as luxury goods (Dietze, 2007). In addition, the plants contributed to scientific and academic enlightenment, with the emphasis on botany. At the start of the century, plant importation was generally the business of wealthy merchants, and few imported plants were to be found in the ordinary markets at that time. With an increase in established plant nurseries, by the mid-nineteenth century any garden owner had the opportunity to acquire the exciting new plants that were for sale. Civil servants, well distributed throughout the country, made up the majority of the middle class (Skard, 1963). Educated in Copenhagen—the only university in Denmark–Norway

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until 1811—and inspired by Danish gardens, they made important contributions to national garden culture during the development of small villa gardens (Bruun, 2007).

The way introduced plants are perceived today appears to be very different from opinions back in the nineteenth century. At present, there is an increasingly negative perception of plants introduced after the year 1800. Even though problems caused by introduced species were already observed in the nineteenth century, the concern has risen merely over the past two decades. The first law to regulate species introduction in Norway was established in 1997. Since then, it has become a national duty to protect native species, due to the legal nationalising of biodiversity. This in turn may have contributed to increased awareness among the general public that some introduced plant species may cause changes to Norwegian nature. Even though the legislation only concerns plant species introduced after the year 1800, it might contribute to fostering a general opposition towards introduced plants, as policy-makers apply terms to them such as alien and black listed (Qvenild, 2013).

In order to map how people perceived introduced plants before 1800 and throughout the nineteenth century, one can study attitudes expressed in the use of terminology and the history of the trading of plants.

The aim of this article is to show how attitudes have changed towards plants introduced in the years 1750–1900. This study focuses on garden owners, as customers in the plant market; plant nurseries as the suppliers of plant materials; and gardening professionals, represented here by authors that, in addition to writing, also gardened in practice. The latter category is the main target of the discussion that follows; exploring their attitudes towards introduced plants, comparing their use, and the development of terminology. The analysed literature relates to gardens and gardening in Norway.

The rise in the demand for plants in the late eighteenth century

In the 1770s, Norway had reached a turning point in garden culture. With a poor native assortment of plants, the romantic breeze of the English landscape style brought with it demands for beautiful and challenging plants from abroad (Bruun, 2007). European colonies in North and South America, Africa and Asia contributed to an increasing supply of introduced plants. The variety of introduced plant species was important (Dietze, 2005).

In the late eighteenth century, there were a limited number of plant nurseries. As communication links by land were poor, commercial plant traders reached communities along the west coast by boat (Skard, 1963). Norwegian merchants generally conducted plant importation privately in combination with the shipping of wood (Dietze, 2007). By the late 1700s, an increased number of private traders demonstrated positive attitudes towards introduced plants.

Norwegian merchants were mainly made up of the wealthy middle class and some of these middle class families were very much Europe orientated when it came to the subject of contemporary garden art. The politically active merchant and landowner Peder Anker (1749–1824) was a representative of the bourgeoisie or middle class. He owned large areas of woodland and his main income derived from selling timber to Great Britain (Dietze, 2004). In 1773, he acquired the manor house at the Bogstad estate, located outside the contemporary capital Christiania (now Oslo) in Southern Norway. He was a private dealer on the European plant market, a typical example of a 'pioneering agent' (Dietze, 2007, p. 112), contributing to putting Norway on the European map of garden culture. He was in regular contact with plant nurseries and other private traders abroad (in Great Britain, Germany, and Holland), which he had established contact with during his 'Grand Tour' (Dietze, 2007, p. 112).

Having made a fortune from successful timber trading, Anker belonged to a category of the Norwegian middle class that contributed to the nation's economic welfare. This category of social class was clearly in touch with other European countries and well informed about developments in garden art. Garden design and the plants used therein were a matter of competition between garden owners. As merchants were in a leading position to keep up with the latest gardening trends, other members of society copied their styles when creating their own pleasure gardens (Dietze, 2007). When it came to new plant discoveries, Norwegian merchants wanted the most up-to-date and cost was no object.

Impressive plantings appeared at that time as a way to obtain admiration from visitors and other garden owners. The latest seeds were ordered and planted without the merchants even knowing the plants' appearance (Dietze, 2005).

A plant list from 1792, containing all plants with scientific information in the gardens of the Bogstad estate, sheds light on Bogstad as a scientifically successful garden (Hammer, 1794). Many of the introduced species from Bogstad were relatively new to science, or at least new to Norway. The relationship with botany as a science was important for the Norwegian bourgeoisie. Their scientific interests were bringing them into an age of botanic enlightenment and soon Norway's first scientific societies were founded. Two examples of such societies include the Useful Society in Bergen (*det Nyttige Gesellschaft*, founded in 1774) and the Royal Norwegian Society for Development (*det Kongelige Selskap for Norges Vel,* founded in 1809). Individuals such as Anker were particularly interested in education and the dissemination of botanical knowledge to the general public; the Anker family, for example, led the proposal to establish a university in Christiania, as well as public libraries and other academic institutions (Dietze, 2007). Another way to reach out with botany skills was through botanical gardens, where each plant could be exhibited individually or in groups. In 1794, Anker intended that Bogstad would be an important locality for such purposes and huge efforts were made towards cultivating and storing introduced plants (Dietze, 2005).

In addition to botany, other scientific fields were also related to the use of introduced plants, such as forestry, plant ecology, and the binomial naming of plants in Latin. Founded by Carl von Linné (1707–1778), the systematic method of classifying plants was an important addition to the botanical world (Jørgensen, 2007). Botanists had previously struggled when trying to establish a way to logically group and identify plants. After 1735, botanists and gardeners were united across professional fields through the use of universal binomial naming (Hobhouse, 2002).

Debating terms used to address introduced plants

The term 'indigenous plants' does not represent a reliable point of reference (Cooper, 2003), since it also embraces naturalised cultural plants from abroad. The concept 'foreign plants' has also become a somewhat imprecise point of reference. In addition to meaning something brought to Norway from abroad, the term can be used synonymously with a diversity of related terms. A more in-depth look at different meanings and associations appears challenging.

Qvenild (2013, p. 6) writes that 'The perception of alien species as unwanted has emerged in the context of gardens'. According to Gederaas et al. (2012), an 'alien species' (*fremmede art*), is defined as 'a species, subspecies, or lower taxon occurring outside of its natural range (past or present)' (p. 12). Gederaas et al. (2012) maintain that the term 'alien' is 'considered to be more neutral' in relation to introduced species (p. 11). Further, they refer to 'non-native, non-indigenous, foreign and exotic species', as synonymous with 'alien species'. As policy-makers, they can use the term pejoratively in ways that may influence the audience. Perhaps introduced plants were termed 'alien' as they started to dominate natural environments (Qvenild, 2013).

Whilst 'alien plants' appear to mean any unwanted plant species from abroad, 'exotic plants' are described in Norwegian dictionaries as 'strong foreign touch (particularly about something that belongs to tropical countries) … originating from, reminiscent of warmer countries' (*'sterkt utenlandsk preg (særlig om det som hører til tropiske land) … stammer fra, minner om varme land'*, Ordnett.no, 2015).

Looking back in time, the negative tone connected to the terms 'alien plants' and 'exotic plants' appears to be rather modern in the Norwegian language. In the late eighteenth and the early nineteenth centuries, the term 'exotic plants' was used in particular to describe the new and exciting plants that were brought to gardens associated with the curious and unusual. One can sense a positive tone connected to the term.

In this section, the article approaches historical Norwegian literature—such as general dictionaries, botanical contributions and literature within gardening and garden art—to explore how the term

'exotic' and the attitudes to introduced plants have changed in the years 1750–1900. The emphasis is on garden literature and literature with impacts on gardening and garden culture.

In common dictionaries from the eighteenth century, when Norway still belonged to Denmark, one finds neither *exotic* nor *exotica*. It seems that it was not until 1851 that one could find descriptions of the term exotic in a common dictionary. Exotic was explained as 'foreign ([particularly] about plants)' ('*udenlandsk [især] om vækster*'; Hansen, 1851). In 1885, the German word *Exotisch* was translated as 'exotic, foreign' (*'exotisk, udenlandsk'*) in a German–Danish–Norwegian dictionary (Kaper, 1885, p. 194). The 1891 book *Norwegian Pocket-conversations* (*Norsk lomme-konversations lexicon*) defines exotic as 'foreign, from temperate countries' ('*udenlandsk, fra varme land*', Konow, 1891, p. 260).

The term 'exotic plants' was little used in Norwegian primary sources concerning gardening and garden art in Norway from the eighteenth and nineteenth centuries. One person that was familiar with the term was the land surveyor and writer Christoffer Hammer (1720–1804). He made significant distinctions about gardening in his literary work the *Norsk Huusholdings-Kalender* (1773). Therein he shed light on exotic plants in a chapter about 'Orange trees and foreign plants' ('*om Orange-træer og udenlandske vækster*', Hammer, 1773, p. 144). Hammer presented this specific plant category—not adapted to the Norwegian climate—as 'woody foreign plants, Plantae exotica perennials' ('*vedvarende udenlandske vækster, plantæ exoticæ perennes*', Hammer, 1773, p. 150). As he read scientific literature and plant catalogues from abroad, he exposed himself to new terms concerning introduced plants. The work of Carl von Linné was probably an important contribution to the use of the term 'exotic' in relation to plants. Among others, the plant catalogue *Hortus upsaliensis* contains a list of 'exotic plants', which Linné had procured from 1742 to 1748 for the botanical garden of Uppsala (Linnæi, 1748).

Hammer was curious about introduced plants and referred to a great number of species from abroad. When visiting the Bogstad estate, he came across several plant species that required greenhouses to survive during the cold season (Hammer, 1794). Those plants' origins were probably tropical or subtropical. Hammer described the introduced plants he had noticed at Bogstad as either foreign (*udenlandske vækster*), or strange (*rare planter*) and remarkable plants (*mærkværdige planter*; Hammer, 1794). Hammer seemed impressed by their unique characteristics; from having lovely scents, culinary or healing properties, to very exquisite appearances. He even encountered one plant species moving by itself, like a living creature. Those species he came across illustrated something unique and unusual, compared to plants people were familiar with in Norway. Examples of exciting plants to impress visitors were plants such as *Hedysarum gyrans* (now *Desmodium gyrans*), which reacted to its surroundings by moving its leaves, and *Dionaea muscipula* (Venus flytrap).

Hammer seemed to be positively disposed toward the use of such introduced plants in gardens, as he took on the challenge of cultivating these plants himself. When he wrote in Danish, he usually indicated plants' foreignness by mentioning their geographical origin and used terms other than 'exotic plants'. One example is from a dissertation about botanical gardens, where he expressed his delight about an exciting diversity: '241 strange and remarkable American and other foreign plants' (*'241 rare og mærkværdige Americanske og andre udenlandske vækster',* Hammer, 1794, p. 17). Even in Norwegian Flora (*Floræ Norvegicæ Prodromus*; 1794), which contained binomial names in Latin, Hammer again indicated 'exotic plants' by other terms when presenting Norwegian botanists; 'among them is Jonas Ramus, illustrious because of many strange plants found by him' ('*blandt dem er Jonas Ramus berömmelig formedelst mange rare planter funde af ham*', Hammer, 1794, p. 10).

In the late eighteenth century, some of Hammer's contemporaries were Norwegian writers who showed passion for gardening. To illustrate their experience of introduced plant species they used a variety of terms. An early plant enthusiast in the Bergen region, Niels Knag Jæger (1706–1780) contributed in 1778 with a pamphlet where he distinguished the 'wild-growing native and foreign' ('*viltvoksende innfødte og udlændinge*') among trees (Moe, 2004).

The civil servant Claus Fasting (1746–1791) was an enthusiast of English landscape style, and was well-versed in contemporary European literature on garden art (Moe, 2000). He was one of the important contributors in Norway's attempt to keep pace with the contemporary development of European garden art (Bruun, 1987). In the journal *Provinzialblade*, founded by Fasting, he wrote about cultivated plants

and their cultural history (Fasting, 1781, 1791a, 1791b). One senses a positive attitude in his writings toward introduced plants. In an essay, he stated that several ornamental plants are indigenous, 'but many have come to us from America and mostly from the Eastern countries' (*'men flere ere komne til oss fra Amerika, og de fleeste fra Østerlandene'*, Fasting, 1780, p. 265). He was restrained with his descriptive terms, using 'strange plants', for example, and 'indigenous and foreign' (*'indenlandske og fremmede'*, Fasting, 1791a, p. 84) to highlight strikingly new and exciting species.

