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Veli-Matti Kangas

GENETIC AND PHENOTYPIC VARIATION OF THE MOOSE (*ALCES ALCES*)

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GENETIC AND PHENOTYPIC VARIATION OF THE MOOSE (*ALCES ALCES*)

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Abstract

Spatial and temporal variation is a universal feature in most organisms in nature, commonly reflecting the past evolutionary history of the species as well as the prevailing environmental conditions. The purpose of this doctoral thesis study was to investigate the genetic and phenotypic variation, and to assess the roles of the different processes affecting them in the moose (*Alces alces*). Altogether 809 DNA samples of moose, gathered throughout Finland and the Republic of Karelia in Russia, were analysed with a variety of population genetic methods. Furthermore, the shape of the moose mandible was investigated with the help of geometric morphometrics using a subset of samples gathered from 179 moose in Finland. This study showed that the Finnish and especially the Karelian moose population harboured relatively high genetic diversity, albeit with clear regional differences in its spatial distribution. In the northern half of Finland, a secondary contact of two diverged mitochondrial lineages was revealed. The presence of the two lineages was interpreted to reflect the existence of allopatric refugia of moose during the Last Glacial Maximum and the subsequent bi-directional recolonisation of Fennoscandia. Furthermore, a spatially explicit Bayesian clustering analysis suggested existence of three genetic clusters, which were estimated to have split after the post-glacial recolonisation. The results also showed that past declines in the moose numbers during the 18^{th} and 19^{th} centuries led to population bottlenecks, leaving a genetic imprint. Thus, the present moose population in eastern Fennoscandia carries the signs of both ancient and more recent events in its genetic composition. Finally, a significant latitudinal shift was revealed in the shape of the moose mandible. The pattern was considered independent of the genetic clustering of the population. The main changes included an enlargement of the attachment surfaces of the muscles controlling biting and mastication, implying more effective mastication in the north compared with the south, possibly an adaptive response to a longer period of hard wintertime diet. The results of this thesis encourage continuation of studies on the moose in order to fully reveal the impact of particular historical events and especially anthropogenic factors on the genetic and phenotypic variation of this species. They also provide the starting point for ‘genetically enlightened’ moose management and conservation in Finland.

Keywords: Alces alces, genetic diversity, genetic structure, mandible shape, phenotypic variation, population bottleneck

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Tiivistelmä

Lähes kaikilla eliölajeilla esiintyy ajallista ja paikallista muuntelua, joka on seurausta lajin evolutiivisesta historiasta ja vallitsevista ympäristöoloista. Tässä väitöskirjatutkimuksessa tutkin hirven (*Alces alces*) geneettistä ja fenotyyppistä muuntelua sekä niitä selittäviä taustatekijöitä populaatiogeneettisillä ja geometrisen morfometrian menetelmillä. Geneettisen aineiston muodostivat Suomesta ja Venäjän Karjalasta kerätyt 809 hirven DNA-näytteet. Fenotyyppisenä ominaisuutena tutkittiin hirven leukaluun muotoa yhteensä 179 alaleuasta. Geneettinen monimuotoisuus oli tutkimuksen mukaan Suomen ja erityisesti Karjalan hirvipopulaatiossa verrattain korkea, joskin alueelliset erot olivat varsin selviä. Pohjoisesta Suomesta löytyi kahta erilaistunutta mitokondrion DNA:n sukulinjaa, joiden arvioin erilaistuneen viimeisen jääkauden aikana, todennäköisesti erillisissä refugioissa, ja saapuneen aikoinaan Suomeen eri reittejä pitkin. Tämän ohella tuman DNA paljasti lisää alueellisia rakenteita; bayesilainen ryhmittelyanalyysi havaitsi hirvellä kolme erillistä alapopulaatiota. Näiden ryhmien arvioin kehittyneen vasta Suomen uudelleenasuttamisen jälkeen. Tämän tutkimuksen tulokset osoittivat myös, että historiallisesti tunnetut kannanromahdukset 1700- ja 1800-luvuilla johtivat populaation pullonkaulaan, joka jätti jälkensä hirven perimään. Itäisen Fennoskandian hirvipopulaation geneettiseen muunteluun ovat siis vaikuttaneet sen historian aikana niin jääkauden aikaiset kuin tuoreemmatkin tapahtumat. Tämän lisäksi hirven alaleuan muodossa havaittiin merkitsevä etelä-pohjoissuuntainen muutos. Tulosten mukaan purentaa ohjaavien lihasten kiinnityspinnat laajenevat pohjoista kohti siirryttäessä, mikä viittaisi siihen, että hirven leukojen puruvoima on pohjoisessa suurempi kuin etelässä. Ilmiö oli riippumaton populaation geneettisestä ryhmittyneisyydestä, ja se on mahdollisesti seurausta kovemman talviruokavalion aiheuttamasta adaptiivisesta vasteesta. Tämän väitöskirjan tulokset rohkaisevat jatkamaan aiheen tutkimusta, jotta eri historiallisten tapahtumien sekä eritoten ihmisvaikutuksen merkitys lajin geneettiseen ja fenotyyppiseen muunteluun voitaisiin selvittää perin pohjin. Lisäksi tulokset muodostavat lähtökohdan ’geneettisesti valistuneelle’ hirvikannan hoidolle Suomessa.

