

Department of Natural Sciences, Tromsø University Museum

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Invasive *Heracleum* in northern Europe: Introduction history and impact on native plant diversity

Dilli Prasad Rijal

A dissertation for the degree of Philosophiae Doctor – Autumn 2015



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Cover image: Dense stand of *Heracleum persicum* along with most frequently co-occurring *Anthriscus sylvestris* along Kvaløyvegen road near Åsgård, Tromsø, Norway

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30 November 2015, Tromsø

Dilli Prasad Rijal

List of papers

This thesis is based on the following papers that are referred to by their Roman numerals in the text:

Paper I: Rijal, D.P., Falahati-Anbaran, M., Alm, T. & Alsos, I.G. (2015) Microsatellite markers for *Heracleum persicum* (apiaceae) and allied taxa: Application of next-generation sequencing to develop genetic resources for invasive species management. *Plant Molecular Biology Reporter*, **33**, 1381-1390.

Paper II: Rijal, D.P., Alm, T., Jahodová, Š., Stenøien, H.K. & Alsos, I.G. (2015) Reconstructing the invasion history of *Heracleum persicum* (Apiaceae) into Europe. *Molecular Ecology*, **24**, 5522-5543.

Paper III: Rijal, D.P., Alm, T., Nilsen, L. & Alsos, I.G. (2015) Giant invasive *Heracleum persicum*: Friend or foe of plant diversity? Manuscript.

The following table shows the contributions of authors to the various components of each paper.

	Paper I	Paper II	Paper III
Concept and idea	DPR, IGA, TA	DPR, HKS, IGA, TA	DPR, IGA, TA
Study design and methods	DPR, IGA, TA	DPR, HKS, IGA, TA	DPR, IGA, LN, TA
Data gathering and interpretation	DPR, IGA, MFA, TA	DPR, HKS, IGA, SJ, TA	DPR, IGA, LN, TA
Manuscript preparation*	DPR	DPR	DPR

*All the co-authors commented on the respective manuscripts.

DPR = Dilli Prasad Rijal, HKS = Hans K. Stenøien, IGA = Inger Greve Alsos, LN = Lennart Nilsen, MFS = Mohsen Falahati-Anbaran, SJ = Šarka Jahodová, TA = Torbjørn Alm

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Summary

Exotic invasive giant hogweeds are infamous in Europe for their ecological and economic damage; however, the magnitude of their impact on plant diversity has not yet been fully explored. In addition, due to sparse and incomplete historical records of such invasive species, tracing the source and route of introduction becomes challenging, which in turn impedes management interventions. In such cases, molecular markers may be instrumental in bridging gaps between invasion history and management by providing insight into the complex history of biological invasions. However, molecular markers for the genetic analyses of non-model organisms are limited.

This thesis developed a microsatellite library for one of the giant hogweeds, *Heracleum persicum* (Paper I). A set of markers were first validated on *H. persicum* and cross-amplified with other giant hogweeds, i.e., *H. mantegazzianum* and *H. sosnowskyi*, a native hogweed *H. sphondylium*, and the putative hybrid *H. persicum* × *H. sphondylium*. Ordination based on a set of 25 polymorphic microsatellite markers clearly discriminated the genetic structure of exotic invasive giant hogweeds, a native hogweed, and their invasive hybrids.

The set of validated microsatellite markers were then used to trace the introduction history of *H. persicum* into Europe (Paper II). Microsatellite markers revealed a significantly higher genetic diversity of *H. persicum* in its native range, and the loss of diversity in the introduced range may be attributed to a recent genetic bottleneck. Approximate Bayesian computation indicated two independent introductions of *H. persicum* from Iran to Europe: the first one in Denmark and the second one in England. English populations subsequently colonized Finland. In contrast to the contemporary hypothesis of an English origin of Norwegian populations, Finland appeared as a more likely source. Also, genetic diversity *per se* is not a primary determinant of invasiveness in *H. persicum*.

This thesis further evaluated the impact of *H. persicum* invasion on Norwegian plant diversity (Paper III). There was a consistent negative impact of *H. persicum* invasion on native

plant diversity. Within invaded plots, the cover of *H. persicum* had a strong negative effect on the native cover. The invaded plots had on average nearly two native species less than the non-invaded plots. Plant communities containing only native species appeared more susceptible for the further invasion than those that included exotic species, especially *H. persicum*. The invasion history of *H. persicum* shapes the invasion dynamics rather than genetic diversity *per se*. Overall, the impact of *H. persicum* on native plant diversity outweighs the invasion resistance it offers.

In conclusion, the strong negative impact of *H. persicum* on the Norwegian plant diversity justifies the need for the urgent management interventions to control and eradicate *H. persicum*. By tracing the route of introduction and identifying vital regional source populations of *H. persicum*, this thesis provides important cues, which may be useful in controlling further introductions. High invasiveness in Norwegian populations of *H. persicum* despite low levels of genetic diversity indicates that even a small founder population may cause high impact. Thus, managers should give priority to eradicate larger populations for the effective control of *H. persicum*. The developed set of microsatellite markers may serve as an important genetic resource for understanding taxonomy, population genetics and phylogeny of giant hogweeds and their hybrids, which in turn, are expected to contribute to biodiversity conservation by invasive species management.

Introduction

The habitat invasion by non-native species is one of the largest threat to biodiversity (Baillie *et al.* 2004; CBD 2010). Different components of biodiversity provide food and medicine thereby making human survival possible. Ironically, human activities constitute the greatest threat to global biodiversity (Baillie *et al.* 2004; Butchart *et al.* 2010; CBD 2010; Powell *et al.* 2011). With the increased access to transportation and mobility of people, species are transported away from native ranges accidentally or deliberately. Some of these may expand their populations so rapidly that they become problematic pests. Because most food plants and industrial crops are exotic in origin and keys to sustain human population, there is still controversy regarding the negative role of exotic species (Davis *et al.* 2011). However, it is certainly not exotic species *per se* that affect biodiversity and ecosystems but those which are invasive (Lambertini *et al.* 2011).

It is widely recognized that invasive exotic species affect biodiversity at all organizational levels from genes to ecosystems (Vitousek & Walker 1989; Vilà *et al.* 2011), and cause significant damage to environment and economy (Pimentel 2011). The harmful impacts of already introduced species will definitely increase in the near future when localized and innocuous introduced species start expanding their ranges (Crooks 2011; Simberloff 2014). We are paying some of the “invasion debt” now ,and future generations will be paying even more if the management of biological invasions is overlooked (Essl *et al.* 2011). Thus, the challenge is to fulfill the demands of ever-increasing population by exploiting both native and exotic species and to maintain the biodiversity of the earth. Humankind has a moral responsibility to mitigate the ‘ecological explosion’ with best possible effort to minimize the ‘impressive effect’ of such explosion, i.e., biological invasion (Elton 1958). However, invasive exotic species generally remain in concealment before their population explodes. Due to the lack of the historical records and poorly understood demography, management of invasive exotic species becomes challenging.

Meanwhile, indirect methods based on molecular genetic markers have proved effective in bridging such gaps between invasion history and management by providing insight into the complex history of biological invasions (Lombaert et al. 2014). According to the unified framework for biological invasion, a species should cross several stages and overcome different barriers within each stage before becoming a successful invader (Blackburn *et al.* 2011; Lockwood *et al.* 2013) (Figure 1). Thus, proper understanding of invasion process may provide cues for better management of invasive species.