Not all attitudes concerning imported plants were positive. The scientist and priest Jacob Nicolaj Wilse (1735–1801) seemed to regard botanic curiosities with interest. But he had strong opinions concerning the use of introduced plant materials, believing that it would be better to utilise native Norwegian plants. Bringing newly introduced species from warmer latitudes was, in his view, like working against nature (Wilse, 1777). He strongly recommended the use of native plants above the use of those that had been introduced, 'One uses those plants, that can be planted, instead of specimens that will not thrive here' (*'Man betiene sig af saadanne planter, som kand settes i steden for dem som her ey vil trives'*, Wilse, 1777, p. 110).

In spite of his antipathy, Wilse also showed a somewhat positive reaction towards introduced curiosities. Some years later, after a visit to the Bogstad estate where Wilse had observed a coffee tree and a tea shrub, he seemed delighted. He stated 'probably the only ones in Norway; whether one wants to go with various rare plants … but very entertaining it is, that here they are trying [to grow] the most remarkable kinds of plants' (*'nok de eneste i Norge; hvorvidt man vil komme her med andre sieldne planter … men meget roesværdigt er det, at man her forsøger de merkeligste slags udenlandske planter'*, Wilse, 1790, pp. 229, 230). In his book series *Reise-lagttagelser* (1790–1798) about his journeys through Europe, Wilse described several introduced species that were present at places he visited. In Hamburg, he received plant catalogues with 'all kinds of flowers and bulbs, strange fruit trees and more' (*'alle slags blomster og svibler, rare frugttræer med mere'*, Wilse, 1792, p. 427). In the same edition of the journal, he also mentioned a number of newly discovered plant species from New Zealand and Japan in Hamburg, which he assumed to be planting experiments. In addition to 'foreign plants' (*'udenlandske planter'*), Wilse seemed to use the terms 'strange plants' (*'rare/sieldne planter'*) and 'remarkable plants' (*'merkelige planter'*) to point out introduced species with unique qualities, especially those differing from plants he had experienced before. Among the plant species he mentioned, several originated in other continents, but not necessarily tropical regions (Wilse, 1793).

Wilse also seemed concerned with keeping pace with botanical knowledge, as he went abroad to learn about the latest in botany. After visiting Hamburg, he anticipated that planting experiments would be undertaken with 'some of the newest plant discoveries' (*'nogle af de nyeste opdagede planter'*, Wilse, 1792, p. 427).

After the turn of the century (1800), interest in introduced species continued to flourish. Frederik Christian Schübeler (1815–1892) was an outstanding representative of the enlightentment in nineteenth century garden culture. Schübeler was a professor in botany who became a leading researcher in the field of experimental planting in Norway. He had a profound impact on the development of Norwegian horticulture (Mørkved, 2015). With an ambitious desire to learn how far north in Norway introduced plant species could be cultivated, Schübeler expanded his studies by sending seeds to selected vicarages, farms, and research stations throughout the country (Schübeler, 1889). Through correspondence with his selected localities, he learned about the results from each planting experiment. The new knowledge also contributed to mapping cultivating zones in Norway.

It appears that Schübeler was positive about the introduction of foreign species. The presentation of his planting results often highlighted that a species 'deserves to be commonly planted as an ornamental plant' (*'fortjener at blive almindelig dyrket som prydplante'*, Schübeler, 1888, p. 540). One can assume that a particular species' appearance, and its ability to be cultivated, played important roles in Schübeler's opinion. His literary works in botany embraced plant species from all over the world, and many of them were new to science. He was restrained when using descriptive terms, simply calling plants 'either indigenous or foreign' (*'enten indenlandske eller fremmede'*, Schübeler, 1888, p. 551).

It seems that it was not until 1900 that 'exotic plants' appeared in common Norwegian garden literature. During research for a book about the history of Norwegian garden art, the art historian Carl W. Schnitler (1879–1926) found conspicuous collections of exotic plants at some garden localities he visited: 'an extensively rich vegetation … an exotic tree growth … delights every botanist' ('*en myldrende rik vegetation … en eksotisk trævekst … fryder enhver botaniker*', Schnitler, 1915, p. 251). By using this term, it seems Schnitler intended to illustrate plants that were once new, and extraordinary additions to Norwegian gardens.

Looking at descriptions of introduced plants, a variety of terms was commonly used before and after 1800. The terms 'foreign' (*utenlandsk, fremmed*) and 'outlandish' (*utenlandsk*) were often used by Hammer, Fasting, Wilse, and Schübeler about introduced plants. While the terms 'foreign' and 'outlandish' might appear neutral, denoting a plant's origins without any particular value judgement (the Norwegian word utenlandsk, 'outlandish', does not carry the same connotations as the English word), other terms seem more loaded. 'Strange/rare plants' (*rare/sieldne planter*), with the emphasis on unusual and odd plants, seem more akin to Wilse's somewhat negative approach. In the context of gardening, those terms give the impression of difficult and problematic plants; i.e. too challenging for Norwegian gardeners. In contrast, 'remarkable/notable plants' (*merkelig*, *merkverdige planter*) appear as positive temptations, worth trying to cultivate. The term 'strange plants' also appears in contexts that suggest that these plants were viewed as unique and exciting, in a way that no one had experienced before. The majority of such plant species were also often new, or relatively new, scientific discoveries (Hammer, 1794; Wilse, 1792). This is in line with Schnitler's use of the term 'exotic plants' in 1915. He continued a trend that one could also find in Britain, for example, where novelties from abroad were commonly called 'exotic plants'. Keeping plants in winter gardens was an exciting and challenging concept (Dixon Hunt, 1993).

There were terms that illustrate how introduced plants were perceived, and what these plants meant for garden culture in the nineteenth century. It is challenging to investigate whether and why the term 'exotic plants' was applied to plants introduced in the eighteenth and nineteenth centuries. In addition to being new to science, it seems that plants called 'exotic' had exciting appearances in terms of their beauty, strange morphology or were challenging to cultivate. Apart from 'foreign plants', it does not appear self-evident to interpret the terms above as being synonymous with the modern usage of 'alien', 'exotic' and 'non-native plants'.

There is little evidence about whether gardeners and other professionals that handled introduced plants in the past were familiar with such terms as 'exotic' and 'alien'. However, a clue can be found in the way introduced plants were represented for sale in Norwegian plant catalogues, which is explored in the following sections.

The increasing plant trade

In the late eighteenth and early nineteenth century, there were a small number of plant nurseries and markets in Norway. Plants were mainly bought from plant nurseries abroad (Dietze, 2005). From 1789 to 1806, Anker ordered frequent deliveries of plants from the company Rosenkrantz & Son in the Netherlands. The Dutch plant nursery delivered an assortment of seeds, bulbs, flowers, trees, fruit trees and vines (grapes). There was also an exchange of seeds between Bogstad and Rosenkrantz's plant nursery. In addition, Anker ordered plants from a trade contact he had in Great Britain, the company Georg and Ernst Wolff in London. Among others, common tree species ordered included *Fagus sylvatica* (Beech), *Crataegus oxyacantha* (Hawthorn) and *Thuja aucdentalis* (Thuja; Dietze, 2004).

Another example of contact with plant nurseries abroad is the Knardal estate in Southeast Norway, which ordered plants from the James Booth & Söhne nursery, in Germany. Their orders contained limited but varied plant categories such as *Dahlia* (dahlia), *Dianthus* (gilly flowers), *Camellia* (camellia), *Rosa* (rose) and stocks of various trees and shrubs. Examples of trees were *Pinus larix* (European Larch) and *Fraxinus excelsior pendula* (Ash; Dietze, 2004). This contact was frequent, and became intense in the period 1840–1860. Founded in 1797, *James Booth & Söhne* was a company with international recognition and was used by the royal households in Denmark and Sweden. James Booth & Söhne also appeared

at the Hamburg Garden and Flower Association (*Hamburger Garten- und Blumenverein*) in 1836, which contributed to their recognition (Dietze, 2007).

Another firm that appeared important for Norwegian customers was the seed trade firm J.G. Booth, also established in Hamburg. Sources from 1833 show that *J.G. Booth* was selling seeds to the Nes Verk estate in Southern Norway. The owner of Nes, Jacob Aall (1773–1844), seemed interested in introduced plants. His son Nicolai Aall (1805–1888) took this interest further and a plant catalogue from 1856 displays a diverse plant collection at Nes. Represented plant categories were, among others, orchids, geranium, chrysanthemum, fuchsia, gloxinia, erica, azalea, rhododendron, camellia, and rose. Though of different species, the plants had their recent arrival in common. In addition to Germany, orders and invoices show that Nes Verk had trade contacts abroad in Denmark, Great Britain, Australia, and Chile (Dietze, 2007).

Also worth mentioning is the estate of Ullevold outside Christiania, owned by the timber merchant John Collett (1758–1810). He lived in London for ten years before returning to Norway in 1793. He redesigned a landscape park at Ullevold, filled with introduced plants (Dietze, 2007; Schnitler, 1916). In an article about the orangery in Ullevold, Martin Flor (1772–1820), a teacher of natural history at Katedralskole in Christiania, described how 300 types of mainly introduced plants could be found there (Flor, 1813). Among Norwegian traders, Collet was outstanding in plant importation, particularly from Great Britain. He was in the lead when it came to contact with plant nurseries abroad. As there were hardly any plant nurseries in Norway, countries like the Netherlands, Germany and Great Britain became important suppliers of introduced plants.

Knowledge of plants and their specific requirements probably also reached Norway via foreign gardeners. For instance, Anker at the Bogstad estate hired the German gardener Johan Reinhold Grauer (1755–1819), whom he sent to London to learn about the latest developments in English gardens (Hammer, 1794). After returning from London, Grauer created a park in the English style at Bogstad (Dietze, 2004). In addition to the park, there were two other differently designed gardens containing a distinctive assortment of plants; i.e. a kitchen garden and a formal pleasure garden (Wilse, 1790).

Due to increasing numbers of customers, plant nurseries and market gardens became a growth business after the turn of the century (1800). In the beginning it was a slow process with challenges along the way. Following the outbreak of the Napoleonic wars (1805–1814) Norway lost its trading business with Great Britain, specifically England. As a result, trading in wood almost stopped completely until around 1840. This led to a severe economic depression for Norwegian merchants and many went bankrupt (Dietze, 2007).

The Norwegian plant trade and the establishment of plant nurseries had a significant breakthrough ca. 1850. From this time onwards, the number of inhabitants in both urban and rural areas increased. The economy was on the rise and a growing number of employment opportunities attracted people into industry and handiwork services (Skard, 1963). In the garden business, there was increasing demand for gardeners and plant materials. A new middle class gave rise to a sudden increase of suburban villas with small gardens (Bruun, 1987). Due to increased assortments of introduced plants for sale, one can assume that a romantic version of the English landscape style still had an impact on customers' demands. It was characteristic for the small villa gardens to be filled with as many garden elements as possible; the greater plant diversity the better in order to create romantic atmospheres (Bjerke, 2002). There was a significant increase in the establishment of market gardens and plant nurseries, as well as the variety of plants available, between 1851 and 1901; the number of plant nurseries trebled from 30 to 129 and the number increased further during the first half of the twentieth century (Skard, 1963).

Plant nurseries were widely distributed throughout the country in almost every province, from Vest-Agder in the south (58°–59° N) to Troms in the north (68°–70° N). An increase in the number of customers and demands for plant materials was reflected through a growing assortment of newly introduced plants. One of the largest and most well-known plant nurseries belonged to the Agricultural University of Aas (founded 1859) in Akershus, Southeast Norway. The assortment of introduced plants for sale increased significantly after the mid-nineteenth century. In 1874, the categories 'deciduous trees' (*løvtrær*), and 'smaller trees and shrubs for garden and park establishments' (*lavere træer og busker*

til park- og haveanlæg) consisted of 71 introduced species and varieties (Aas Høiere Landbrugsskole, 1874). In 1899, these categories had merged into 'deciduous trees and ornamental shrubs' (*løvtrær og prydbusker*) with 111 introduced species and varieties (Norges Landbrugshøiskole, 1899). In total, including Norwegian plants, this assortment had grown from 124 to 237 plant species for sale. The variety of coniferous trees also increased: from 1875 to 1899 the number grew from 14 to 38 species and varieties, of which 13 and 37 respectively had been introduced to Norway (Aas Høiere Landbrugsskole, 1874; Norges Landbrugshøiskole, 1899).