Asiasanat: alaleukaluun muoto, Alces alces, fenotyyppinen muuntelu, geneettinen monimuotoisuus, geneettinen rakenne, populaation pullonkaula

Äidille ja isälle

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Oulu, October 1st, 2015 Veli-Matti Kangas

Abbreviations

A	Allelic richness
AIC	Akaike information criterion
AMOVA	Analysis of Molecular Variance
b	Slope of regression line
BP	Before present
DNA	Deoxyribonucleic acid
F_{ST} / φ_{ST}	Fixation index; a measure of genetic differentiation
$\hat{h}$	Haplotype diversity
H_e	Expected heterozygosity
HWE	Hardy-Weinberg equilibrium
IBD	Isolation by distance
K	Maximal number of genetic clusters
mtDNA	Mitochondrial DNA
mtN_e	Mitochondrial effective population size
n	Sample size
N_e	Effective population size
Nh	Number of haplotypes
p	Level of statistical significance
PA	Private allelic richness
PCA	Principal component analysis
PC	Principal component
PCR	Polymerase chain reaction
sPCA	Spatial principal component analysis
z	Z test statistic
π	Nucleotide diversity
θ	Theta; an index of mitochondrial genetic diversity

List of original articles

This thesis is based on the following publications, which are referred to throughout the text by their Roman numerals:

I Kangas V-M, Kvist L, Laaksonen S, Nygrén T & Aspi J (2013) Present genetic structure revealed by microsatellites reflects recent history of the Finnish moose (*Alces alces*). European Journal of Wildlife Research 17(4): 15–22.

II Kangas V-M, Kvist L, Kholodova M, Nygrén T, Danilov P, Panchenko D, Fraimout A, Aspi J (2015) Evidence of post-glacial secondary contact and subsequent anthropogenic influence upon the genetic composition of Fennoscandian moose (*Alces alces*). Journal of Biogeography 42(11): 2197–2208.

III Kangas V-M, Rytkönen S, Kvist L, Nygrén T, Käpylä T & Aspi J (2015) Latitudinal variation in the shape of the moose mandible: indications of an adaptive trend. (*Manuscript*).

Contributions

The following table shows the contributions of authors to the original articles/manuscripts

Paper	I	II	III
Original idea	VMK, LK, JA	VMK, LK, JA, TN, MK	VMK, LK, JA, TN
Sample collection	SL	TN, DP, PD	TN
Laboratory work	VMK	VMK, MK, LK, AF	TK
Data analyses	VMK, LK, JA	VMK, LK, JA	VMK, SR
Manuscript preparation	VMK, LK, JA	VMK, LK, JA	VMK, LK, JA, SR

VMK: Veli-Matti Kangas, LK: Laura Kvist, JA: Jouni Aspi, TN: Tuire Nygrén, SL: Sauli Laaksonen, MK: Marina Kholodova, DP: Danila Panchenko, PD: Pjotr Danilov, AF: Antoine Fraimout, TK: Teemu Käpylä, SR: Seppo Rytkönen

Table of contents

1 Introduction

Spatial and temporal variation in genetic and phenotypic traits is a universal feature in most organisms in nature (Lowe *et al*. 2004). This variation is the product of past evolution, and also a prerequisite for further adaptive change (Hartl & Clark 2007, Frankham *et al*. 2009). Describing the different patterns of variation and disentangling the underlying processes continue to provide an endless source of challenge for biologists. The vast quantity of analytical tools available at present helps us in this task, however, enabling us to widen our knowledge of the different evolutionary processes as well as to learn about the history of populations and to gain prospects for the future (e.g. Avise 2000, Guillot *et al*. 2009, Luikart *et al*. 2010, Zelditch *et al*. 2012).