Population genetics and invasion history

Information about population genetics, introduction history and identification of source populations are crucial in understanding the invasion process (Cristescu 2015). The genetic diversity of a species indicates its evolutionary potential to adapt to a novel environment (Sakai et al. 2001). This may be especially important for exotic invasive species as they have to adapt to and survive in novel environments. Genetic diversity of introduced populations largely depends on the number of founders and the number of introductions from the genetically differentiated source populations (Kolbe et al. 2004; Lavergne & Molofsky 2007; Ward et al. 2008; Simberloff 2009). Genetically diverse populations may have higher establishment success if they contain genetic variants more suited to the new environment, thereby posing greater invasion risk (Lee 2002; Forsman 2014; Bock et al. 2015).

Although introduced invasive species suffer from genetic bottlenecks, they often overcome adverse effects of population reduction by genetic admixture via multiple introductions from the native range (Kolbe et al. 2004) and/or other successfully established populations (invasive bridgehead effect, Lombaert et al. 2010; Benazzo et al. 2015). As multiple introductions and genetic admixture may enhance invasibility (Kolbe et al. 2004; Roman & Darling 2007; Marrs et al. 2008; Ward et al. 2008), the number of introductions may indicate risk of further regional spread of a species. Better understanding of the genetic diversity of introduced populations and vital source populations along with the number of

introductions may be used to prevent further introductions and/or spread of invasive species by designing monitoring and quarantine strategies targeting the source area and the important vectors (Estoup & Guillemaud 2010). The change in effective sizes and ranges of natural populations in the past leave signatures in their genetics (Cornuet et al. 2010), and this historical signature can be inferred by examining genetic variation among populations (Lawton-Rauh 2008). For example, genetic differentiation among populations is considered a product of limited dispersal and gradual genetic drift. As a result, genetic similarity becomes correlated to geographic distance (isolation by distance, Wright 1943). Thus, genetic diversity of invasive populations may be used as a tool for inferring invasion history and risk assessment.

Hybridization and invasiveness

Interspecific hybridization has often been reported as promoting invasiveness (Ainouche *et al.* 2009; te Beest *et al.* 2011). Invasive species generally produce entirely new transgressive phenotypes through hybridization (Hufbauer 2008). Due to the disruption in chromosome pairing and assortment, hybrids are generally sterile (Craig S 2001). However, such sterility may be removed in hybrids through the fixation of 'permanent heterozygosity' (see Craig S 2001 for the details), which is responsible for hybrid vigor. The hybrid can evolve as a separate species with additional quantitative and genetic traits to either parent (Brennan *et al.* 2012). Genomes of related species are permeable to alleles of each other. If so, hybridization enables genome exchange through which hybrids can achieve advantageous phenotypes (Baack & Rieseberg 2007). Interspecies hybridization between invasive species may also enhance invasiveness in hybrids (Ellstrand & Schierenbeck 2000; Schierenbeck & Ellstrand 2009). On the other hand, hybridization can impede management interventions through creation of unique characteristics, e.g. production of novel chemicals, which in turn makes hybrids unrecognizable or unpalatable to specific herbivores or biological control agents (Schoonhoven *et al.* 2005; Williams *et al.* 2014).

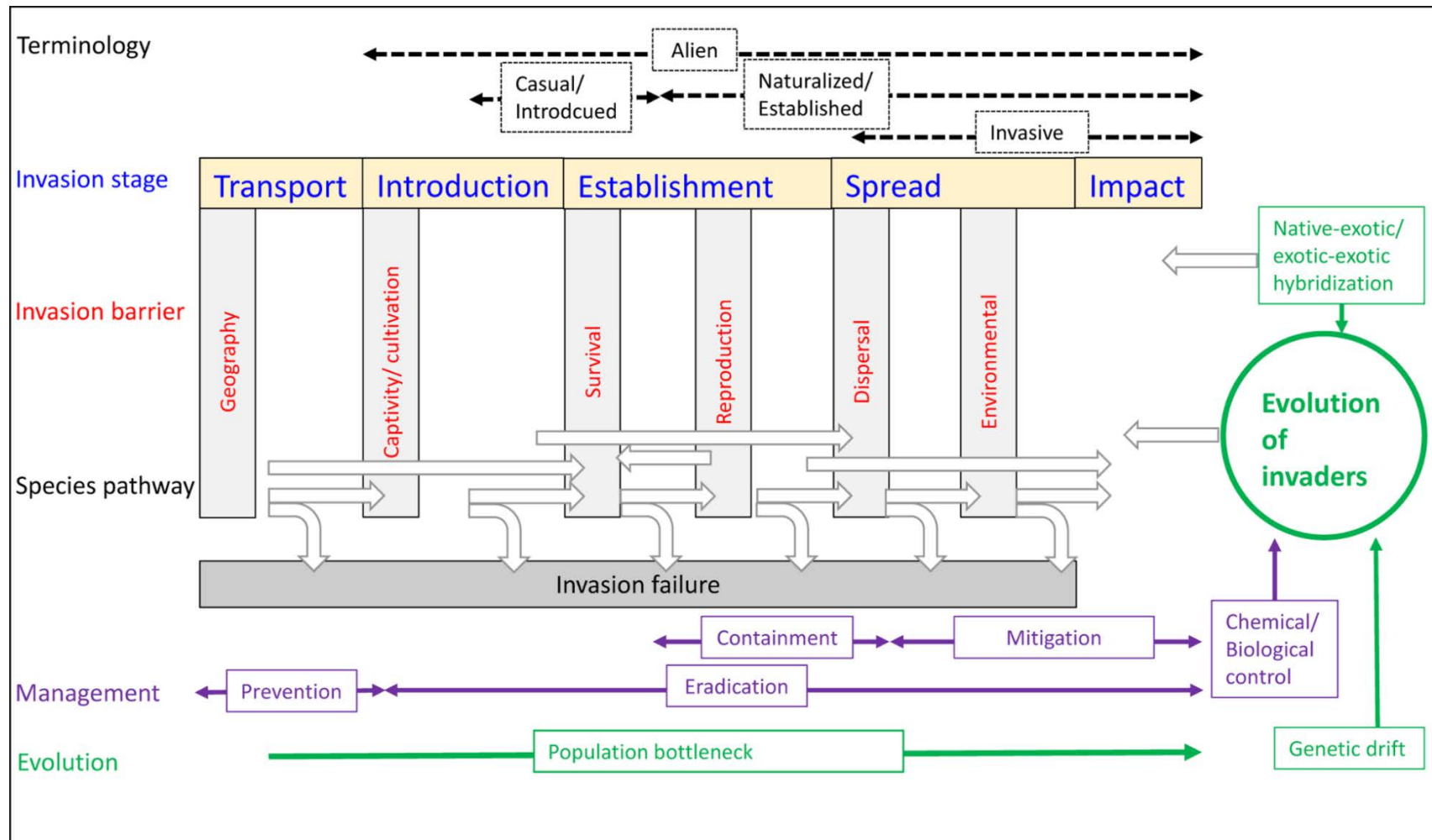


Figure 1 A modified version of unified framework for biological invasion proposed by Blackburn *et al.* (2011) and further edited by Lockwood *et al.* (2013). The model recognizes different stages of invasion and the respective barriers that need to be overcome by alien species in each stage. It also proposes different terminology for a species in invasion continuum as well as indicates appropriate management strategies for respective invasive stages. I included evolutionary aspect of invasive species. Note population bottleneck in each stage of invasion and possibility of hybridization between native-exotic/exotic-exotic species that may induce evolution in invaders.