Another interesting example is one of the earliest and most well-known plant nurseries, *Olsen's Enke* (established 1833) in the capital, Christiania. It started as a small market garden, mainly selling seeds and soon expanded its range. In the spring of 1868, the assortment mainly contained fruit and vegetables, seeds, and pot plants for sale. There was also a small selection of ornamental pot plants, garden roses, shrubs, and trees (Handelsgartner J. Olsens Enke, 1868). Available plant categories included *Aloe* (aloe), *Rhododendron* (azalea), *Geranium* (geranium), *Fuchsia* (fuchsia) and *Chrysanthemum* (chrysanthemum). Once privately ordered only by Nes Verk from the firm *J.G. Booth*, in the 1860s these introduced plants were, in addition to the bourgeoisie traders, within easy reach of anyone. Further, Olsen's Enke could offer introduced plants for winter gardens, such as orchids and other heat-loving plants. With an emphasis on ornamental plants, in 1890 the range presented a large diversity of 89 species and varieties, the majority of which were from geographic localities outside of Norway. There was also an appreciable increase in varieties of garden rose with 43 types available (J. Olsen's Enke Frøhandel og Handelsgartneri's, 1890).

It seems that professionals dealing with plants in nurseries and markets were not familiar with the use of specific terms concerning introduced plants. In plant catalogues from the Agricultural University of Aas, the only distinction marking out introduced plants was the mention of an origin other than Norwegian. The foreign origins of 'smaller trees and shrubs' were presented separately under 'Native country' (*Hjemland*). For some reason, such information disappeared in 1875. Instead, foreign origins started to appear as additional notes, e.g. Siberian shrub, Californian tree, or 'common' (*alm./almindelig*). The latter probably denoted that a plant species was either commonly cultivated, or perhaps accepted as 'belonging' to Norwegian flora.

Demand for introduced plants seemed to increase until the start of the twentieth century (Skard, 1963). However, by glancing at the range of plants for sale in 1923, one can sense a significant decrease in deciduous trees and ornamental plants from the 1920s (Norges Landbrukshøiskole, 1923). The reason for that is as yet unclear and needs further analysis of plant introduction during the twentieth century.

Conclusion

In spite of difficult growing conditions, it seems that positive views used to dominate concerning introduced plants during the time period 1750–1900. One gets the impression that plants introduced for garden purposes were an exciting challenge, something very different from the already established cultivated plants. Having unique and challenging requirements for survival, it was impressive when garden owners succeeded in growing these newly introduced plants. In addition, the plants were also like tools that could help demonstrate the wealth and knowledge of the garden owners. With a unique history behind a particular species discovery, this possibly also contributed to the kudos associated with owning it. Hence, introduced plants were a positive contribution that could show botanic skills of the garden owners and their success in cultivating the plants.

The increasing demand for new plants from abroad reflected the positive attitude among both professional and amateur gardeners in the nineteenth century. After 1850, the boom in plant imports began for common people. The plant nurseries offered people the opportunity to get beautiful and exciting plants. One could also make a living cultivating and selling introduced plants. With the romantic approach of the English landscape style, demand for different types of plants increased. Trees and shrubs were particularly important for creating mood, atmosphere, and colourful effects. As the variety of plants available grew during the latter half of the nineteenth century, in every new edition of a plant catalogue one could sense something exciting and positive concerning the new types of plants for sale.

A change in term use also indicates a change in opinions towards introduced plants. Despite a few sceptics in the late eighteenth century, bourgeois academics wrote about newly introduced plant species with enthusiasm and curiosity. Positive tones continued to dominate in the nineteenth century, when many 'foreign plants' were recommended as modern ornamental plants, leading to growing demand for introduced plants. At the start of the twentieth century, 'exotic plants' appeared as a positive element, associated with exciting plants from abroad.

As this article intended to show, attitudes towards introduced plants certainly changed throughout the period 1750–1900. In contrast with the 'exotic' introduced plants, which were then something desirable to attain and show, there is at present a noticeably negative approach to introduced plants. In the current legislation which regulates future use of alien species, introduced plants are now looked upon as a problem. In the legislation the term 'exotic plants' is synonymous with 'alien plants', which has a rather uncomfortable tone; 'alien', in its own context appears as a rather strange adjective for an introduced plant species. Gederaas et al. (2012) consider that 'alien species' is a neutral term to be used in the context of introduced species. But the term can be used derogatorily, with the intention of inducing scepticism towards introduced plants.

Policy-makers selected the year 1800 to delimit the use of introduced plants. In this way, it seems that an important era of plant importation is in danger of being wiped away. With respect to the variations in climate and ecology in different parts of Norway, it would be relevant to compile a more differentiated legislation. More research is needed for each introduced species, the actual impact of which is dependent on their availability to spread and survive in nature. Further research will not only gather new knowledge, but also contribute to new attitudes concerning plant introductions.

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PAPER II

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A Battle of Values: a Case Study of a Blacklisted Heritage Tree represented by European Silver fir *Abies alba* Mill. in a Protected Landscape in Norway

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Abstract

Old trees in protected landscapes may be historically important, but in some cases problematic if naturalising. In this study, we investigated how a blacklisted heritage tree is valued in a protected landscape, with focus on its cultural history, invasiveness, and general management of the area. We used one European Silver fir *Abies alba* Mill. planted in the 1890s as a case plant. A historical literary approach included the landscape history, cultural values, and introduction history of *Abies alba*. We accessed management information from management plans, floristic reports, and the supervisory manager. The present spreading of *Abies alba* was recorded with GPS along transects. In an area constituting approximately 13,600 m^2, vegetation clearing and grazing have contributed to limit the invasion of *Abies alba*. Most offspring (88%) were less than 15 cm tall and found within 30 m of the parent in half-shade positions. *Abies alba* belongs to the area's cultural historical identity, but has attracted more attention as a threat for plant species richness and habitats. Cultural and historical values are generally less prioritised in the management, which is, at present, mainly the responsibility of ecological conservationists. We therefore see a need for interdisciplinary collaboration to equally consider cultural and historical values.

Keywords: introduced plants; invasive plants; heritage trees; management; *Abies alba*

Introduction

The management of protected landscapes with introduced tree species is a challenging issue, as individual trees may represent historical events and contribute to natural values. At the same time, they might be able to naturalise and spread. Native plants may suffer a major decline due to introduced plants invading their habitats (Myers and Bazely, 2003). This can be exemplified with the introduced conifer European silver fir *Abies alba* Mill., which is blacklisted in Norway due to its potential invasiveness (Gederaas et al., 2012). On the contrary, trees planted in the past in cultural landscapes are historically and ecologically important (Rossi et al., 2016).

The aim of this study was to investigate how such an introduced tree species is valued as a heritage tree in a protected biocultural landscape, with emphasis on its cultural historical background, ability to invade and management of the area. The goal is to equally consider historical, cultural and natural values in the management and conservation of introduced trees.

We found it adequate to use a protected landscape (*landskapsvernområde*) with only one remaining mature *Abies alba* specimen from the 1890s as a case plant. Historical trees in a historic site are often limited in number and usually represented by a few single specimens. There can be different reasons for this:

1. The decline of a site with less maintenance or the replanting of destroyed or dead trees (Blicharska and Grzegorz, 2014).
2. Single or few trees were planted (with special shapes and layout) to create viewpoints and special attractions during many epochs in garden history, for instance, in the 18th and 19th centuries (Hobhouse, 1992).
3. A single or a few species were planted to ‘collect’, exhibit and try out new introduced plants in parks, arboretums and gardens (known from Bogstad in Norway for instance; Dietze, 2007).

When evaluating potential risks and future problems concerning *Abies alba*, the conclusions are mainly based on examples from forestry (Øyen et al., 2007). At present, there is a lack of evidence on how *Abies alba* affects habitats and botanic species richness on a smaller scale, such as in parks or other small biocultural areas.

Abies alba is native to mountainous areas in Central Europe and was one of the earliest introduced tree species for small-scale plantings in Norway (Dahl Kjær et al., 2014). The earliest known plantings for forestry took place in the mid-1700s in Kongsberg, southeast Norway

(Schübeler, 1862; Elieson, 1881). The interest in *Abies alba* as an ornamental tree in Norway probably arose with influences from the English landscape style in the late 18th century. One of the earliest evidences of *Abies alba* for sale as an ornamental plant is a plant catalogue from 1874 (Aas Høiere Landbrugsskole, 1874). The species appeared particularly popular as an ornamental plant in parks, arboretuma and gardens in central western Norway (Schübeler, 1862).

To clarify which introduced species does not belong in the Norwegian flora, Gederaas et al. (2012, p. 12) selected the year AD 1800 as 'a historical cut-off point'. Some plant species that were introduced earlier, such as *Abies alba*, and are not considered to have established reproductive populations until after 1800, are also categorised as non-native (Gederaas et al., 2012, p. 12).

In this article, we use the term 'introduced species' as defined by Richardson et al. (2000), i.e. a species that has overcome 'a major geographical barrier' fuelled by human activity (p. 97) and relates to plant species 'associated with deliberate actions', i.e. intentionally introduced by humans (Gederaas et al., 2012, p. 11). We use the term 'non-native' synonymously with the term 'alien species', defined as follows in accordance with the International Union for Conservation of Nature (IUCN):

'A species, subspecies, or lower taxon occurring outside of its natural range (past or present) and dispersal potential (i.e. outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans) and includes any part, gametes or propagule of such species that might survive and subsequently reproduce (Invasive Species Specialist Group, 2000, p. 5–6)'.

The term 'biocultural landscape' here represents any landscape shaped by human impact over long periods of time, which has contributed to a cultural landscape with high biodiversity that depends on continued traditional use (Rotherham, 2015). We use the term 'heritage tree' to address old trees that have historical and cultural values (Blicharska and Grzegorz, 2014).

Materials and Methods

Case area

The protected landscape Austråttlunden is situated on the peninsula Ørland (63.71°N, 9.72°E) in central western Norway (Fig. 1). The area has a typical oceanic coastal climate, characterised by mild winters (mean temperature –0.2°C, December–February) and cool summers (mean temperature +12.5°C, June–August) (eKlima, 2016). Precipitation and humidity are relatively high throughout the year. As the landscape is relatively flat, winds have a strong impact. Some low hills and ridges in the northern part of Austråttlunden are natural wind barriers (Moen, 1986).

Austråttlunden covers 616,000 m^2 of forested area (Engan and Bratli, 2003) and is a remnant of a former forested landscape (Stusdal, 2006). The forest grows on low ridges that consist of loose rock materials, such as gravels from the former solid bedrock of the Devonian conglomerate and sandstone. Mires and swampy areas fill up the gaps between the ridges (Moen, 1986). Pine forest covers the larger forested parts, where Scots pine *Pinus sylvestris* L. is the dominating tree species (Skogen, 1974; Holten, 2010). Among the native deciduous trees, the dominating species are aspen *Populus tremula* L., downy birch *Betula pubescens* Ehrh., goat willow *Salix caprea* L., grey alder *Alnus incana* (L.) Moench and rowan *Sorbus aucuparia* L., which are common to boreal deciduous forests (Opheim, 1977; Engan and Bratli, 2003). Hazel *Corylus avellana* L. is very common on sunny spots (Holten, 2010).

Austråttlunden is among the prioritised floristic localities in the province Sør-Trøndelag, housing over 600 vascular plant species (Skogen, 1974). It has been a protected landscape since 1975, with the aim to "conserve a forest landscape … a rich flora and fauna and the area's valuable cultural historical traditions" (Opheim, 1977, p. 1). The purpose was also to make the area more attractive for recreational purposes (Opheim, 1977; Gangås, 1988).

The cultural history of Austråttlunden dates back to the Viking Age AD 997 (Moen, 1986). The area is an important part of the region's history, together with the nearby Austrått Manor, originally built in the 17th century (Fig. 1). It seems that local people have used Austråttlunden as a recreation area during the last 400 years. Parts of the landscape are mainly a result of long-time grazing, with a long tradition of keeping cattle and horses (Opheim, 1977). In the late 18th century, the Danish historian Schøning described Austråttlunden as a beautiful forest with

diverse tree growth and noted that it had once been an area for keeping animals (‘*dyrehave’*) (Schøning, 1910). One can interpret this as either a zoological or a hunting park, which was the first one of this kind established in Norway (Bruun, 2007). At that time, it was common to have fenced deer parks at Norwegian and Danish manors (Ordbog over det danske Sprog, 1921). Moreover, the remains of fencing from the 16th century, found in mires in the northwestern part of Austråttlunden, also indicate former animal husbandry (Gangås, 1988).

The occurrence of oak *Quercus robur* L., small-leaved lime *Tilia cordata* Mill. and wild cherry *Prunus avium* L. is a result of plant introduction. These species are probably the remains of tree plantings to increase tree diversity. Two heritage trees, one *Tilia cordata* (> 200 years old) and one *Quercus robur* (> 350 years old), are protected by law from clearing (Skogen, 1974). Currently, these trees are the only specimens preserved as heritage trees of importance to the natural qualities of Austråttlunden (Holten, 2010).