Significant geographic variation is common especially in species occupying vast areas described by varying environmental conditions. In the northern hemisphere, such species include several cervids (Cervidae; Geist 1987, Geist 1998), whose evolutionary history has been impacted immensely by the repeated glaciations during the Pleistocene and by subsequent human actions (Randi *et al*. 2004, Lister 2005 Roed *et al*. 2008, Linnell & Zachos 2011, Zachos & Hartl 2011). This thesis utilises genetic and geometric morphometrics tools to investigate the genetic and phenotypic variation and the factors behind this variation in the largest living representative of the deer family, the moose (*Alces alces*).

1.1 Distribution of genetic variation

1.1.1 Genetic diversity

Genetic diversity refers to the variation of different alleles and genotypes present in an individual, population, species or a group of species. This diversity can be roughly divided into two classes: adaptive diversity affecting the fitness traits of the individual and neutral diversity (Lowe *et al*. 2004). Adaptive diversity is most essential as it is the raw material for natural selection, and hence for adaptive evolution in a changing environment. Consequently, the loss of adaptive diversity is often associated with reduction in reproductive fitness (Frankham *et al*. 2010). However, selectively neutral diversity is also valuable, especially from a research point of view, in helping to interpret the evolutionary processes besides selection (Avise 2000).

The level of genetic diversity present in a population is a result of the interaction of different evolutionary forces - mutations, selection, chance and gene flow - as well as population demography and reproductive system (Hartl & Clark 2007). Mutations are the ultimate source of all diversity, whilst selection together with chance and gene flow cause changes in the allele frequencies in time and space. The element of chance is introduced during reproduction as the random sampling of parental gametes within the population causes allele frequencies to fluctuate over generations. This process is called (random) genetic drift, which affects both adaptive and neutral genetic diversity (Frankham *et al*. 2010).

Genetic drift is the dominant evolutionary force especially in small populations, where the average time between the emergence of a new allele and the subsequent fixation or disappearance is shorter than in large populations (Hartl & Clark 2007). As a consequence, processes such as loss of genetic diversity and genetic differentiation among groups are also more rapid in small populations (Frankham *et al*. 2010). However, rather than census size, it is the effective size of the population (N_e; Fisher 1930, Wright 1931) that determines the strength of the genetic drift. N_e can be defined as the size of an ideal population that has the same rate of change as the observed population. Typically, it is substantially smaller than the census size as natural populations deviate from the assumptions of the idealised population, including e.g. an equal sex ratio, no variance in family size, non-overlapping generations and a constant population size across generations. N_e is a fundamentally important concept and parameter in predicting genetic change, particularly in evolutionary and conservation biology (Frankham *et al*. 2010). Furthermore, N_e can be used retrospectively to explain the observed patterns of genetic variation. Respectively, genetic variation within a population can be utilised in estimating its effective size (e.g. Luikart *et al*. 2010, Serbezov *et al*. 2012).

A population bottleneck is a term referring to a significant drop (either temporary or permanent) in the effective size of a population leading to a loss of genetic diversity due to increased drift (Nei *et al*. 1975, Hartl & Clark 2007). Consequently, bottlenecks can result in a fixation of deleterious alleles and random changes in allele frequencies (Luikart *et al*. 1998). However, the genetic impact of the bottleneck depends on the speed and duration of the population decline; a rapid fall is expected to affect a population more than a gradual one, and more alleles will be lost the longer the bottleneck lasts (Frankham *et al*. 2010). Similar reductions in the effective population size and subsequent genetic effects can occur during colonisation of new areas by a small number of individuals, a phenomenon known as founder effect (Lowe *et al*. 2004).