Impact of invasion on diversity and invasibility

Exotic invasive species may reproduce and spread quicker than the native species as they are resistant to strong disturbances and lack natural enemies in the introduced ranges (Keane & Crawley 2002; Tilman 2004; Moles *et al.* 2012). However, due to the complexity of invasion, not all introduced species can become successful invaders (Williamson 1993; Williamson & Fitter 1996). Due to species specific nature of impact of invasive exotic species, it is often difficult to generalize the effect of individual exotic species (Hulme *et al.* 2014) and predict the vulnerability of a community to further invasion.

Meanwhile, recent progress in theoretical and experimental ecology makes it possible to predict invasibility based on the interplay among the intrinsic characteristics of a community (Chytrý *et al.* 2008; Rejmánek 2013; Guo *et al.* 2015). The impact of invasion reflects the level of dominance, constrained by biotic interactions, of exotic species once they become invasive (Williamson & Fitter 1996; Theoharides & Dukes 2007). Thus, further growth and spread of new invaders largely depend on the biotic interactions, especially competition for light and resources, within a community. Whether a species can significantly impact a community also depends on the vegetative and reproductive capacity of that particular species (Hejda *et al.* 2009; Gooden & French 2015). The impact of invasion is likely to be higher in a community if the invader is a superior competitor (for resources) to the resident species. In general, highly invasive exotic species maintain their dominance over native congeners across wide environmental gradients e.g. moisture and light via continuous growth over the entire growing season (Čuda *et al.* 2015). Cover difference between native and exotic species may be considered a measure of the impact of invasive species (Pyšek & Pyšek 1995; Hejda *et al.* 2009). Invasive exotics may reduce abundance of native species locally, which in turn may decrease species diversity (e.g. Shannon's diversity index) and evenness of the invaded system (Pyšek & Pyšek 1995; Hejda *et al.* 2009). As a consequence of invasion by a dominant invader, there should be noticeable decrease in abundance of native species long before the species richness starts declining (Mulder *et al.* 2004). The overall impact of invasion depends

on the strategies of dominant invaders. The invaders occupying high position along the trait hierarchies are 'exploiters' that can reduce native diversity; however, those that occupy intermediate trait positions are 'coexisters' which generally have no impact on the native diversity (Lai *et al.* 2015).

Invasibility, the susceptibility of a community to biological invasion, is primarily an intrinsic characteristic of a community that reflects the number of vacant niches, which in turn is largely determined by the available resources (Davis *et al.* 2000; Guo *et al.* 2015). Resource availability is influenced by the interplay of species composition, diversity and biomass of a particular community (Catford *et al.* 2012). The invasibility depends on whether characteristics of a community favours 'establishment' of invaders or not (Williamson & Fitter 1996; Theoharides & Dukes 2007). A stable community in a mid to late successional stage may be more resistant to biological invasion due to the establishment of competitively stronger native species (Pino *et al.* 2006). Similarly, due to the analogy between species diversity and genetic diversity, the latter is expected to resist invasion (Vellend & Geber 2005; Vellend 2006), although diversity-resistance hypothesis (Elton 1958; Kennedy *et al.* 2002) has not yet been established firmly (Levine *et al.* 2004; Harrison *et al.* 2015). While few studies have reported how genetic diversity of native species influences the establishment success of exotic species (e.g. De Meester *et al.* 2007), whether genetic diversity of a dominant exotic invader shapes the future of invasion dynamics is rarely emphasized. It, therefore, remains unclear whether invasion history or resident time of dominant invader, or genetic diversity *per se*, shapes invasion dynamics.

Statement of the problem

A group of large hogweeds, commonly known as "giant hogweeds" in Europe (*sensu* Nielsen *et al.* 2005), include three invasive species of *Heracleum* (Apiaceae), i.e., *H. mantegazzianum*, *H. persicum*, and *H. sosnowskyi*. The first two species were famous garden plants during the 19th century in Europe, and the latter was introduced to North-West Russia as a forage crop

at the end of the 1940s (Nielsen *et al.* 2005; EPPO 2009; Alm 2013). The taxonomy of giant hogweeds remained controversial in Europe, particularly discrimination of *H. persicum* and *H. mantegazzianum*, and remains unresolved in the UK (Sell & Murrell 2009; Stace 2010; Denness *et al.* 2013). Within less than two centuries of introduction, giant hogweeds became some of the most prominent invasive species in northern Europe (Nielsen *et al.* 2005; EPPO 2009; Alm 2013). They possess some typical features of invasive species, e.g., early and fast growth, high stature, huge biomass production, extensive cover, and abundant seed production.

Invasive giant hogweeds and their hybrids can pose serious threats to the European biodiversity thereby needing urgent management interventions (Nielsen *et al.* 2005; EPPO 2009). However, morphological similarity, taxonomic uncertainty and hybridization among giant hogweeds impede the management process. In such cases, understanding population genetics of the giant hogweeds should be helpful. However, studies in population genetics of giant hogweeds are limited due to paucity of genetic resources (Walker *et al.* 2003; Jahodova *et al.* 2007; Henry *et al.* 2009).

This thesis considers giant hogweeds as a model system and attempts to resolve some of the important aspects of the invasion process including evolutionary changes in giant hogweeds during the course of invasion (see Figure 1). Giant hogweeds may hybridize with each other or native species and produce vigorous hybrids, which in turn may augment pressure on native diversity (*sensu* Ellstrand & Schierenbeck 2000). The study generated genetic resources that may be useful in addressing the taxonomic problem and issue of hybridization within and between hogweeds. It is important to note that population size of giant hogweeds is reduced after crossing each barrier in the invasion continuum. This reduction in number alters the allelic frequency due to the genetic drift (Allendorf & Lundquist 2003). Thus, there should be a series of genetic changes in giant hogweeds before they become successful invaders. This thesis further explores the population genetics of one of the less studied giant

hogweeds, i.e., *H. persicum* to explore issues such as what shapes the genetic diversity of invasive species, and, In particular, whether or not genetic diversity promotes invasiveness in *H. persicum*. In addition, by assessing the impact of invasion of *H. persicum* on native diversity, my study provides clues as to why is it important to control and manage *H. persicum*.

The specific aims of this thesis were:

- (i) Generating tools for genetic analysis of hogweeds in general and invasive giant hogweeds in particular (Paper I),
- (ii) Detecting the vital source populations of *H. persicum* by reconstructing the route of introduction to Europe (Paper II),
- (iii) Assessing the impact of a massive plant invader, *H. persicum*, on the diversity of native vascular plants by considering case study from Norway (Paper III).

Material and methods

Study species (Paper I, II & III)

Heracleum persicum, commonly known in Norway as tromsøpalme, is a native of Iran and introduced invasive in Nordic countries. This herbaceous polycarpic species is generally 2 m tall and sometimes reaches up to 3 m with large leaves of up to 2.5 m long. A germination rate of 4% was observed in a phytotron trial for seeds collected in early November 2012 (n = 72, 2 month stratification at 2-4°C in moist sterilized soil). The giant hogweed *H. mantegazzianum*, derives from western Caucasus and has aggressively colonized most of the Europe (EPPO 2009). It is monocarpic and can grow up to 5 m with leaves reaching up to 3 m. Similarly, *H. sosnowskyi*, commonly known as Sosnowsky's hogweed, is a native of Caucasus and Transcaucasia which has colonized most of the Baltic region (Nielsen *et al.* 2005; EPPO 2009). This species, which also grows up to 3 m tall, is also monocarpic and morphologically closer to *H. mantegazzianum*. All hogweed species are perennial seed-propagated plant. *Heracleum mantegazzianum* has been listed as an invasive alien plant in Europe (EPPO 2009) and as a federal noxious weed in USA (USDA 2012). *Heracleum persicum* and *H. sosnowskyi* have been recommended for regulation as quarantine pests in Europe (EPPO 2009). Due to their negative ecological and biological effect, *H. persicum* and *H. mantegazzianum* are both black-listed in the 'very high risk' category in Norway (Gederaas *et al.* 2012).