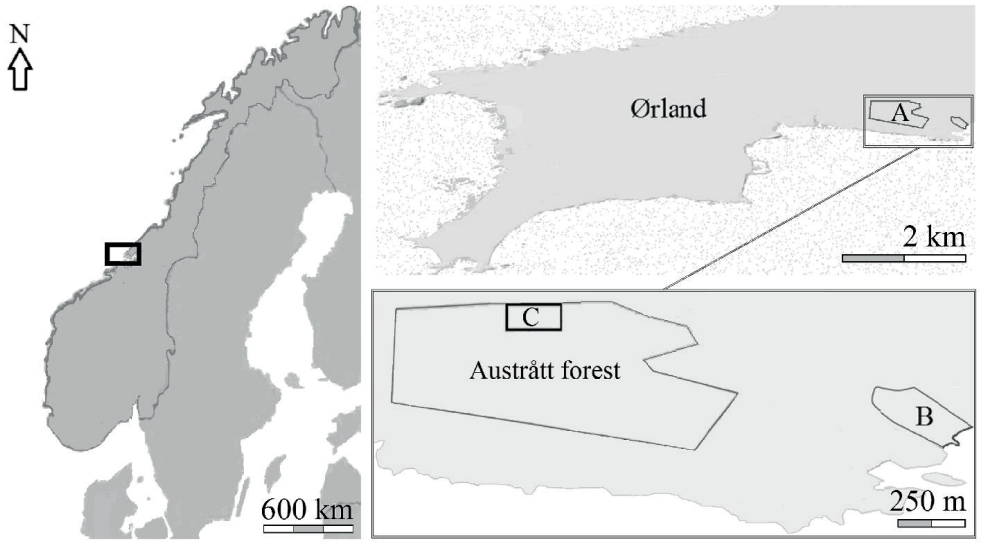

Figure 1. Location of the case area in Ørland, central coastal Norway: Austrått forest (A), Austrått Manor (B) and the transect area (C) (adapted from Kartverket 2016).

Experimental planting of *Abies alba* in Austråttlunden was presumably one method to test new species for forestry (Njøs, 1963). Because of the location and climate, a limited assortment of trees was suitable for planting. *Pinus sylvestris* and introduced Norway spruce *Picea abies* (L.) H. Karst. were the main tree species used in forestry. Another introduced conifer species in the area is European larch *Larix decidua* Mill. (Gangås, 1988).

In the last management plan of Austråttlunden from 1988, there was a description of an *Abies alba* grove. Today, however, only one historical specimen remains, which has reached an impressive growth and age.

Data collection

Initially, this study applied an ecological approach to reflect on the invasiveness *and* management of *Abies alba* in Austråttlunden. To include cultural values, we used a historical literary approach, which included the landscape history and introduction history of *Abies alba*.

Management

To assess the management strategies in Austråttlunden the past 45 years, we consulted the management plans of the periods 1977–1987 and 1988–1998 and reports based on biodiversity mapping in the municipality Ørland; in addition, we reviewed flora investigations and vegetation reports for Austråttlunden. Information regarding the present maintenance was obtained through personal communication with the supervisory manager of the area (2016). In addition, we accessed public documents from the local Department of Environmental Protection (*Miljøvernavdeling*) regarding the new management plan for Austråttlunden in 2011.

In this case study, we placed emphasis on measures [acts] to safeguard natural and historical values, with a focus on introduced plants and maintenance actions, i.e. vegetation clearing and grazing (by cattle and sheep).

Invasiveness

We collected data with a focus on the present spreading and distribution of *Abies alba* in Austråttlunden. In December 2015, with the remaining *Abies alba* (parent tree) specimen as a central starting point, we recorded offspring of *Abies alba* along 18 transects in the north–south direction. Each transect was about 90 m long. The size of the transect area covered

approximately 13,600 m^2, which corresponds to 2% of Austråttlunden. In the north, we selected the edge of Austråttlunden as a natural border to the transect area. The hill rising in the southeastern corner of the area was a natural limitation and slightly shortened the length of the last five transects in the eastern direction (Fig. 2). The distance between each transect was 10 m. We used a compass and GPS to keep straight transects. To cover as much of the selected area as possible, we recorded offspring on both sides of each transect up to about 1 m from the central line. We recorded *Abies alba* by marking the coordinates of each offspring with the help of the GPS and processed the geographical data in ArcMap 10.3.1. The exactness of the GPS coordinates varied by +/– 5 m. In addition, we recorded the following ecological parameters for each offspring:

- Height (m);
- distance to the closest tree (m), independent of species;
- estimated light conditions at each recorded offspring in the following scale: 1 ‘very dark’, 2 ‘quite dark’, 3 ‘half-shadow’, 4 ‘light’, 5 ‘very light’;
- dominant vegetation at each recorded offspring.

The term ‘seedling’ represents any offspring of *Abies alba* with a height below 15 cm. Offspring >15 cm high are referred to as saplings.

Results

Management

Since the protected landscape was established in 1975, the management of Austråttlunden has focused on natural values such as plant species richness. Cultural values are considered by making the area more accessible as a recreation area, which includes the protection of historical objects by the Norwegian Cultural Heritage Act (*Kulturminneloven*). Maintenance actions in the transect area have primarily involved the clearing of vegetation and the keeping of grazing animals (Table 1). To safeguard plant species richness and to keep an open landscape with good access to the protected heritage trees and the tombs from the Viking Age, shrubs and trees have been continuously cleared in and around the transect area in the period from 1976 to 1998. The maintenance plans exhorted clearing of particularly introduced fir trees, as they were foreign

elements and impede the development of light-demanding species (Opheim, 1977; Gangås, 1988; Table 1). In 1980–1981, the maintenance of walking tracks involved reconstructions for better access and the clearing of vegetation to keep the tracks open (Gangås, 1988). A large number of trees fell in storms in 1991 and 1992, resulting in intensive clearing in a large part of Austråttlunden (G. Bangjord, personal communication, August 8, 2016). Cattle were kept from 1978 to 1986 and replaced by sheep in 1988 (Gangås, 1988).

At present (2017), there is no management plan for Austråttlunden, since the last plan has expired in 1998. Inventories made in 2009 by Holten (2010) included assessments of maintenance strategies as a basis for a new management plan. The local Department of Environmental Protection initiated work on a new management plan in 2011, in collaboration with the Ørland municipality (Fylkesmannen i Sør-Trøndelag, 2011). In the beginning of 2013, the Ørland municipality presented a time schedule for the progress of the the new management plan (Langdahl Andresen and Arneberg, 2013). However, the plans were stalled in 2013 by the Ørland municipality (G. Bangjord, personal communication, October 4, 2017).

In the absence of a management plan, the Department of Environmental Protection has given directives on the clearing of vegetation that tends to dominate and on the continued keeping of sheep in Austråttlunden. An *Abies alba* grove was cleared in the late 1990s, but one reproductive individual remained. In the last seven to eight years, invasive introduced species, primarily *Abies alba*, Sitka spruce *Picea sitchensis* (Bong) Carrière and Norway maple *Acer platanoides* L. were regularly cleared (G. Bangjord, personal communication, August 8, 2016).

Spreading of *Abies alba*

In total, including the reproductive parent tree, 114 individuals of *Abies alba* were recorded on the transects (Fig. 2). We recorded 100 seedlings with a height from 0.05–0.15 m, which constituted the majority (88%) of the total number of records. Thirteen saplings with a height from 0.15–3 m were recorded. None of the tallest saplings had reached the reproductive age.

About 84% of the offspring occurred northwest of the parent tree, where the ground was dryer, and 65% were located within 30 m of the parent tree (Fig. 2). Offspring most distant from the parent tree were about 75–80 m away.

There was conspicuous damage due to grazing on some saplings with a height of 0.15–1 m, probably caused by elk *Alces alces*, deer *Cervus elaphus*, roedeer *Capreolus capreolus* or sheep.

Such damage appeared more extensive in the northwestern part of the transect area, where saplings were exposed without any protection from the surrounding vegetation.

The relatively dense vegetation offers sufficient shade, and the majority of the offspring (54%) grew in 'half-shade' positions, while a large number (35%) grew in 'quite dark' spots. We recorded two offspring in 'very dark' spots and eleven in 'light' spots.

Table 1. Management strategies in the transect area.

Time period	*Grazing*	*Clearing of vegetation*	*Reference*
Before 1900	For centuries, grazing by cattle and horses has presumably been a major factor that has given the forest the open grove appearance.		(Opheim, 1977)
1900–1945	Grazing which contributed to an open parklike forest, without undergrowth vegetation.		(Opheim, 1977)
1945–1976	Overgrowing, dominated by deciduous trees due to the absence of grazing.	Anthropogenic activities. Protected reserve since December 1975.	(Engan and Bratli, 2003)
1977–1978	Clearing of particular trees.	Ditch cleaning; improved drainage.	(Gangås, 1988)
1978–1986	Continuous grazing of cattle (5–10 animals, 1978–1979) and sheep (10–22 animals, 1980–1986).	Clearing of undergrowth vegetation and trees, in particular *Picea abies* and *Abies alba*.	(Opheim, 1977; Gangås, 1988)
1991–1992		Intense clearing of undergrowth and various trees (of which many broken stems due to hurricanes).	(Bangjord, 2016)[1]
1988–1998	Grazing by sheep (15–20 animals). Even grazing pressure over time.	Clearing of trees and undergrowth vegetation to prevent overgrowth, particularly new sprouts of *Picea abies* and *Abies alba*[2]. Keeping funerary monuments visible and clear from the undershrub.	(Gangås, 1988)
1984–2009	Relatively intense grazing by sheep (unknown number of sheep, 1999–2009).		(Holten, 2010)
2014–2015	Grazing by a small number of sheep from spring to autumn.	Clearing of *Abies alba, Picea sitchensis*, *Acer platanoides* and undergrowth vegetation.	(Bangjord, 2016)[1]

[1] G. Bangjord, personal communication, August 8, 2016.

[2] Njøs (1963) observed a grove of several large *Abies alba* in Austråttlunden in 1962.

The average distance between offspring of *Abies alba* and the closest tree (any species) was 1–1.5 m. The forested part of the transect area was mixed with both deciduous and evergreen trees, of which *Betula pubescens*, *Corylus avellana*, *Picea abies* and *Pinus sylvestris* were the dominant species. The great wood-rush *Luzula sylvatica* (Huds.) Gaudin was the dominating herbaceous vascular plant in the transect area.

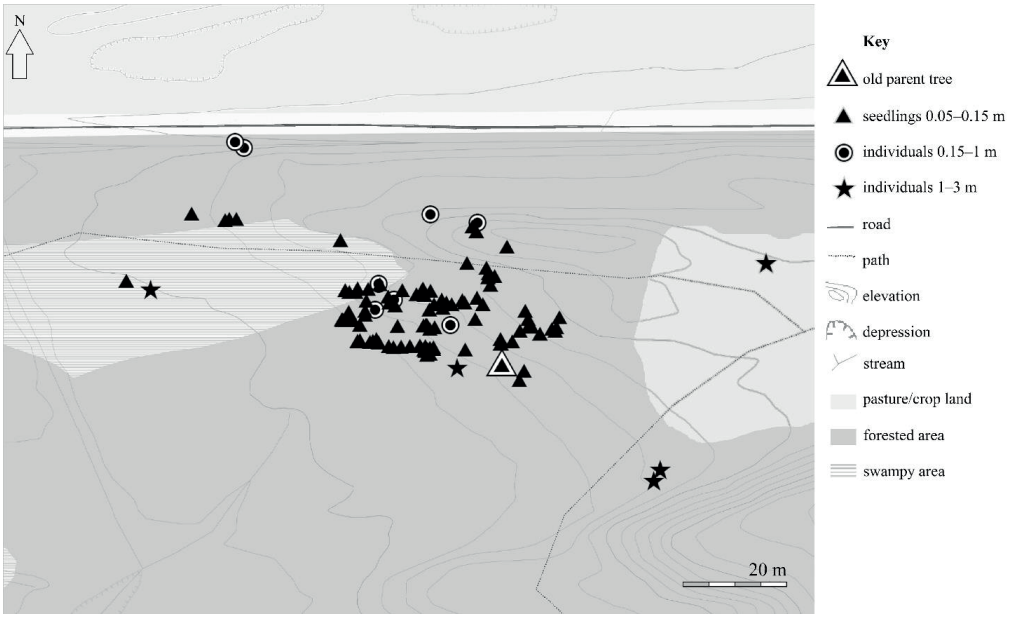

Figure 2. Recorded offspring of European silver fir (*Abies alba* Mill.) in the Austrått forest (processed in ArcMap 2016).