1.1.2 Genetic population structure

The spatial genetic structure of a species, i.e., the distribution of genetic variation among populations, is determined by the forces generating differentiation (mutations, disruptive selection and genetic drift) and those reducing it (balancing selection and gene flow), together with geographic and ecological factors (Slatkin 1987, Frankham *et al*. 2010). In nature, populations are rarely fully panmictic, but rather genetically subdivided, at least to some extent (Hartl & Clark 2007). This is most apparent with populations separated by geographic barriers; without the homogenising effect of gene flow, the subpopulations will evidently diverge over time due to random genetic drift. As a consequence, distinct genetic clusters are formed, which can persist through time even after the initial barrier has disappeared (Slatkin 1985).

In continuously distributed populations where obvious barriers to gene flow are lacking, genetic differentiation can exist due to behavioural and/or historical factors. One such phenomenon is called isolation by distance (IBD), which rises from geographically limited dispersal diminishing the exchange of genes between the opposite ends of the species' range (Wright 1943, Guillot *et al*. 2009). As a result, the level of genetic differentiation becomes positively correlated with the geographic distance between the subpopulations and/or individuals (Slatkin 1993). Similar structures exhibiting gradual genetic change across the landscape may also result from a secondary contact and admixture of subpopulations diverged in the past, for example in different glacial refugia (Barton & Hewitt 1985, Hewitt 2000, Durand *et al*. 2009) or alternatively, gene flow among subpopulations subjected to differential selection along an environmental gradient (Frankham *et al*. 2010).

1.1.3 Molecular markers

Molecular markers are polymorphic proteins and DNA sequences (nuclear or organelle) utilised as indicators of the genome-wide genetic variation of an individual organism, population or species (Avise 1994, Frankham *et al*. 2010). At present, multiple marker types with varying features are available for different study purposes. Using a combination of genetic markers and/or analytical methods that are effective over different temporal scales, it is possible to capture signatures of population processes over a wide time frame during evolutionary history (Avise 1994, Storfer *et al*. 2007, Wang 2010).

Microsatellites are short DNA sequences that consist of 1–6 nucleotide tandem repeats, scattered frequently throughout the nuclear genome of most taxa. Due to their

many advantageous features, microsatellites are amongst the most popular markers (Selkoe & Toonen 2006, Storfer *et al*. 2010, Guichoux *et al*. 2011). First of all, microsatellites are very variable with a high mutation rate of approximately 5 x 10^{-4} per locus per generation, which makes them suitable especially for inferring recent/contemporary evolutionary processes (Selkoe & Toonen 2006, Wang 2010). Additionally, the co-dominance of this marker enables the distinction between heterozygotes and homozygotes. Microsatellites utilised as molecular markers exist mainly in the noncoding (i.e., neutral with respect to selection) regions of the genome, but they can be found in the protein-encoding regions as well (Ellegren 2004). Like all markers, microsatellites have their drawbacks, one being the existence of null alleles: unamplified alleles at a locus, due to mutations at the primer-binding regions or suboptimal amplification conditions. As a consequence, heterozygotes can be falsely genotyped as homozygotes, leading to heterozygote deficit and thus, possibly erroneous conclusions on the obtained data (Selkoe & Toonen 2006).

Mitochondria, cytoplasmic organelles found in most eukaryotic cells, contain a double-stranded circular DNA of their own (mitochondrial DNA, mtDNA), which differs greatly from its nuclear counterpart: mtDNA is haploid and predominantly inherited only maternally without recombination (Avise 1994). Hence, the effective population size for mtDNA is four times smaller than that of nuclear DNA, making it more prone to genetic drift. MtDNA contains several gene-encoding sequences in addition to one noncoding sequence, the control region, which has been widely utilised as a molecular marker (Avise 2000, Galtier *et al*. 2009). This region is usually highly polymorphic, but with a lower mutation rate of approximately 6 x 10^{-8} (Haag-Liautard *et al*. 2008) compared with microsatellites. Therefore, mtDNA is considered especially well-suited for phylogeographic studies investigating historical evolutionary processes (Avise 2000, Wang 2010).

1.2 Phenotypic variation

Genetic variation within populations is typically manifested as phenotypic variation in size, shape and colour. However, most phenotypic traits are quantitative by nature and emerge as the complex interplay of multiple loci and different environmental factors (Hartl & Clark 2007). Therefore, the correlations between variation estimated with molecular markers and that observed in quantitative traits, respectively, are fairly poor (Reed & Frankham 2003). Nevertheless, investigation of phenotypic variation together with neutral genetic variation helps to assess the contribution of different biological processes that may have contributed to the studied population(s).