The giant hogweeds often hybridize with *H. sphondylium* L. (common hogweed), a rather smaller plant which reaches up to 1.4 m in height (Fröberg 2010). *Heracleum sphondylium* is considered as indigenous to most European countries. Scattered natural hybrids of giant hogweeds with native *H. sphondylium* have been reported from the British Isles (Sell & Murrell 2009; Stace 2010) as well as Scandinavia (Fröberg 2010). Several well-established stands of natural hybrids have been observed in northern Norway, which are sometimes morphologically very similar to *H. persicum*. Norwegian hybrids are as vigorous as *H. persicum* and equally invasive (Alm 2013). Some of the intermediates have been

interpreted as hybrids of *H. persicum* and *H. mantegazzianum* by Elven (2005). However, these species are not sympatric in the native range and the distribution ranges in Europe hardly overlap (Fröberg 2010). Thus, it is questionable whether hybridization occurs between *H. persicum* and *H. mantegazzianum*.

Heracleum persicum was included in all three papers whereas *H. mantegazzianum*, *H. sosnowskyi*, *H. sphondylium*, the hybrid of *H. persicum* and *H. sphondylium*, and a more distant species *Anthriscus sylvestris* from Apiaceae, were included in paper I. For general morphology of five taxa of hogweeds growing in Europe and included in this thesis, except *H. sosnowskyi*, see Figure 2.

Leaf sample collection and molecular methods (Paper I & II)

Leaf samples were collected from the entire distribution range of *H. persicum* between 2012 and 2014 (Figure 3), except Iraq and Iceland, for which the species has only recently been found (Wasowicz *et al.* 2013; Ahmad 2014), and Turkey, from where export of plant material is now prohibited. Four samples and one representative herbarium voucher were collected from 5 different spots at 5–10 m intervals per population, and care was taken to avoid resampling from the same genet, resulting in 1-20 samples per population. All samples were dried on silica gel. A few populations collected during 2003-2004 were retrieved from the material of Jahodova *et al.* (2007) and herbarium vouchers for those samples are deposited with the original collectors. Representative samples of other taxa were collected from England, Georgia, Norway and Russia following the same protocol as described above.

DNA was extracted using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following manufacturer's protocol. DNA concentration of each sample was measured using NanoDrop 2000 (Thermo Scientific, Waltham, USA). The quality of DNA was further checked in 2% agarose gel. High quality DNA of ten individuals from Norwegian, Danish and English populations of *H. persicum* were pooled for microsatellite library preparation (Paper I). All the DNA samples were normalized to 10 ng/μl for downstream analyses.

High-throughput DNA sequencing was performed by 454-GS-FLX Titanium chemistry (Malausa et al. 2011) at GENOSCREEN (Lille, France) to prepare microsatellite library and design primers (Paper I). Thirty pairs of newly designed primers and four pairs of primers each described by Walker *et al.* (2003) and Henry *et al.* (2008) were selected for initial screening (Paper I). The cost effective polymerase chain reaction (PCR) approach was used while testing primers (Blackett *et al.* 2012). Multiplex manager was used to accommodate polymorphic markers into different multiplexes (Holleley & Geerts 2009). The electrophoresis was performed on a 3130xL genetic analyzer (Applied Biosystems).

Vegetation sampling (Paper III)

Vegetation was sampled during July-August 2012 and August 2013 (only Ibestad) in areas where *H. persicum* is most frequent (Figure 3). The sampling approach was to compare species richness and diversity estimates between *Heracleum* invaded and non-invaded plots. We sampled five invaded and five non-invaded plots in each location (Figure 4), except Bjørnevatn where only two plots were sampled due to the sparse stands of *H. persicum*. The non-invaded plots were established as close as possible to the invaded plots for minimizing variation in site conditions and also to increase the chance that the non-invaded plots represent a vegetation before the invasion of *H. persicum* (space-for-time substitution approach, Pickett 1989; Pyšek & Pyšek 1995). We selected homogenous stand of *H. persicum* wherever possible and covered variation in the growth form of *H. persicum* while sampling. The percent cover of each species within 2 × 2 m² plot was visually estimated from 56 invaded and equal number of non-invaded plots.

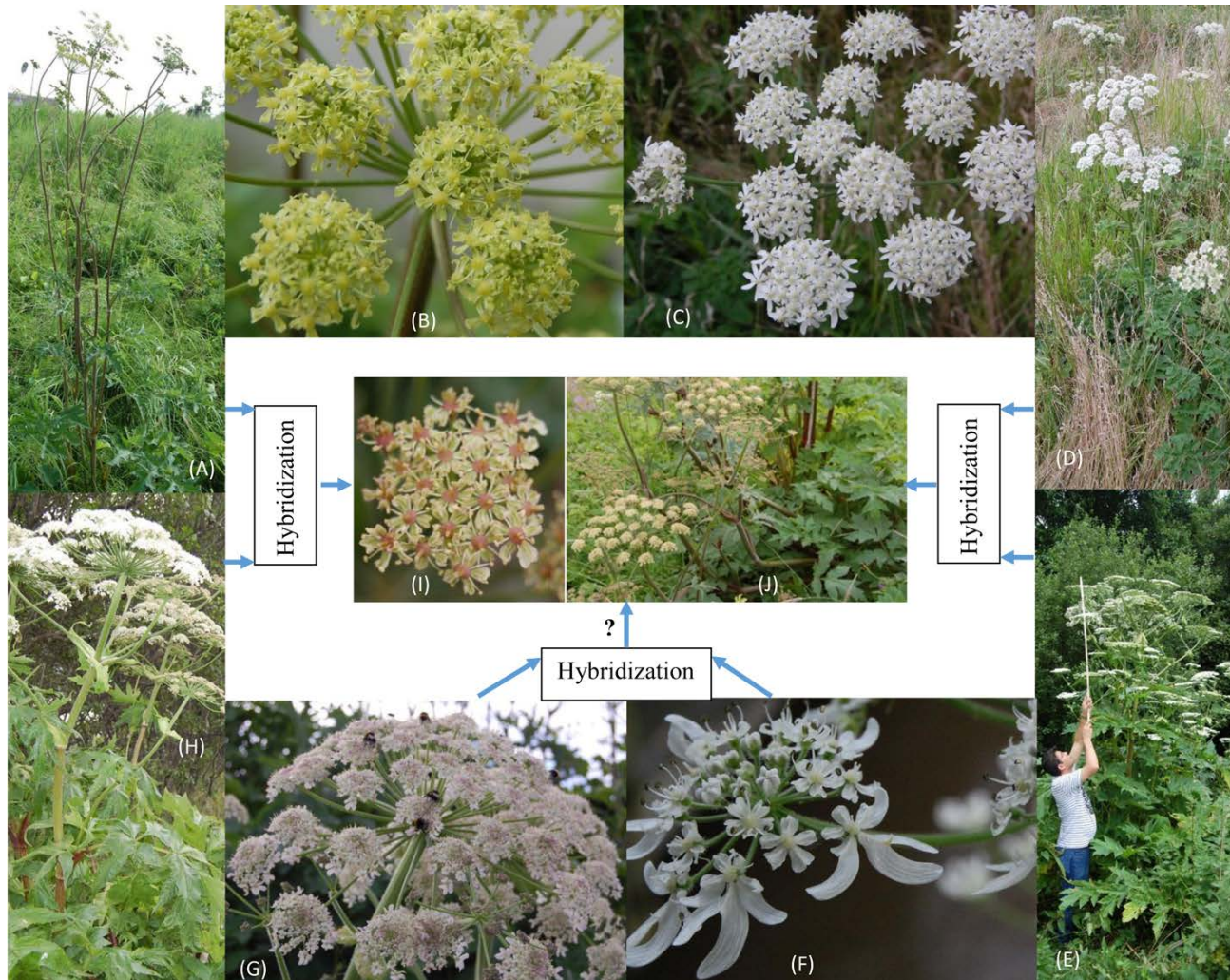


Figure 2 General morphology of the European hogweeds included in this thesis: *Heracleum sphondylium* subsp. *sibiricum* (A & B), *H. sphondylium* subsp. *sphondylium* (C & D), *H. mantegazzianum* (E & F), *H. persicum* (G & H), and the hybrid *H. persicum* × *H. sphondylium* (I & J).