Discussion

The ability to invade

Due to small windborne seeds, a juvenile period shorter than 15 years and short intervals between large seed crops, some conifers are excellent in colonising new areas once established (Richardson and Rejmánek, 2004). The risk assessment of *Abies alba* in the Norwegian Black

List states that it has a high invasion potential, but a minor effect on native species and habitat types (Gederaas et al., 2012). When conifers invade an area, this can cause rapid and substantial changes in the affected habitat (Saure et al., 2013), alters the distribution and dynamics of vegetation lifeforms and affects nutrient cycles and hydrological conditions (Carrillo-Gavilán et al., 2010).

Richardson and Rejmánek (2004) characterise *Abies alba* as less invasive (negative Z-score) than many other conifer species. Richardson et al. (2000) define invasive plants as 'naturalised plants that produce reproductive offspring, often in large numbers, at considerable distances from parent plants … and thus have the potential to spread over a considerable area' (p. 98). The present situation with *Abies alba* appears not that dramatic in Austråttlunden, since few or no offspring have reached the reproductive age.

In this study, we recorded 113 offspring of *Abies alba* along the transects. As we did not cover the area completely, several seedlings were probably left out. In spite of effective spreading, the seedlings are vulnerable and grow slowly in the first five to six years (Roll-Hansen, 1956). Among offspring established in recent years in Austråttlunden, few (12%) have survived to reach a height of more than 15 cm.

Our study shows that the most intense establishment of seedlings occurs close to the parent tree, within a radius of 30 m. A rather high seed mass (on average 43 mg) may prevent the seeds from spreading far, compared with many other conifer species (Rejmánek and Richardson, 2003). As the ground southeast of the parent tree seemed more disturbed by grazing and clearing, the conditions seemed more favourable for *Abies alba* seedlings to establish northwest of the parent tree (Fig. 2).

The grazing pressure by cattle (1978–79) and sheep (1980–present) has been more or less continuous during the last three decennia (Table 1). In addition to sheep, wild ungulates occur in the area. It seems that *Abies alba* attracts deer, elk and roedeer, which is supported by observations by Østraat (1999), Skre (2001) and Tonjer (2011). Häsler and Senn (2012) suggest that *Abies alba* is primarily an occasional food eaten by ungulates when other food is scarce, which can limit the survival of saplings.

Light condition is another factor that influences the regeneration of *Abies alba* (Santopuoli et al., 2016). Most of the offspring that we recorded grew in half-shade and relatively dark locations in Austråttlunden. Boncina (2011) supports the statement that *Abies alba* is a

remarkable shade-tolerant species. Even under conditions in which light is reduced by 80–95%, saplings of *Abies alba* may survive for 10–20 years (Robakowski et al., 2004). Considering the number of deciduous trees in the transect area, this may also contribute to the thick ground cover of organic litter, which, together with mosses, can limit the soil contact for seeds (Vikane et al., 2013).

According to the last management plan, the pressure from grazing by sheep was too low in the period from 1980 to 86. As a result, the suggestion to clear *Abies alba* remained in the last management plan (1988–1998) in order to facilitate the growth of deciduous trees (Gangås, 1988). We assume that maintenance actions suggested in the last management plan were carried out, considering the low number of *Abies alba* saplings >1 m (Table 1). In recent years, vegetation clearing has primarily covered invasive species, including *Abies alba* (G. Bangjord, personal communication, August 8, 2016).

In terms of the management of introduced conifers, careful observations are necessary to prevent invasions in areas that are sensitive to disturbance (Carrillo-Gavilán et al., 2010; Saure et al., 2013; Vikane et al., 2013). Even though today, the spread of *Abies alba* seems to be under control in Austråttlunden, we hardly know how the species would interact with its environment if it spreads more aggressively. There is little expectation in Norwegian forestry that the presence of *Abies alba* will affect native species (Myking, 2013). This may, however, change over a longer period if *Abies alba* successfully reproduces, with little competition with other species, and benefits from climate change.

In western coastal Norway, investigations on the spreading of introduced Sitka spruce *Picea sitchensis* in heathlands provide an idea of how an invasive conifer could potentially affect its environment (Saure et al., 2013; Vikane et al., 2013; Saure et al., 2014). The location of these studies is quite similar to the region where Austråttlunden is located, with a similar climate with mild winters and high precipitation. Saure et al. (2013) found that the number of light-demanding species decreased below the canopies of *Picea sitchensis* in invaded heathlands. Their study corresponded to other studies of invading tree species in formerly treeless habitats (see e.g. Richardson et al., 1989; Jäger et al., 2007) where plant species richness was reduced. Nevertheless, there was an increased number of shade-tolerant plant species and liverworts (Saure et al., 2013). Vetaas et al. (2014) argue that introduced conifers, in exceptional cases, may even contribute to ecological restoration.

Management of natural, cultural and historical values

The conservation of different values in Austråttlunden is a subject of debate and tension. Important natural values are plant species richness, which involves red-listed species such as the marsh orchid *Dactylorhiza majalis purpurella* (T. and T.A. Stephenson) Soó (Skjoldager, 2012) and unique and vulnerable habitats dependent on continued traditional activities. Cultural values are reflected in the local people's relation to Austråttlunden. Most people use the area for recreation and nature experience (Skanke, 2014). Recreational activities are, among others, walking, horse riding and hunting. Many people are emotionally connected to the area and perceive it as an important historical site. The unique history is part of the area´s identity, and the lack of maintenance negatively affects Austråttlunden. With respect to the area´s historical character, according to local people, the clearing of vegetation must be discrete to not affect or destroy historical values (Skogheim et al., 2017).

A small part of Austråttlunden (*Lundahaugen*) is conserved as an open cultural landscape, whereas the remaining part of the area is to be preserved as a 'natural forest'. The border between these areas is diffuse and challenges the maintenance of the area (G. Bangjord, personal communication, October 4, 2017). Skanke (2014) argues that the protection regulation (*vernebestemmelse*) of Austråttlunden is more suitable for a primeval forest than a historical and recreational landscape, by prohibiting activities that might affect the area in a way that can harm its ecological environment. This also applies to the removal or destruction of plants, dead wood and fallen trees, except for the vegetation cleared in accordance with a management plan.

Among the protected areas in Europe, several permit certain activities to maintain historical and human-modified landscapes and traditional activities. The management of historical values is, however, not a top priority in these cases, compared to the management of natural values such as biodiversity (Linnell et al., 2015). Skjoldager (2012) found that there are significant differences between the conservation of natural and historical values in Austråttlunden. This supports our findings that the management has, to a large degree, focused on plant species richness rather than on historical objects. It seems that the conservation of natural values reduces the meaning of cultural values. The natural values are well mapped and protected by the Norwegian Nature Diversity Act (*Naturmangfoldloven*), whereas the conservation of historical

values is fortuitous and less prioritised (Skjoldager, 2012). The Norwegian Cultural Heritage Act protects only cultural heritage that can be dated back to 1537 or earlier (Lovdata, 2015b).

Plant introduction is an important part of the cultural historical traditions in Austråttlunden, although it is presently not valued as that. As the interests in forestry have diminished, the remaining *Abies alba* specimen represents a monument from the time of experimental plantings. In addition, it may house sentimental values for local people. In this sense, G. Bangjord (personal communication, October 4, 2017) expressed that cultural historical nostalgia has led to the protection of this historical *Abies alba* tree.

If all values are of equal importance, can an invasive heritage tree such as *Abies alba* be an important contribution? Large old trees in good condition are, with their impressive stature, beautiful and majestic. Solitary trees may serve as 'heritage trees' and 'living history trees' with cultural historical as well as ecological functions (Blicharska and Mikusinski, 2014, p. 1561, 1563). Because *Abies alba* is a potential threat towards plant species richness and habitats, the values which make the historical specimen interesting have been strongly reduced. For a visitor, a historical *Abies alba* tree may appear as interesting as the preserved and protected *Quercus robur* and *Tilia cordata*. There are signs presenting natural and historical values along a walking track that runs through Austråttlunden. The *Abies alba* specimen cannot be easily accessed from the walking track, and its historical background is presently not indicated.

To cover cultural, historical and natural interests, collaborations between local representatives, the municipality and the Department of Environmental Protection are required. In accordance with the protection regulation of Austråttlunden, a committee, consisting of four people, is currently responsible for the maintenance of the area. Appointed by the municipality, the County Board and the Department of Environmental Protection, it appears that the people currently involved in the management of Austråttlunden are mainly professionals in nature conservation (Skanke, 2014). In order to equally address the different values of interest in Austråttlunden, management strategies that cross the boundaries of different disciplines are required

Conclusion

This study found that the historical values attract less attention than natural values in protected biocultural areas such as Austråttlunden. *Abies alba* is part of the area's cultural historical

identity, but has attracted more attention as a threat towards native plants and their habitats. However, the variation in the landscape, including rare and historical trees, also is part of the people's cultural identity. In order to safeguard the diversity of natural, historical and cultural values, the management plans need an interdisciplinary approach. In this context, the recognition of values is the first step and requires the involvement of professionals from different disciplines.

Legislations such as the Norwegian Black List focus on the impacts of invading trees, esp. when they appear in large numbers. However, mainly in historical sites, the impact is usually low. Our study shows that single trees with the ability to spread have less impact as long as they are carefully managed. In Austråttlunden, such management mainly involves vegetation clearing and grazing by cattle and sheep. In addition to limit the invasion of *Abies alba*, continued maintenance is necessary to prevent overgrowth by other plant species and to conserve an open cultural historical landscape. This requires a sufficient allocation of resources to manage both cultural and biological diversity.

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PAPER III

Past anthropogenic dispersal of introduced European silver fir *Abies alba* Mill. in Norway was revealed by reduced representation sequencing

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Abstract

Many old trees may remain as monuments from a time of experimental and ornamental plantings, but their historical records are often few, little explored or missing. In Norway, few studies combining historical records with genetic data have been conducted to resolve dispersal routes for introduced plants. The aim of this study was to investigate dispersal routes of the European silver fir, *Abies alba* Mill., by investigating the genetic relatedness between old trees, using genotyping by ddRAD sequencing. For this study, we collected plant material from eight trees planted in the late 1800s and the early 1900s in central coastal and southeast Norway. Literary sources were studied to obtain information about the historical background of each sampling site. The ddRAD libraries were established from total genomic DNA isolated from needles of each sampled tree and sequenced. Genetic diversity, phylogenetic analysis and population structure results allocated these eight trees to three populations. Close genetic relatedness was revealed for three trees in one population, which supported historical literary records on collaborations regarding the plantings of these trees. The remaining five trees were allocated to two populations, which reveal possible dispersal scenarios of *Abies alba* to these sampling sites. In cases where historical data is missing, we find that genotypic data from ddRAD sequencing can reveal origin and help to predict past dispersal of introduced trees.

Keywords: introduced plants; introduction history; plant genetics; RADseq; *Abies alba* Mill.

Introduction

Determining the place of origin of introduced plant species and specimen is of interest primarily to understand the history of the introduction. In particular, it helps to determine how, why and when a new plant species was introduced to a particular locality.

During the last two decenniums, methods and techniques that generally appear in natural sciences have been involved in research related to the use of plants in garden history and garden plant history (Moe et al. 2006). Regarding the dispersal of introduced plants, historical sources are limited and may be hard to access. The involvement of new research techniques has provided significant amounts of new data (van Etten and Hijmans 2010). Among other disciplines, archaeology has, until now, been particularly involved in the investigation of former gardens that have disappeared or that might exist below a present younger garden in a layer below the visible ground surface. In terms of garden plants, pollen analysis has become an important contribution, albeit dependent on the representation of the produced pollen spectra (Grüger 2013). Other micro-botanical remains are silica-formed phytoliths, which exist in many higher plants and are particularly useful when studying the origins and dispersal mechanisms of plants (Horrocks 2013a). Under certain conditions, plant macroremains may be well preserved. There are various techniques to recover different kinds of soils and sediments in order to identify plant remains to the species level (Horrocks 2013b).

Another discipline that plays an important role in historical research is genetics. For example, in anthropology, the combination of genetics and archaeology is a well-established method to reconstruct the origins and migratory patterns of modern humans (Black et al. 2006). In studies of lines of family descent for individuals with unknown origin, genetic data have become a commonly used tool to estimate genealogical relatedness (Kalinowski et al. 2006). This is particularly helpful when studying a species' introduction history, where genetic data can help to clarify dispersal routes hypothesised through historical records of anthropogenic actions (Willows-Munro et al. 2016).

The use of genetics in botany had a new breakthrough in the 1990s (Nybom et al. 2014). As archaeobotany and zooarchaeology are the primary means of documenting historical flora and fauna, genetic data is another evolving source of evidence to identify species introduced in the past (Witcher 2013). Regarding the dispersal of introduced plants, genetics can contribute with new sets of data linked to and compared to historical records.