Clinal phenotypic variation along environmental gradients is fairly common in continuous populations with large geographic ranges. Similar trends observed in several species led to the constitution of the so-called ecogeographic rules, such as Bergmann's and Allen's rules of increasing body size and shortening appendages towards the poles in homeotherms, respectively (Bergmann 1848, Mayr 1963, Avise 2000). Such trends can develop as a result of evolutionary adaptation through selection favouring different genotypes along the gradient, or alternatively, similar genotypes can produce different phenotypes as a response to the varying environmental conditions. This phenomenon is referred to as phenotypic plasticity, which is a property of an individual or genotype that may be adaptive, maladaptive or neutral with respect to the fitness of the individual (Ghalambor *et al*. 2007). In addition, the genetic structure, a reflection of the history of the population, can influence the distribution of phenotypic variation (e.g. Herfindal *et al*. 2014); e.g. the secondary contact of radiated lineages may lead to formation of a clinal pattern in morphological variation, even in the absence of a readily observed environmental gradient (e.g. Geist 1987).

1.3 The moose (*Alces alces*)

The moose (*Alces alces* Linnaeus, 1758) is the largest extant species of the deer family (Cervidae) and the sole representative of its genus. Traditionally, this circumboreal species (Fig. 1) is divided into up to eight subspecies (Peterson 1955), but an alternative dichotomous classification between European and Asian-American moose has also been proposed on morphological and behavioural grounds (Geist 1987, Geist 1998). Furthermore, the nominate subspecies, *A.a.alces* (the European moose), has a karyotype of 2N = 68 while the other subspecies, sometimes referred to as the American moose group, have 2N = 70, which is why a split into two separate species has been suggested (Boeskorov *et al*. 1996, Boeskorov 1997). Yet, these moose karyotypes live sympatrically in Western Siberia, with no verified reproductive isolation, keeping the debate unsettled for the present (Hundertmark & Bowyer 2004). In this thesis, the name 'moose' is used narrowly, referring only to the European subspecies (unless stated otherwise), for simplicity.

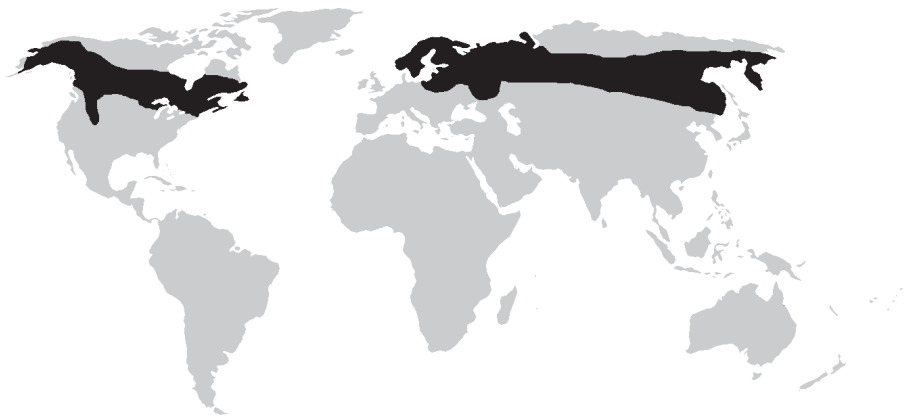

Fig. 1. The global distribution area of the moose (*sensu lato*). The map was downloaded at Wikimedia commons on 13th of July 2015.

The moose is a typical browser herbivore and can be considered a keystone species in the boreal ecosystem (see Melis *et al*. 2007, Suominen *et al*. 2008, Mathisen *et al*. 2010, Mathisen *et al*. 2012). The moose is traditionally associated with mires and early succession stage forests (e.g. Nikula *et al*. 2004), feeding mainly on various species of herbs, shrubs and sprigs during the summer, while the shoots and twigs of trees and shrubs compose its wintertime diet (Telfer 1984, Shipley *et al*. 1998, Mysterud 2000, Wam *et al*. 2010, Milligan & Koricheva 2013). Recent studies have shown the species to exhibit a very flexible behaviour in habitat selection and use, being well-adapted also to human-altered and dominated landscapes (Bjørneraas *et al*. 2011, Bjørneraas *et al*. 2012, Eldegard *et al*. 2012, Melin *et al*. 2014). Described as a serially monogamous species, moose possesses high reproductive potential, enabling fast population growth under good environmental conditions (Bubenik 1985, Nygrén 2009).