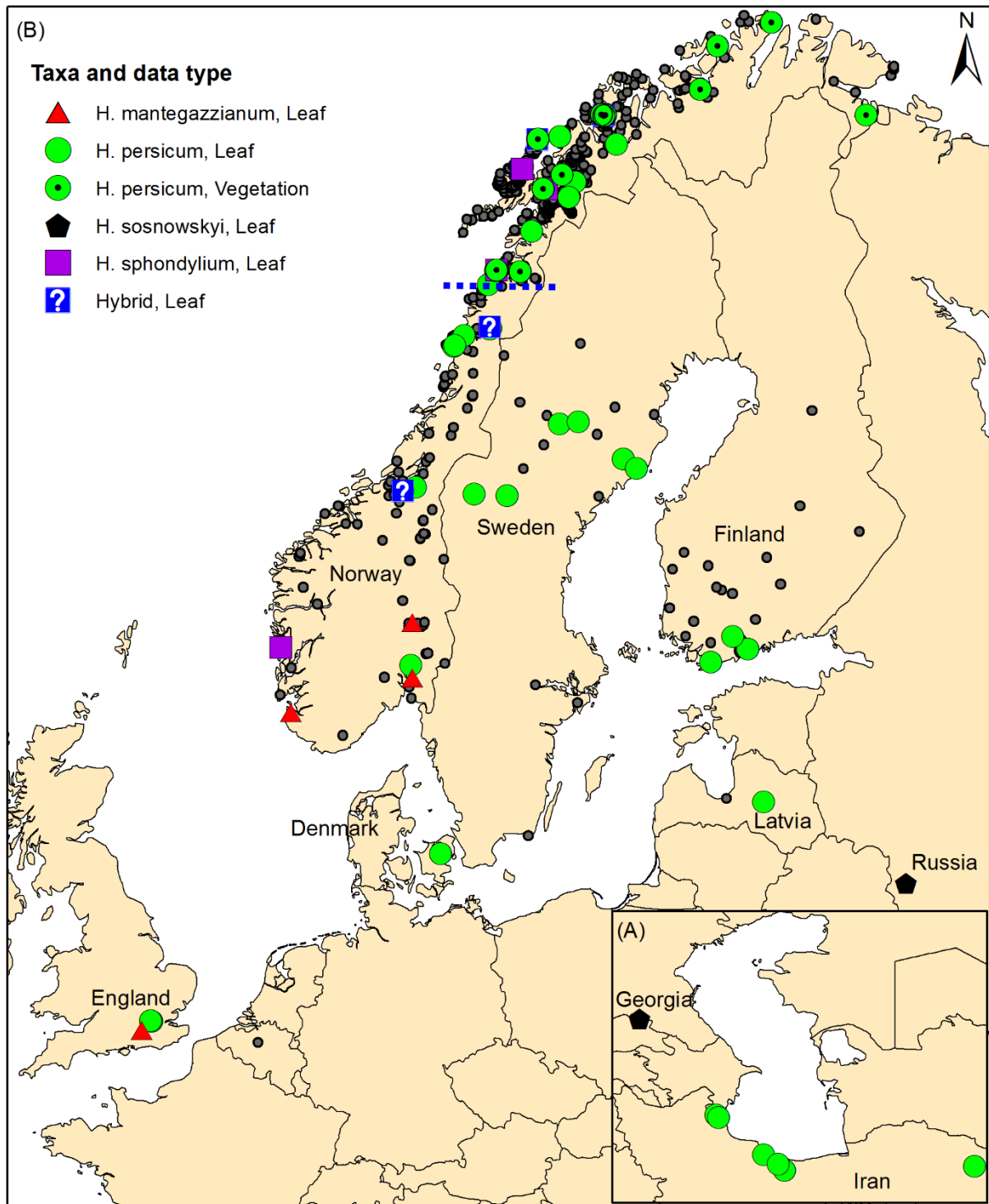


Figure 3 Map of sites for vegetation and leaf sampling of different taxa of *Heracleum* from (a) the native, and (B) the introduced ranges. Vegetation data were collected from *H. persicum* invaded and adjacent non-invaded plots mainly from northern Norway (north of the dashed line). Historical records of *H. persicum* are provided in the background (small circles).