Historical records may contribute with information about local history and activities that occurred; such information may involve how landowners used their land and why they introduced plants. When such records are hard to access or are completely lacking, genetic data may be able to complement and support existing knowledge or to indicate the origin of

introduced plants, their dispersal and the relatedness to other plants of the same species within a particular region or country. In addition, such data may also indicate whether landowners collaborated.

As reflected on above, the combination of information based on genetic data and historical records is not a new approach. In Norway, a limited number of studies have been carried out to investigate the introduction history of ornamental plants. One example is Salvesen et al. (2009), who used amplified fragment length polymorphism (AFLP) to fingerprint and examine if this could support the provisional classification of the genus´ *Buxus* L. based on morphological characteristics and further to substantiate whether the investigated specimens represent ancient cultivars.

Studies of genetic relatedness among plants are usually approached through phylogenetic analyses, aiming to deduce accurate and comprehensible relationships among taxa. In the early 1990s, systematists started to use polymerase chain reaction (PCR) for amplification of DNA polymorphism and utilisation in phylogenetic analyses (Chase et al. 1993).

However, phylogenetic studies are generally expensive and labour-intensive. Miller et al. (2007) therefore presented a high-throughput, low-cost method to identify and type numerous RAD (restriction-site associated DNA) markers on a microarrays, which are easy to produce for any kind of organism. Since its development in 2008, RADseq (Restriction-site associated DNA sequencing) has emerged as a cost-effective genotyping method (Ree and Hipp 2015; Andrews et al. 2016). Today, RADseq and a modification of this approach, ddRAD (double-digest RAD; Peterson et al. 2012), are widely used for the discovery and genotyping of SNPs (single nucleotide polymorphisms) and allow investigators to detect and score SNPs randomly dispersed across a target genome (Baird et al. 2008; Davey and Blaxter 2011).

In recent years, quite a few phylogenetic studies involving RADseq have been published (Ree and Hipp 2015). Eaton and Ree (2013) used RADseq data to resolve recalcitrant phylogenetic relationships within the angiosperm genus *Pedicularis* L. (Orobanchaceae, the broomrape family). In spite of relatively short sequences, RADseq generates data sets from a large number of loci (Eaton and Ree 2013), and accesses more nuclear genome markers than microsatellites (simple sequence repeats; Ree and Hipp 2015).

The tools for high-throughput genotyping (for example SNP arrays) are, however, limited for non-model organisms, i.e. a category of less studied organisms (da Fonseca et al. 2016), among others, many plant species. Due to the amount of information one can obtain rapidly with a small budget, RADseq data has quickly become widely used in studies of genetic relatedness (Ree and Hipp 2015; Eaton et al. 2016), regardless of the studied organisms (da Fonseca et al. 2016) and irrespective of the taxonomic level (Zimmer and Wen 2015). Based on these favourable properties, we applied RADseq in this study.

The demand for introduced plants in Norway considerably increased in the 19th century. In garden art, for instance, the plants could contribute to the people's social status (Dietze 2007). As the Norwegian economy was on the rise at the mid-1800s, forestry was an important contribution. *Abies alba* Mill. (European silver fir) has a natural distribution in the Central European mountainous regions, with its most northern natural range in central Germany (Parducci et al. 1996). It was a popular timber tree over centuries (Farjon 2014), introduced to Norway in the mid-1700s as a forestry tree (Schübeler 1862; Elieson 1881). *Abies alba* (*A. alba*) was then a promising timber tree due to its fast growth and excellent wood (Elieson 1881). In addition to forestry, *A. alba* also found its way into Norwegian garden culture. As influences from the English landscape style dominated Norway in the mid-1800s, it seems this might have fuelled the interest for *A. alba* as an ornamental tree. Soon, it appeared as an ornament in many gardens, parks and arboretums (Schübeler 1862). A plant catalogue from 1874 reveals its popularity as a garden tree in the 19th century (Aas Høiere Landbrugsskole 1874). In a region with a harsh climate and difficult conditions for growing introduced species, *A. alba* appeared as a good substitute for exotic tree species.

Even though several old *A. alba* trees have survived as living monuments from the late 1800s, there are few historical records regarding their introduction and life histories. Such knowledge appears relevant to conserve, as large old trees can function as important cultural historical heritages (Blicharska and Mikusinski 2014). Plant species introduced and distributed in Norway may originate from the same local plant nurseries, planted with seeds from the same or closely related parent trees.

In this study, we determine the genetic relatedness between old trees of *A. alba* in order to provide new insights on the anthropogenic dispersal routes of this species. This study also functions as an evaluation of the methodological approach, with reflections on combining historical records and genetic data when investigating possible dispersal routes.

Materials and Methods

Table 1. Material and biometric data of *Abies alba* Mill., European silver fir, used in the study.

Sampled tree	Collector and date	Locality were collected	Circumference (metres)	Height (metres)	Planting year (estimated)
1	Ridbäck U 10.29.2015	Austråttlunden, Brekstad	3,6	16 (top broken)	1890s (Njøs 1963)
2	Ridbäck U 10.29.2015	Reins Kloster, Rissa	1,4	14	Century turn 1900/early 1900s[1]
3	Ridbäck U 10.30.2015	Fjæraskogen, Rotvoll, Trondheim	2,5	22	Late 19th century (Fremstad 2009)
4	Ridbäck U 10.30.2015	Elsterparken, Ila, Trondheim	2,6	24	1871–1896 (Jansen and Svendsen 1954)
5	Ridbäck U 10.28.2015	Skånes, Levanger	1,6	12	Century turn 1900/early 1900s[1]
6	Ridbäck U 10.28.2015	Skånes, Levanger	1,8	13	Century turn 1900/early 1900s[1]
7	Ridbäck U 10.28.2015	Skånes, Levanger	1,6	15	Century turn 1900/early 1900s[1]
8	Ridbäck U 11.13.2015	Fougnerhaugen, Aas	2,2	25	Later half of the 1800s (Misvær 1926)

[1] No reference to support approximate time of planting.

Figure 1. The sampling sites of *Abies alba* Mill. in central coastal Norway (1–7) and southeast Norway (8). The complete arrow is based on historical sources and dashed arrow shows assumed collaboration indicated by sources.

Plant material

Fresh needles from eight *A. alba* trees, situated in five localities in central coastal Norway and one locality in southeast Norway (Fig. 1), were collected in October 2015 and immediately dried in silica gel. In addition, biometric data were recorded from measurements of stem circumference (1.5 meters above the ground) and height (estimated). As old stems of *A. alba* are not evenly round, the exactness of the circumference varied +/- 5 cm (Table 1).

The distances between the localities in central coastal Norway varied by about 10–70 km. The region has a long history of plant introductions, and a local garden culture was established in Trondheim in the late 17th century (Balvoll and Weisæth 1994). It seems that *A. alba* became a particularly popular tree in forestry as well as an ornamental plant in alleys, parks and gardens in the 19th century (Schübeler 1862).

Austråttlunden (sample 1; Fig. 1) is a recreation area situated about 4 km outside Brekstad municipality, on the peninsula Ørland (63.70°N, 9.71°E). It has a long history as a recreation area; former landowners used parts of it as a pleasure park back in the 17th century (Bruun 2007). The Danish historian Gerard Schøning described the area in the late 18th century as a beautiful forest with a diversity of trees. He indicated that animals were kept in the areas, either in a zoological park or for husbandry (Schøning 1910). Austråttlunden is, at present, mainly covered by native forest, dominated by pine trees (*Pinus sylvestris* L.) and complemented by a variety of native deciduous tree species. There is also a cultural historical part, marked by grazing and forestry.

Abies alba was introduced in Austråttlunden in the late 19th century in the context of a planting experiment (Njøs 1963). Today, only one old tree remains.

Reins Kloster (sample 2; Fig. 1) is a recreation site located on the remains of a former monastery, later developed into a landscape park with an arboretum. The area is situated outside the municipality Rissa (63.56°N, 9.91°E). In the years 1864–1899, Thomas E. Horneman (1819–1899) owned the manor at Reins Kloster (Horneman 2016). He planted a diversity of introduced pines and conifers in the late 1800s, with the aim to establish an arboretum on his property; *A. alba* was only one of many introduced conifers. Horneman received help from the Trondheim-based city engineer Cark Adolf Dahl (1828–1907), who collaborated with the forester Johannes Schiøtz (1835–1897) (Horneman H, personal communication, 18 January 2016). Dahl and Schiøtz organised experimental plantings in and outside Trondheim in the period from 1860 to 1880 (Bull and Jansen 1926). Horneman is assumed to have been involved in the contemporary plantings of *A. alba* in Austråttlunden, as the owners of Reins Kloster and Austråttlunden at this time knew each other (Johansen D, personal communication, 1 Dec 2015).

Elsterparken (sample 4; Fig. 1) is situated at Ila, the western part of Trondheim (63.43°N, 10.35°E). The area is part of Bymarka, where a large planting project took place from 1871 to 1896, led by Schiøtz and his assistant Kristian Elster (1841–1881), after whom the park is named (Jansen and Svendsen 1954). Until 1921, about 25,000 specimens of *A. alba* were planted in Bymarka (Fremstad 2008). One of the oldest trees that remains from the original plantings of *A. alba* still grows in Elsterparken, next to a monument in the remembrance of Schiøtz (author's comment).

Fjæraskogen (sample 3; Fig. 1) is situated in the area Rotvoll, the eastern part of Trondheim (63.43°N, 10.48°E). *Abies alba* occurs in an area which probably was a part of a park established there around 1800. It is assumed that the conifers, in particular Norway spruce (*Picea abies* (L.) H. Karst), are remains of plantings by Grev Schmettow (Fremstad 2009). The introduction of *A. alba* might also have been part of the contemporary planting projects in Trondheim.

Skånes (samples 5, 6 and 7; Fig. 1) is a recreation area in Levanger, northeast of Trondheim (63.77°N, 11.38°E), situated northwest of the Levanger city centre (Nilsen 1996). The area houses a cultural historical landscape with prehistoric attractions, among others, a former fortification (1643/1645– 1746/1747) (Hallan 1969; Kolberg 2011). The area has a long history of farming, with remains of a former windmill, an old farmhouse and pastures with high plant diversity, indicating significant and long-term grazing (Nilsen 1996). *Abies alba* was likely introduced to the area as a forestry tree at the century turn 1900.

The locality in southeast Norway, *Fougnerhaugen* in Ås municipality (sample 8; Fig. 1), is located about 450 km away from the other localities in this study (59.66°N, 10.76°E). Fougnerhaugen is known as the arboretum of the former Agricultural University of Norway

(presently Norwegian University of Life Sciences) and is located 2 km west of the centre of Ås. It is an interesting site for this study, as there used to be a plant nursery (established 1858) at the agricultural univerity (Misvær 1926), which appears as an important distributor of introduced plants, particularly in southern Norway (Skard 1963). Several conifer species that were for sale were also planted in the arboretum. We expected that the selected *A. alba* trees in Fougnerhaugen were less related to the trees from the other localities. In a phylogenetic perspective, this tree may function as an 'outgroup' in comparisons.

Historical sources

Literary studies on cultural history and plantings of *A. alba* were carried out for each sampling locality. With emphasis on the introduction of forestry and ornamental tree species, historical records were accessed from the Department of Plant Sciences at the Norwegian University of Life Sciences in Ås and from the National Archives in Oslo. Printed material, such as plant catalogues and booklets about forestry, constituted the main sources found in the archives. With an emphasis on the potential genetic relatedness between the trees selected for this study, a hypothetical dispersal route of the sampled trees was established, based on the historical sources (Fig. 1).

DNA extraction, ddRAD library preparation and sequencing

Total genomic DNA (gDNA) was isolated from needles of each of the eight trees, using the DNeasy® Plant Mini Kit (Qiagen), following the manufacturer's instructions with minor variations in order to recover a sufficient amount of genomic DNA. The quality of the gDNA was determined by agarose gel electrophoresis and UV absorbance (NanoDrop, Thermo Scientific) and quantified using fluorescence measurement (Qubit®, Invitrogen, Thermo Fisher). The high-molecular weight DNA samples were normalised to 500 ng and prepared for sequencing, according to the ddRAD protocol described by Peterson et al. (2012). Briefly, DNA was digested to completion, using the restriction enzymes *EcoR1* and *Msp1* (NEB), uniquely barcoded and size-selected by running the samples on a 2% agarose cartridge on Pippin Prep (Sage Scientific) to isolate fragments in the 500-650 bp range. The final library was validated by quantification using a Qubit® 2.0 Fluorometer and the Qubit® dsDNA BR Assay Kit (Invitrogen™, Thermo Fisher); size analysis was performed using a 2100 BioAnalyzer system with a DNA High Sensitivity Kit (Agilent Technologies). Sequencing was performed using a MiSeq Sequencer (Illumina) and a 600-Cycle MiSeq Reagent Kit v3 in a paired-end mode, generating 2 x 250 bp reads.