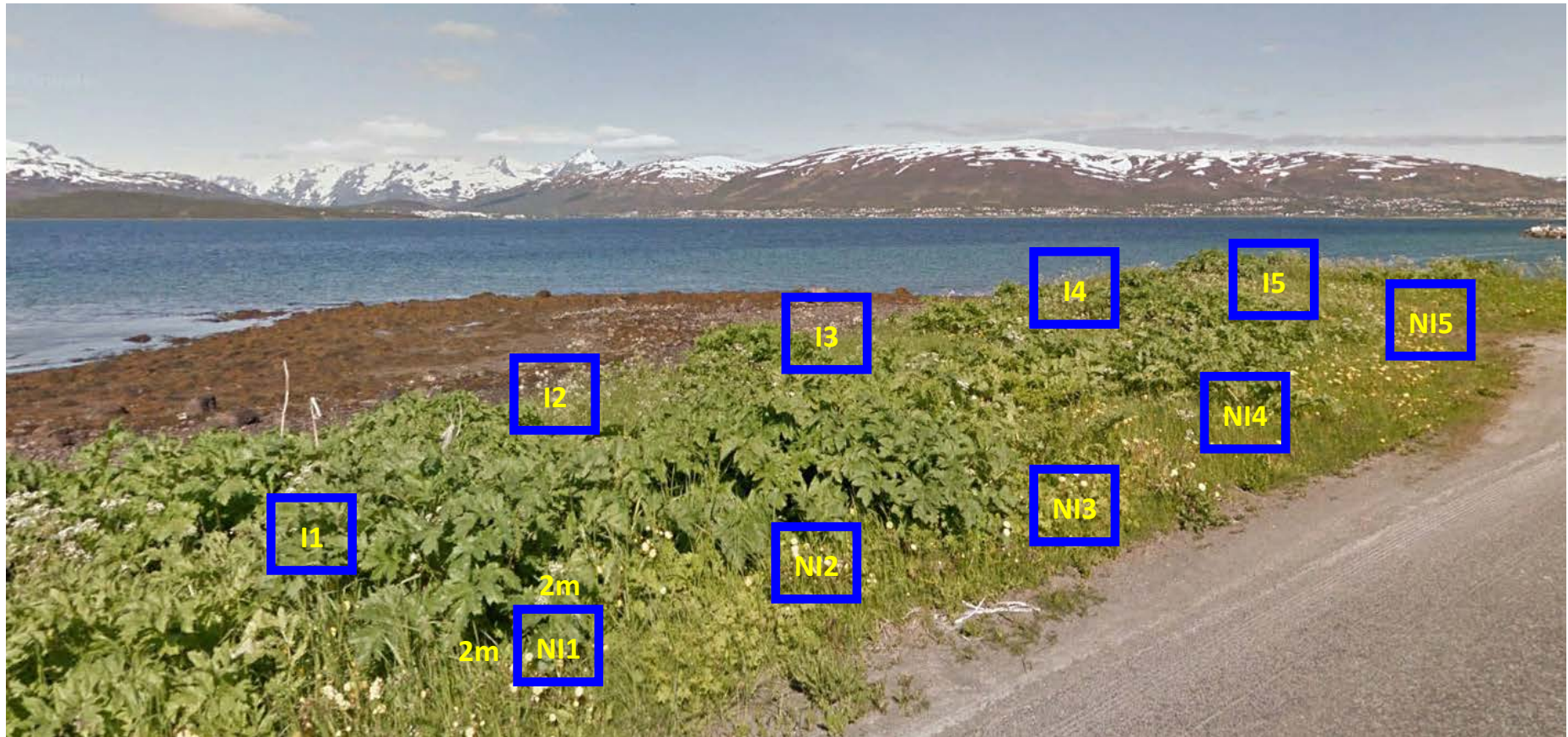


Figure 4 Illustration of vegetation sampling. Data were collected from equal number of *Heracleum persicum* invaded (I1-5) and adjacent non-invaded (NI1-5) plots of 4 m² from northern Norway. Photo © 2015 Google.

Molecular data analysis (Paper I & II)

Most of the methods described in this section were pertinent to paper II and any method applicable to paper I will be indicated in parentheses. The genotype data were generated using GENEIOUS (Biomatters Ltd, New Zealand) following 3rd Order Least Squares method implemented in microsatellite plugin for allele calling (Paper I). PGDSPIDER (Lischer & Excoffier 2012), MICROSATELLITE TOOLS (Park 2001), and GENALEX (Peakall & Smouse 2012) were used as data conversion tools; and the latter two were also used to check errors in genotypic data (Paper I). GENALEX (Peakall & Smouse 2012) was used for estimating genetic diversity e.g. average and effective number of alleles, and observed and expected heterozygosity (Paper I). Allelic richness and the pairwise population genetic differentiation were estimated in FSTAT (Goudet 1995). The tests of heterozygosity excess, deficiency and mode shift in allele frequencies, as signatures of population bottlenecks, were performed in BOTTLENECK (Piry *et al.* 1999).

The genetic relationship among different taxa and among different population within a species was evaluated by principal coordinate analysis (Paper I) in GENALEX (Peakall & Smouse 2012). The number of genetic clusters in *H. persicum* was estimated in STRUCTURE (Pritchard *et al.* 2000) using the Lifeportal computing platform (<https://lifeportal.uio.no/>). To trace the most likely introduction route of *H. persicum* in Europe, the Approximate Bayesian Computation (ABC) approach as implemented in DIY-ABC (Cornuet *et al.* 2014) was used. Four competing scenarios were tested by considering Iranian populations as the native source of the introduced populations (see Fig. 2 in II). The migration rate between Norway and Finland was estimated using isolation with migration analysis in IMA software (Nielsen & Wakeley 2001; Hey & Nielsen 2004,2007).

Vegetation data analysis (Paper III)

Presence/absence of *H. persicum* was the primary factor to discriminate invaded and control plots. Thus, we excluded *H. persicum* while calculating species richness and multivariate

analyses. Species were classified into native and exotic based on their origin (indigenous or native) following Gederas *et al.* (2012). All species were further classified into the functional groups grasses and forbs. The adjusted biomass volume of each plot was estimated following Axmanová *et al.* (2012).

Species richness, Shannon's diversity index, evenness, and taxonomic diversity were calculated and compared between control and invaded plots. The environmental variables of the invaded and the control plots were compared by paired t-test (Crawley 2013, pp. 362-363). Pearson's product-moment correlation was calculated between all pairs of variables.

To discriminate the relative contribution of native and exotic species in community richness and abundance, relative exotic richness and abundances were calculated (Catford *et al.* 2012). To evaluate susceptibility to further invasion, invasibility was calculated following Guo *et al.* (2015). All the analyses were performed in R (R Core Team 2014).

Results and discussion

Invasion history (Paper II)

The results based on genetic structure and ABC analysis indicate that *H. persicum* was introduced twice into Europe from Iran. The species was first introduced to Denmark and then to England. Finland and Norway were subsequently colonized by English and Finnish propagules respectively. Genetic markers are considered as reliable tools for tracing the invasion history when the historical records are sparse and incomplete (Estoup & Guillemaud 2010; Cristescu 2015). Historical records shows that *H. persicum* was introduced to Norway from England (Alm 2013 & references therein) and based on the most extensive populations in Norway, further spread in Europe was assumed to have occurred through Norway (EPPO 2009). However, the results of this thesis contradicts the historical records, and identify the most likely native source range (Iran) of introduced populations. The higher migration rate from Finland to Norway than vice versa further supported Finnish origin of the Norwegian populations.

The routes of introduction of *H. persicum* inferred by this thesis appear reasonable as reflected by the distribution of genetic diversity within the introduced range. Population size of invaders generally remain smaller during initial introduction (Sakai *et al.* 2001; Blackburn *et al.* 2015). If we consider smaller population size and following genetic drift as the cause of loss of genetic diversity during invasion (Allendorf & Lundquist 2003; Cristescu 2015; Dlugosch *et al.* 2015), then there should be a pattern of subsequent loss of genetic diversity after each introduction, i.e., the source population has higher genetic diversity than the recipient population (Cristescu 2015). In the case of *H. persicum*, the pattern of loss of the genetic diversity in the introduced range closely resembled the introduction events indicated by the ABC analyses. For instance, Danish and English populations had lower genetic diversity than the Iranian source populations. The genetic diversity of the Finnish populations was lower than the English source and that of the Norwegian populations was lower than the

likely Finnish source. Thus, genetic diversity patterns of *H. persicum* appear to have been shaped largely by diversity of the source and the introduction history.

Genetic diversity and invasiveness (Paper II & III)

More frequent genetic bottlenecks and significantly lower genetic diversity were observed in the introduced range of *H. persicum* compared to the native range. In general, genetically diverse populations may have higher evolutionary potential than genetically depauperate ones (Sakai *et al.* 2001) and may drive invasion success of an exotic species due to higher possibility of adaptability in wider environmental gradients (Lavergne & Molofsky 2007). However, there are several examples of exotic species that are genetically depauperate but successful invaders (Henry *et al.* 2009; Hagenblad *et al.* 2015), thus, challenging the genetic diversity-adaptability hypotheses (Sakai *et al.* 2001; Kolbe *et al.* 2004; Lavergne & Molofsky 2007). Although *H. persicum* seems to have introduced twice, none of the introduced populations have higher genetic diversity than the native one. Such results may be possible if there is no genetic admixture between multiple introduced populations. The results of this thesis also do not support the diversity-adaptability hypothesis as the most vigorous and invasive populations of *H. persicum* (e.g. Norwegian populations) have the lowest level of genetic diversity. Genetics of invasive species, thus, represents a paradox in terms of the role of genetic diversity in adaptability.

The genetic diversity pattern in invasive species, at least in case of *H. persicum*, suggests that a high level of genetic diversity is not a prerequisite for the success of exotic invaders. Given that the persistence of small populations fundamentally depends on the number of individuals, propagule pressure has been considered as one of the important factors in determining the establishment success of introduced species (Simberloff 2009; Blackburn *et al.* 2015). The propagule pressure may have had an important role in the establishment of *H. persicum*. However, absence of genetic admixture and reduced genetic

diversity in the introduced range of *H. persicum* may indicate that propagule pressure did not have any significant role in the subsequent invasion.

The overall distribution of *H. persicum* (Figure 3) and its wide latitudinal and longitudinal range (Paper III) indicate its tolerance to a broad range of environmental variables. This is one of the characteristics of successful exotic invaders: to acclimate in a wide range of habitats and environment in the introduced range as they are often exposed to sudden change in environmental conditions (Sexton *et al.* 2002; Lande 2015). While exploring the role of genetic diversity in invasion, one would expect a higher establishment success of genetically diverse populations, mainly due to the fact that there will be higher chance of containing genetic variants more suited to the new environment (Lee 2002; Forsman 2014; Bock *et al.* 2015). Despite low level of genetic diversity, *H. persicum* seemingly possessed the required genetic variants needed to adapt to its introduced range. For example, the Norwegian populations of *H. persicum* are composed of quite distinct genotypes (Fig 1, 3, 4 S2 in Paper II), and are genetically highly structured compared to other regions (highest average regional F_{ST} , Table 2 in Paper II), indicating limited dispersal. As reduced gene flow is a prerequisite for local adaptation (Lenormand 2002), the spatially extensive populations of *H. persicum* in Norway may be due to the local adaptations or success of pre-adapted genotypes from Iranian temperate mountains. These genotypes may be favoured in the cool northern Norwegian climate compared to other countries. From its present distribution in Norway, it is evident that *H. persicum* thrives in the humid coastal areas with mild winters, and avoids the drier inland areas with their cold winters, which may also explain the general scarcity of records of naturalized plants in Sweden and Finland. Thus, local adaptation appears more important in determining the invasiveness in *H. persicum* than genetic diversity *per se*.

Impact of invasion (Paper III)

Impact on plant diversity

Dominant exotic invaders have been reported to change the invasion dynamics by facilitating establishment and spread of other exotic species (Simberloff & Von Holle 1999; Ricciardi *et al.* 2013). However, *H. persicum* does not seem to facilitate other exotic species. Overall, only a few other exotic species are found in the plots, and there is no difference in their occurrence between *Heracleum*-invaded and non-invaded plots. Despite an increased number of exotic species in northern Norway, e.g. Troms, during recent years (Alm & Pedersen 2015), their general sparsity may be due the fact that the habitat occupied by the nutrient-demanding gigantic *H. persicum* may not suit other exotic species. From a management perspective, this pattern indicates that there is a relatively low risk of further invasion.

Meanwhile, invasion of *H. persicum* alone seems to have greatly affected the native diversity as indicated by the consistent reduction in all the diversity parameters (Shannon's diversity, evenness, taxonomic diversity, and species richness) in the invaded plots compared to the non-invaded plots. On average, the invaded plots lost two native species compared to the non-invaded plots. The lower relative richness but higher relative abundance of exotic species, as is the case here, indicates that presence of a single dominant exotic invader that can reduce diversity and potentially extirpate native species (Catford *et al.* 2012). Thus, the lower richness in the invaded plots may be the result of high cover of *H. persicum*. Cover of exotic invasive species is considered one of the most important factors in reducing native diversity (Hejda *et al.* 2009). *Heracleum persicum* may reduce species richness of the invaded sites by consuming much of the available resources for high biomass production, shading other native species due to its high stature and dense cover, altering soil characteristics after subsequent decomposition of biomass, and inhibiting the germination of seeds of other species due to its allelopathic effect (Myrås & Junttila 1981). Thus, due to the possession of competitive traits (e.g. early growth, huge biomass production, high seed production and

perennial habit), *H. persicum* appears as an efficient ‘exploiters’ that may reduce native plant diversity

The space-for-time approach is generally used to compare the impact of invasion when historical data are lacking (Pyšek & Pyšek 1995; Hejda *et al.* 2009). This approach assumes that the vegetation composition of invaded and non-invaded plots were similar before the invasion and considers any post-invasion difference in vegetation characteristics as an invasion impact (Thomaz *et al.* 2012). If one sticks to the space-for-time approach to quantify the impact of *H. persicum* invasion on plant diversity, one can conclude that *H. persicum* replaces native species, as indicated by the lower native richness in the invaded plot. In general, a dominant invader may reduce the abundance of native species at local scale and force native species to pass through low-abundance stages with decreased relative distribution long before species richness starts declining (Wilsey & Potvin 2000; Mulder *et al.* 2004). Thus, in this case, the consistently lower natives’ cover may be responsible for reducing Shannon’s diversity, taxonomic diversity and evenness in the invaded plots. The observed pattern was expected as dominant invasive exotic species may reduce the abundance of the native species locally, which in turn may decrease diversity (e.g. Shannon’s diversity index, evenness and taxonomic diversity) of the invaded system (Pyšek & Pyšek 1995; Hejda *et al.* 2009). Thus, the reduced cover of the most native species in the invaded plots indicates that several species are on their way to local extinction if *H. persicum* continually exerts such pressure on the native species.

Impact on invasibility

The vulnerability of a plant community to further invasion depends on the native-native and native-alien interactions as the first invader may potentially alter the invasion dynamics of a community (Catford *et al.* 2012). In this case, the estimated invasibility was significantly higher for the non-invaded plots compared to the invaded plots (Table 2 in Paper III). In addition, there was a negative association between invasibility and cover of *H. persicum* (see Table S2

in Paper III). There is a general agreement that the presence of several exotic species indicates habitat heterogeneity and community saturation, which in turn makes an invaded community less prone to further invasion (Catford *et al.* 2012; Chytrý *et al.* 2012). Given that, *H. persicum* might have extensively consumed the available resources to produce a huge cover or biomass, leaving scanty resources unconsumed, thus, not providing other species an opportunity to establish. On the other hand, high level of invasion also means an increased probability of occurrence of exotic species leading to a higher risk of establishment and invasion by exotic species (Rejmánek & Randall 2004; Chytrý *et al.* 2012). In general, there is still no consensus as to whether exotic species increase or decrease further invasion. The results further suggest that higher variation in total height may indicate resistance to future invasion (Table S2 in Paper III). This result is intuitive in the sense that several native species of smaller size can co-occur with giant *H. persicum*, which ultimately occupy the available space and deplete the resources making further invasion unlikely. In other words, co-occurrence of exotic and native species of varying size may fill the vacant niches and use most of the resources, thus, not allowing further invasion.

Genetic diversity is analogous to species diversity, and accordingly expected to resist invasion because species diversity act as biotic resistance to invasion (Vellend & Geber 2005). In contrast, there was a positive association between the genetic diversity of *H. persicum* and estimated invasibility (Table S2 in Paper III). Cover of *H. persicum* was important determinant of invasibility as reflected by a negative association between cover of *H. persicum* and invasibility. It is noteworthy that the introduction history of *H. persicum* in Norway is more important in determining invasibility than genetic diversity *per se*. The positive association between latitude and genetic diversity appears as a consequence of subsequent loss of genetic diversity during the north-south spread, most likely from an area close to Talvik, of *H. persicum* in Norway (Paper II). This means genetically diverse northern populations of *H. persicum* have had a longer residence time than the recently established populations in southern Norway. This also indicates that, due to succession, competitively strong native

species co-occur with *H. persicum* in historically older sites, which may constrain cover of *H. persicum*. If so, older sites offer less competition and more unconsumed resources compared to the others where *H. persicum* is dominant. This discrepancy in resource availability makes historically older sites, where genetic diversity of *H. persicum* is higher, more invisable than the recently invaded sites.