RAD-seq data analysis

Consensus tags were constructed and SNPs (Single Nucleotide Polymorphisms) detected using STACKS v1.18 (Catchen et al. 2013). Default settings for the denovo_map pipeline were used, with the following exceptions: reads were trimmed to 240 bp and -m and -M values were both set to 4. To simplify the subsequent analysis, stringent filtering was used to identity tags detected in all eight samples and containing only a single SNP.

Phylogenetic and PCoA analysis

The final SNP genotype data obtained for the eight trees from the STACKS program was used to derive the genetic distance matrix, using the GenAlEx software version 6.5 (Peakall and Smouse, 2012). From the obtained distance matrix, a phylogenetic tree was calculated using BIONJ (Gascuel, 1997), which is an improved version of the neighbour-joining algorithm implemented in the program phylogeny.fr (Dereeper et al. 2008). Principal coordinate analysis (PCoA), based on a dissimilarity matrix, was performed for differentiation in trees, using the GenAlEx software version 6.5 (Peakall and Smouse, 2012).

Population structure analysis

To infer the population structure, 642 SNPs were employed and the “admixture” model-based approach, together with the correlated allele frequency model, was implemented in the STRUCTURE software version 2.3.4 (Pritchard et al., 2000), as described by Kovi et al. (2015). Briefly, initial STRUCTURE runs were carried out with a length of burn-in of 10,000 and an MCMC (Markov Chain Monte Carlo) of 50,000. Eight independent simulations were conducted, allowing K (number of subpopulations) to vary from 1 to 8. Once inferring the true K, we implemented more stringent parameters with a length of burn-in and an MCMC of 200,000 each, with eight independent simulations of K, varying from 1 to 8. The best K was determined by the log likelihood of the data (LnP(*D*)) in the STRUCTURE output and an ad hoc statistic ΔK based on the second-order rate of change in LnP(*D*) between successive K values (Evanno et al., 2005), using Structure Harvester (Earl and Vonholdt, 2012) and CLUMPAK (Kopelman et al., 2015).

Genetic diversity and analysis of molecular variance (AMOVA) analysis

The SNPs derived from STACKS program were filtered in order to perform molecular diversity analyses. The SNPs with more than 10% missing genotypes and with minor allele frequency (MAF) <5% were removed. We used the SNP genotyping data, obtained after filtering, for calculating expected heterozygosity (H_e) and observed heterozygosity (H_o), using the ARLEQUIN software 3.5.1.3 (Excoffier et al., 2010). The AMOVA was performed to estimate the variance between

populations and among genotypes within populations, using the ARLEQUIN software 3.5.1.3 (Excoffier et al., 2010).

Results

Historical source

Historical literary sources indicated connections between the people involved in plantings of *A. alba* in Elsterparken (tree 4), Reins Kloster (tree 2) and Austråttlunden (tree 1) in central coastal Norway (Table 1, Fig. 1).

SNP discovery

On average, 2 M sequences (±500 K) were obtained for each sampled tree with the STACKS pipeline. A total of 72,342 tags were constructed from the forward read, with 24% of them (17,202) containing 1 or more SNP variant. Due to a lower sequence quality, fewer tags were generated in the reverse read (11,668), although a similar proportion of these (28%; 3,219) contained one SNP. Monomorphic markers were removed from the analysis. Finally, 642 SNPs were retained for the population genetic analysis.

Phylogenetic and PCoA analyses

The phylogenetic tree calculated using BIONJ (Gascuel, 1997) clearly separated the eight trees into three groups: group 1 (trees 1, 2 and 4), group 2 (trees 3 and 6) and group 3 (trees 5, 7 and 8; Fig. 2). The PCoA based on the dissimilarity matrix also separated the eight trees into three groups; however, tree 8 was located closer to the trees 1, 2 and 4. The first and second principal coordinates explained 23.67 and 20.46%, respectively, of the molecular variance (Fig. 3).

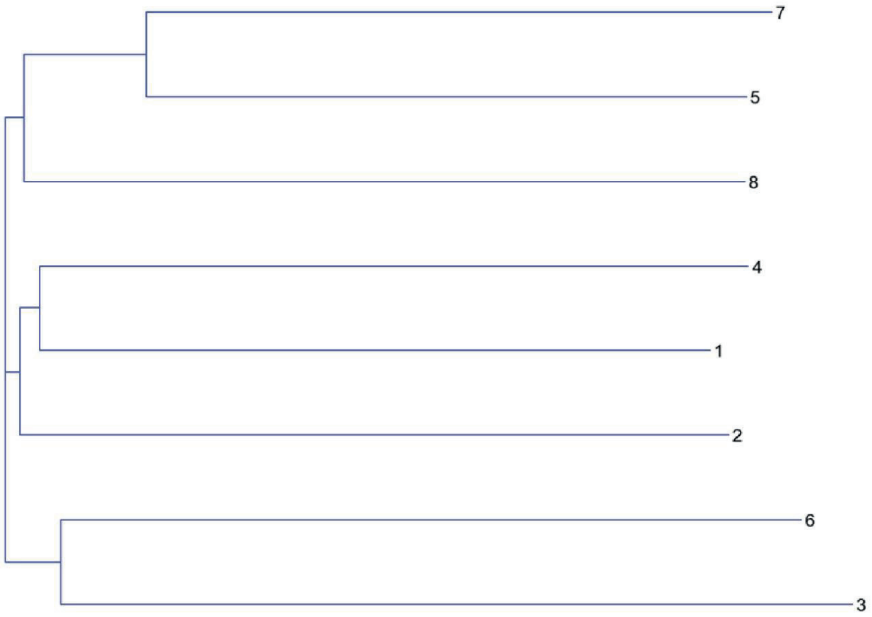

Figure 2. Phylogenetic tree based on the genetic distance between *Abies alba* specimens. Eight trees were classified into three groups (populations).

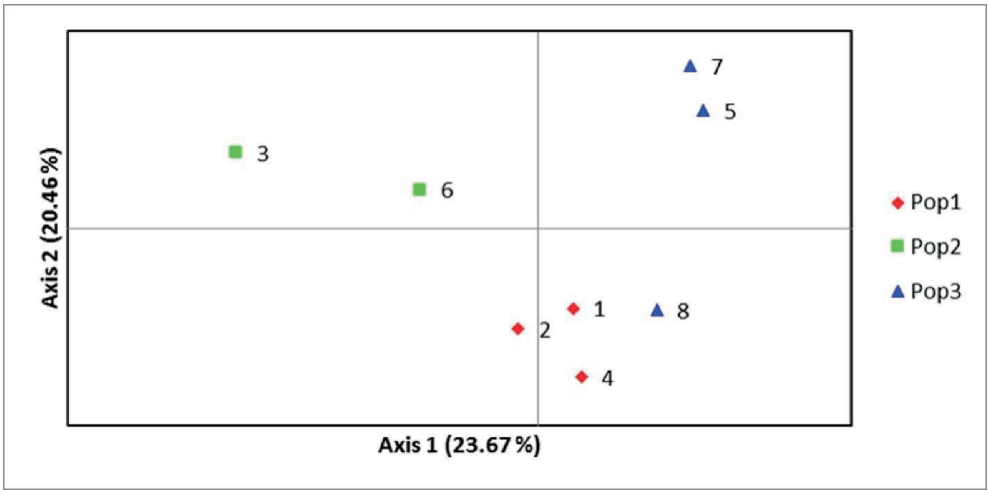

Figure 3. Principal coordinate analysis (PCoA) of eight *Abies alba* trees. The different colours represent the three populations. The first and second principal coordinates account for 23.67 and 20.46%.

Population structure

The LnP(D) value for each given K (number of subpopulations) slightly decreased from 1 to 3 and gradually decreased between 4 and 8 (Fig. 4A). The second-order likelihood (ΔK) was calculated and the maximum ΔK value obtained at K = 3. Both Pritchard's and Evanno's methods confirmed a K-value at 3 (Fig. 4A). This indicates that the most probable genetic subdivision among the eight trees has the statistical K-value 3, and hence best illustrates how the trees are related to one another (CLUMPAK; Fig. 4B). The bar plots at K = 3 showed higher proportions of presumable alleles for trees 5 and 7 (orange) and trees 3 and 6 (black).

Genetic diversity and AMOVA

Based on the phylogenetic and population structure analysis as well as on the results of the PCoA, the eight trees were grouped into three populations. Population 1 (Pop1) consisted of trees 1, 2 and 4; population 2 (Pop2) consisted of trees 3 and 6; population 3 (Pop 3) consisted of trees 5, 7 and 8. The observed heterozygosity was higher than expected heterozygosity in all the three populations (Table 2). F_{IS} (the inbreeding coefficient) was negative in all three populations, implying a considerable degree of outbreeding. The analysis of molecular variance (AMOVA) for the three populations revealed that 93.2% ($P < 0.0068$) of the genetic variation is found within individuals, whereas 6.8% ($P < 0.0001$) of the genetic variation is found among populations (Table 3).

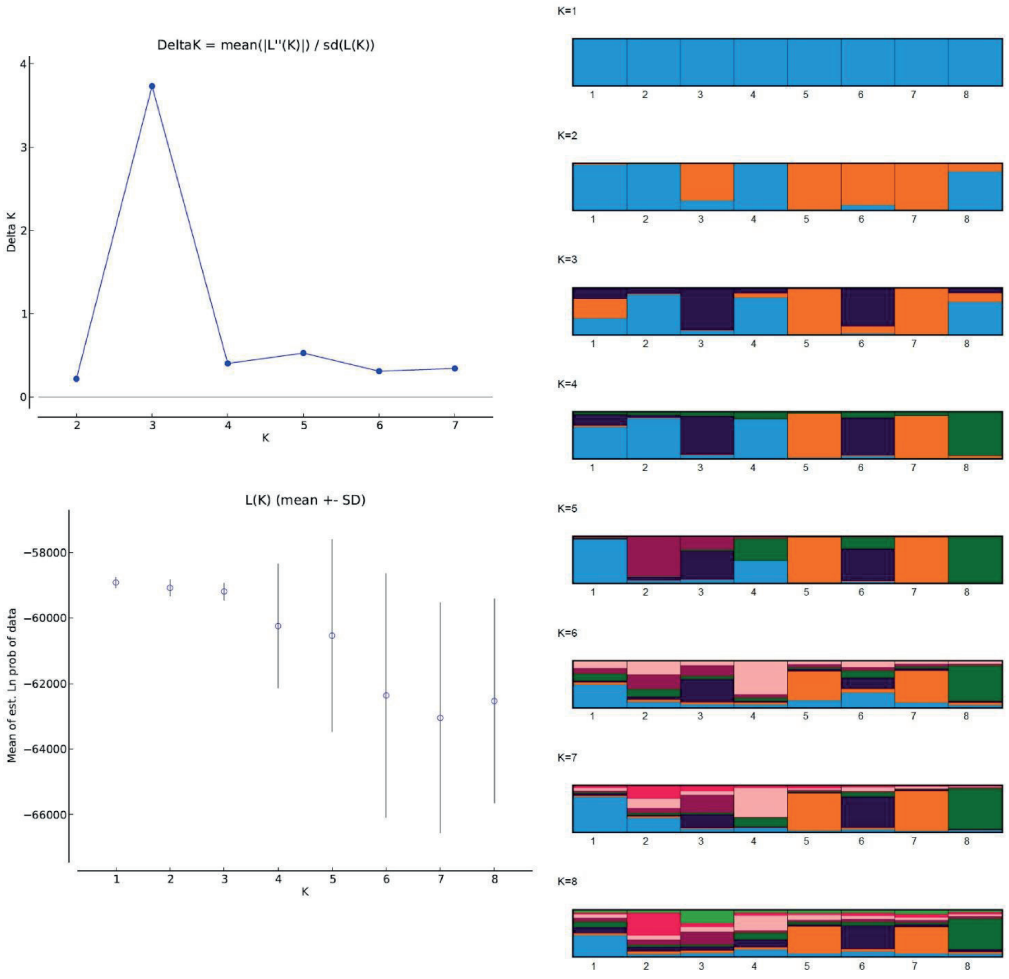

Figure 4. (A). Ad hoc ΔK over eight repeats of STRUCTURE analysis for K = 1–8 subpopulations; below: estimated log likelihood of the data (LnP(D)). **(B)** Genetic subdivision among the eight trees. Bar plots from CLUMPAK results aligning eight structure runs for K = 1 to 8, with an iteration of eight for each run. Each bar plot is accompanied by its statistical K by Pritchard's (Pritchard et al., 2000) and Evanno's method (Evanno et al., 2005). The plots are read from left to right, with each bar (1–8) representing a tree and the colour of the bar representing the proportion of individual markers that originated from a certain tree.