Taxonomy and hybridization (Paper I)

The polymorphic microsatellites developed for *H. persicum* can be used as reliable markers to resolve taxonomy of *Heracleum* in general and of giant hogweeds in particular. It is important to emphasize that the sparse historical record and a general lack of voucher specimens of giant hogweeds directly affect the identification of *Heracleum* species (Fröberg 2010). As a consequence, the taxonomy of the northern Norwegian giant hogweed remained controversial in the past, and *H. persicum* may still to some extent be confused with *H. mantegazzianum* (Fröberg 2010; Alm 2013). The taxonomy of *H. mantegazzianum* is equally controversial in the UK (Sell & Murrell 2009; Stace 2010; Denness *et al.* 2013). These uncertainties clearly show that *Heracleum* is a taxonomically complex genus. Meanwhile, microsatellite markers clustered the controversial samples from England, which have been named either *H. trachyloma* or *H. mantegazzianum* (Sell & Murrell 2009; Stace 2010), with other samples of *H. mantegazzianum* (e.g. from Norway, fig. 1 in Paper I). Similarly, hybrids of invasive species are often unidentifiable and can impede management interventions. Of the microsatellite markers validated on *H. persicum*, 60-76%-were polymorphic for hybrids and all other species of *Heracleum* included in this thesis. The developed suite of markers clearly differentiated the genetic structure of giant hogweeds, a distantly related *H. sphondylium*, and their hybrids (Fig. 1 in Paper I). This indicates that the set of microsatellite markers may be used as an alternative tool in discriminating genetic structure of hogweeds and their hybrids.

These markers were also polymorphic for another genus *Anthriscus* of the family Apiaceae. Although microsatellite markers are often criticized for their application in

phylogenetic analyses due to size homoplasy (Chambers & MacAvoy 2000; Estoup *et al.* 2002), cross-generic amplification of a few markers indicates the possibility of wider application of the designed markers within the Apiaceae. Thus, the suite of microsatellite markers developed and validated in this thesis may be instrumental in resolving *Heracleum* taxonomy, study hybridization between species of *Heracleum*, study of other Apiaceae, and may therefore be useful in management of invasive giant hogweeds and allies.

Recommendation for management (Paper I, II, & III)

Heracleum persicum needs urgent management consideration due to its strong negative impact on the native plant diversity. It is vigorous and highly invasive in the introduced range despite its reduced genetic diversity. This indicates that introduction of few seeds of *H. persicum* may develop into invasive populations. The historical vector (i.e., frequent cultivation in gardens) responsible for the original introduction and dispersal of *H. persicum* is now probably obsolete, indicating no further risk of intentional introductions from the native sources. However, a successfully established invasive population may pose greater risk of spread than the native source as the former is already adapted to be invasive (Estoup & Guillemaud 2010; Lombaert *et al.* 2010). Accidental introduction and expansion of *H. persicum* is quite likely in Europe due to the high frequency of cross-border transportations. I recommend managers to avoid a possible second introduction from the English and the Finnish populations. Otherwise, successive waves of introduction from similar sources may augment further invasions.

Biological control agents are generally chosen from the native range of the invasive species (Roderick & Navajas 2003). A nematode, *Heterodera persica*, has been reported to parasitize on *H. persicum* in Iran (Maafi *et al.* 2006). Thus, *Heterodera persica* may be considered as a candidate bio-control agent in the introduced range of *H. persicum*. However, due to perennial habit, clonal reproduction, and more than two distinct genotypes, a single biological or chemical control agent may be less effective in controlling *H. persicum*. Thus, I

suggest 'shoot first and ask later' approach (Simberloff 2003) to control *H. persicum*. Uprooting the entire plant or mowing/cutting for several years appears as one of the best options to eradicate *H. persicum* as practiced by gardeners at the University of Tromsø.

Hybridization can impede management interventions as they often remain unrecognized. *Heracleum persicum* commonly hybridizes with *H. sphondylium*. Hybrids may further pose management challenges due to enhanced invasive abilities as a consequence of interspecies hybridization (Ellstrand & Schierenbeck 2000; Schierenbeck & Ellstrand 2009). In addition, giant hogweeds and their hybrids may jointly affect the native diversity. Thus, identification of hybrids, using developed markers, and their control is highly recommended for the conservation of native plant diversity.

Conclusions

This thesis developed genetic tools, which is otherwise unavailable for non-model organisms such as *H. persicum*, which may be instrumental in studying population genetics of both useful and noxious species of *Heracleum*. Cross-amplification of few markers with one of the distantly related genera, *Anthriscus*, of the Apiaceae further indicates the possibility of broader application of the developed markers in resolving taxonomic and phylogenetic issues particularly within *Heracleum* and possibly in other genera within the family Apiaceae. By tracing the most likely route of introduction of one of the massive plant invader of Scandinavia, this thesis not only resolved the contradicting introduction history of *H. persicum* but also allowed detection of important source populations of *H. persicum* that may enhance further invasion. The lack of correlation between genetic diversity and invasiveness indicates that even a small founder population may cause high impact. Established populations of an exotic species should not be a management concern unless it affects native diversity. By documenting severe negative impact of *H. persicum* on the native plant diversity, this thesis draws the attention of management authorities to control and eradicate *H. persicum* for the conservation of native plant diversity.

Future perspectives

I recall the taxonomic problem within 'giant hogweeds' and further imagine the complexity within *Heracleum* as there are nearly one hundred species. In addition, identification of hybrids of giant hogweeds would be definitely challenging. This thesis has reported a good number of microsatellite markers that may be useful in identifying other *Heracleum* species. However, due to size homoplasy, microsatellite markers should be cautiously used in phylogenetic analyses. One alternative would be to use as many markers as possible in such analyses. Thus, one can validate rest of the markers if the intention is to study phylogeny within *Heracleum*. Furthermore, due to the poor correlation between neutral and quantitative genetic variation, I recommend using recent genome wide sequencing approaches, e.g. restriction site associated DNA sequencing (Etter *et al.* 2011), to directly measure the quantitative trait variation if the aim is to discern the adaptability of *Heracleum* in the sub-arctic climate. This thesis revealed contrasting but most likely pattern of introduction of *H. persicum* into Europe compared to what historical records were indicating. The current result may be further validated or contrasted by using high-throughput sequencing approaches such as genotyping-by-sequencing (Elshire *et al.* 2011), which involves genomewide markers that provide global view of the genome (Cristescu 2015).

Invasion by *H. persicum* reduces native diversity. On the other hand, it increases community's resistance to further invasion. This discrepancy in the role of *H. persicum* makes it difficult to conclude whether it is friend or foe of native diversity. Personally, I believe that impact of *H. persicum* outweighs the invasion resistance it offers. In addition, the studied sites appear less vulnerable to further invasion as indicated by the general sparsity of other exotic species. Due to the problem of finding appropriate space for establishing invaded/non-invaded plots of large size in the neighbourhood, I ended up choosing a plot size that may not be ideal in order to study giant species like *H. persicum*. I recognize the size of the plot as one of the important factors affecting diversity analyses, and suggest that future researchers use larger plots to make a more precise picture of impact of *H. persicum* visible.

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