Table 2. Genetic diversity of three experimental populations.

Population	n	H_0	H_e	F_{IS}	
Pop 1 (1, 2, 4)	3	0.259	0.218	-0.188	
Pop 2 (3, 6)	2	0.269	0.213	-0.275	
Pop 3 (5, 7, 8)	3	0.246	0.209	-0.181	

n = total number of genotypes; Ho = observed heterozygosity; He = expected heterozygosity; F_{IS} = the inbreeding coefficient. The tree numbers are denoted in the brackets in each population.

Table 3. Results of AMOVA for three populations.

Group	Partitioning	d.f.	sum of squares	Variance components	percentage of variation	P-value
Three populations (Pop1, 2 and 3)	Among populations	2	465.792	6.13416	11	0.00001***
	Within populations	5	873.333	84.24359	89	0.00324
	Total	7	1339.125	90.37775		

Discussion

Historical evidence

As reflected on in this study, historical sources can be lacking or difficult to access. Most of the historical knowledge in this study was obtained from literature and printed sources. There are more archival sources to explore, but this would have been beyond the scope of this study. Further research in archives could possibly provide more valuable information.

With probable encouragement and support from foreign gardeners, it appears as landowners were leading the introduction of new tree species from abroad. Rare trees planted as experiments, ornaments and collections in arboretums and gardens were of importance for the

status of wealthy people, illustrating their botanical knowledge and representing something that can be shown to visitors (Dietze 2007).

In the second half of the 19th century, *A. alba* was available for sale in local plant nurseries as a forestry tree (Aas Høiere Landbrugsskole 1887). Historical and literary sources indicate collaborations between the plantings of *A. alba* in Elsterparken and at Reins Kloster, trees 4 and 2, respectively (Fig. 1). Dahl and Schiøtz, who led the plantings in Elsterparken, and Horneman, who owned Reins Kloster, are assumed to have been involved in the contemporary plantings of *A. alba* in Austråttlunden (Johansen D, personal communication, 1 Dec 2015). For the other localities, there was poor evidence to support that collaborations had occurred.

In accordance with studied sources, we expected that samples 2 (Reins Kloster) and 4 (Elsterparken) originated from the same or from closely related ancestors, which likely was in a local plant nursery. Since the plantings in Elsterparken was a large project that took place over a longer period of time (1871–96), it might be the source of plantings elsewhere in the region. The first plant nursery for forestry trees in Trondheim was established in 1899, near the location of Elsterparken in Bymarka. Shortly after this, during the two following decennia, several other plant nurseries with the same purpose were established in the region (Skogselskapet 2016).

With respect to stem circumference and height, the trees 1 (Austråttlunden), 3 (Fjæraskogen), 4 (Elsterparken) and 8 (Fougnerhaugen) have probably been planted around the same time in the late 1800s, whereas the trees 2 (Reins Kloster), 5, 6 and 7 (Skånes) probably were planted later at the turn of the century or in the early 1900s (Table 1).

Relatedness

All eight trees were distinguished into three groups identified in the phylogenetic tree (Fig. 2), PCoA (Fig. 3) and STRUCTURE (Fig. 4) analyses, i.e. trees 1, 2 and 4 constituting one group (Pop 1), trees 3 and 6 a second group (Pop 2) and trees 5, 7 and 8 a third group (Pop 3). However, the PCoA analysis showed that tree 8 seems to be more closely related genetically to trees 1, 2 and 4 than to 5 and 7.

Regarding the plantings at Skånes, the trees 5, 6, and 7 are similar in terms of their location, age, size. It is therefore likely that they were all planted at the same time, probably even in the same planting operation, but with material from different sources (Table 1). Apart from trees 5 and 7, they are generally not well related. The results of STRUCTURE support the relatedness between the trees 5 and 7 and indicate that these trees originate from a closely related ancestor (Fig. 4B). The results from STRUCTURE and from the phylogenetic analysis (Fig. 2) showed the relatedness between the trees 6 (Skånes) and 3 (Fjæraskogen), which apparently share a dominant genotype, suggesting that these trees may have a common ancestor (Fig. 4B). As the area where tree 3 was collected is a former arboretum with several old 19th century trees, it may

be the source for plantings of *A. alba* at other localities. The plantings in Skånes were seemingly a forestry experiment, and the genetic difference between the trees 5, 7 and 6 suggests that trees with a different origin were perhaps planted by purpose in order to find out which type was best adapted for the locality where it was introduced. The results of STRUCTURE (when K = 2 and K = 4, Fig. 4B) and of the phylogenetic analysis (Fig. 2) support that tree 4 is related to trees 2 and 1, which also suggests that the material was most likely distributed from the planting in Elsterparken to Austråttlunden and Reins Kloster (Fig. 5).

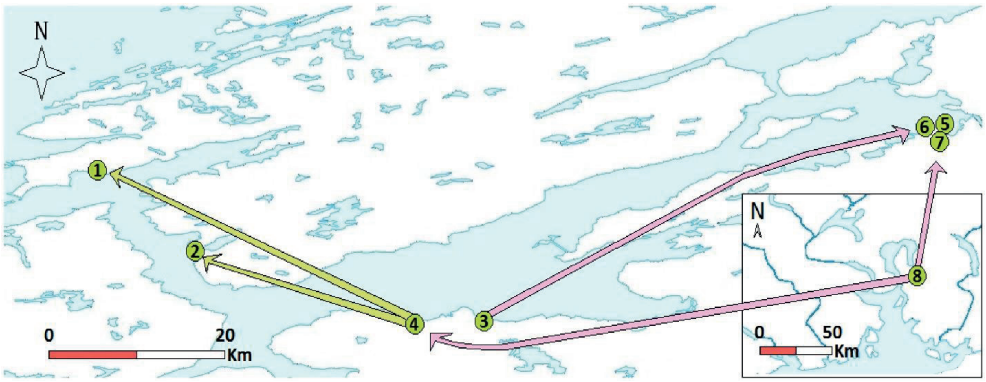

Figure 5. Possible dispersal scenarios of *Abies alba* Mill. based on genetic relatedness. Green lines are supported by historical sources, purple lines are assumed distributions based on the genetic relatedness only.

Dispersal route

Indications from historical literary sources gave the impression that there were connections between people involved in plantings of *A. alba*. We made an attempt to test the theories on the anthropogenic dispersal of *A. alba* by employing ddRAD in the genetic study of single trees. However, with such few individuals, it is challenging to apply the analysis suitable for the population genetics on single individuals. We solved this issue by grouping the single individuals into three groups based on genetic relatedness, i.e. the genetic diversity between each sample.

In spite of the small number of trees included in this study, each one represents an area where *A. alba* was introduced in the past and can contribute with an insight into a possible dispersal route. A possible dispersal scenario for these trees is that the planting of trees 1 and 2 might be the result of a collaboration with the people who planted tree 4 (Fig. 5). The plant nursery in southeast Norway, where tree 8 (Fougnerhaugen) likely originates, was established in 1858, one

decennium before the planting project started in central coastal Norway, i.e. Elsterparken 1871. According to the results of STRUCTURE, tree 8 appears as unique, but with some relatedness to trees 1, 2 and 4 (when K = 2 and K = 3; Fig. 4B). In the phylogenetic analysis, tree 8 is closest related to samples 5 and 7 (Fig. 2), which, to a small degree, suggests that these samples originate from an ancestor related to 8 (Fig. 5).

The results of STRUCTURE, AMOVA and of the phylogenetic analysis support that trees 5 and 7 in Skånes are very similar genetically, indicating that they have an ancestor in common and were presumably not part of the collaboration related to Elsterparken (sample 4) or Fjæraskogen (sample 3). Regarding sample 6 in Skånes, the results indicate that the plant material was distributed from Fjæraskogen (sample 3) (Fig. 5). One can assume that, when trying out new trees in planting experiments.

As a research method, the involvement of genetics did support and complement the historical literary sources, regarding how people accessed, shared and distributed plant materials. This is supported by, among others, Willows-Munro et al. (2016), as they found that genetic data matched findings in historical sources, i.e. how genetic lineages of an introduced species corresponded to the main centres of human settlement. It also supports the value of a multidisciplinary approach regarding the dispersal of introduced organisms.

We demonstrate a possible introduction route where material possibly was brought from southeast Norway to central coastal Norway and further to other localities in the region (Fig. 5). Little or no relatedness between the trees does not exclude collaborations regarding planting projects, but indicates that the specimens came from different origins. This might indicate that landowners obtained their trees from different plant nurseries, either in Norway or abroad.

Salvesen et al. (2009) used AFLP fingerprinting to find genetic relatedness and ancestors of historical cultivars of *Buxus sempervirens* L. (Boxwood). This approach is actually similar to the use of ddRAD: two restriction enzymes are used to cut DNA, but the AFLP markers are dominant (fingerprint). Nybom et al. (2014) claimed that PCR-amplified single-locus microsatellite markers remain more important compared to any of the other traditional DNA fingerprinting methods. However, Eaton et al. (2016) argue that RADseq data sets are useful in resolving extensive phylogenetic relationships, as increased sequencing coverage also may increase the phylogenetic utility.

Conclusion

The overall aim of this study was to provide new information on the introduction of *A. alba* and to test new methods to trace the dispersal of *A. alba* across Norway, as well as to encourage similar studies on the same or on other introduced plants species elsewhere. Although we used

a small number of historical trees in this study, it functions as a basis for further investigations using ddRAD. We consulted historical records that indicated a connection between three of the localities (i.e. trees 1, 2 and 4), which was confirmed by the genetic data (trees 1, 2 and 4 are grouped as one population). Among the other trees, for which we do not have historical data, we can predict that trees 3 and 6 are historically related based on the genetic data. Our findings also indicate that trees 5 and 7 were planted in the same operation and have a common origin. A more in-depth study on a dispersal route would benefit from further archival research and studies on relatedness, involving a larger number of samples. To track the genetic origin, it would be relevant to compare the DNA of planted *A. alba* trees in Norway with the DNA of wild populations in Europe. With reflections from Salvesen et al. (2009), analyses of biometric data (e.g. bark structure, leaf (needle) size and characteristics) would also be useful in a study like this and could provide information about the relatedness of the samples based on morphological differences and similarities.

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07.04.2017

SKJEMA 4.7 Errata

Retting av formelle feil i avhandlingen (jf. §15.3-2 i ph.d.-forskriften)

Ph.d.-kandidaten kan, etter innlevering, søke fakultetet om tillatelse til å rette formelle feil i avhandlingen. En fullstendig oversikt over de feil (errata) som ønskes rettet skal skrives inn i dette skjemaet og leveres fakultetet senest 4 uker før planlagt disputas. Det kan søkes kun én gang.

Avhandlingens tittel:	**On the Complexity of Dealing with Introduced Plants as Cultural Heritage** A historical multidisciplinary study of plants introduced to Norway from 1750 to 1900, exemplified with Abies alba Mill. (European silver fir) as a case species

Side nr	Avsnitt	Endret fra	Endret til
12	Table of contents	Savnet sidehenvisning for Paper III	Sidehenvisning for Paper III tillagt
23	*Turning point in Norwegian garden culture*	targeting alien species rather a very recent issue	targeting alien species is rather a very recent issue
30	*The need for a multidisciplinary approach*	To research as historical park,	To research a historical park,
31	*The need for a multidisciplinary approach*	explore how methods which have been seldom been combined	explore methods which have seldom been combined
37	Theoretical approach	Emphasis was placed on how on middleclass authors	Emphasis was placed on how middle-class authors
40	*Alien plants*	Even though is expresses	Even though it expresses
53	*Introduction notes on Abies alba*	regeneration, is the species is currently	regeneration, the species is currently
57	Natural scientific approach	to map in the spreading of this species	to map the spreading of this species
70	I. Literary reflections on plants introduced as ornaments in the 1800s	romanticism (Bruun 1987, 181), and the term 'exotic plants' was	romanticism (Bruun 1987, 181), the term 'exotic plants' was
81	Conslusions	They were commonly sees as	They were commonly seen as
94	References	Ridbäck, U., Dietze-Schirdewahn, A. and Vike, E. (manuscript (a).	Ridbäck, U., Vike, E. and Dietze-Schirdewahn, A. (Manuscript (a).

Dette skjemaet signeres av ph.d.-kandidat og hovedveileder og oversendes fakultetet for godkjenning. Godkjent errata arkiveres i ph.d.-kandidatens doktorgradsmappe, og legges ved den endelige avhandlingens trykk-versjon som siste side.

Dato og signatur:

Ph.d.-kandidat (forfatter):	21.03.2018 Ulrika Ridbäck
Hovedveileder:	22.03.18

Errata godkjent av fakultetet: Ja ☒ Nei ☐

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