The moose is regarded as a partially migratory species, where most, but not all, populations/individuals migrate between separate summer and winter ranges (Sweanor & Sandegren 1989, Heikkinen 2000, Singh *et al*. 2012), with especially female moose showing high home range fidelity (Tremblay *et al*. 2007). Despite being potentially highly mobile animals able to cover hundreds of kilometres within a short period of time (Hoffman *et al*. 2006), moose exhibit strong philopatric behaviour as juveniles disperse only a short distance from the natal ranges (Cederlund & Sand 1992).

1.3.1 History of moose in eastern Fennoscandia

According to the present knowledge, the modern moose originated in Asia approximately 100,000 years ago (Lister 1993), from where it spread to Europe and North America during the Late Pleistocene (Hundertmark & Bowyer 2004). However, during the Last Glacial Maximum (c. 21,000 years ago; Clark & Mix 2002), when northern and central parts of Europe were covered with continental ice, moose were forced to seek refugia in lower latitudes. Moose fossils from that time have been discovered e.g. in Italy, Balkans, Carpathians, Caucasus and further east in the Urals (Sher 1987, Sommer & Nadachowski 2006). The subsequent climatic warming and ice retreat (c. 10,000 years ago) started a swift re-expansion of Europe. In the early Holocene, moose used to be abundant in most of continental Europe before disappearing in the Middle Ages (Schmölcke & Zachos 2005). Currently, the European moose has a vast and continuous area of distribution westwards from Western Siberia to Northern and Eastern Europe, with an estimated global population of approximately 1.5 million individuals and increasing in 2008 (Henttonen *et al*. 2008).

Following the northward shift of boreal habitats during the Holocene, the moose has been a part of the Finnish fauna at least since 9,000–8,000 years ago (Ukkonen 1993). Among many other taxa, moose are assumed to have colonised this region via two main pathways: east from Russia and south-west from continental Europe via southern Scandinavia (Markgren 1974, Hundertmark *et al*. 2002). However, knowledge on the status of the moose population prior to the 16th century is very scarce (Nygrén 1987). The moose has been a very important game species in Finland since the time of the early hunter-gatherers and apparently, harvesting by humans together with environmental change has had a substantial effect on local moose numbers already for several millennia (Siiriäinen 1982, Ukkonen 1993, Oinonen *et al*. 2014). For example, the species is completely absent in the archaeological refuse fauna in the middle of the Subboreal period (4,000–3,000 years ago), indicating a possible population decline during that time (Ukkonen 1993).

From the 1600s onwards, the Finnish moose population has experienced several declines as well as local extinctions, most probably due to anthropogenic factors (Nygrén 1987). The most drastic times were seen in the mid-1800s, when the whole population in Finland was close to total extinction (Mela 1900, Nygrén 2009). Following protection actions started in 1923, moose were able to recover, after likely having survived in only two separate populations in north-eastern and south-western parts of the country; the latter believed to have gone through a bottleneck of not more

than six individuals (Nygrén 1987, Nygrén 2009). The situation was slightly better on the Russian side, where the moose persisted in the Kola Peninsula and farther south in Karelia around the shores of large water bodies: the Gulf of Finland, Lake Ladoga and Lake Onega (Danilov 2005, Danilov & Panchenko, unpublished). The recovery took several decades and the moose populations started to grow and expand on both sides of the border in the 1950s; in Finland, the population size doubled from ~10,000 individuals to 24,000 within ten years (Nygrén 1987, Danilov 2005).

In the latter half of the 1900s the history of moose took a new course in Finland: benefitting greatly from changes in land use, management and the absence of large carnivores (Nygrén 1987), this previously rare species became highly abundant with increasing ecological, economic and social impact (Nygrén 2009). Firstly, intensified forestry increased the proportion of young forest stands in the landscape from the 1950s onwards, providing more suitable habitats and nutrition for moose. Furthermore, the introduction of age- and sex-specific harvesting regimes in the Nordic countries in the early 1970s (Lavsund *et al*. 2003) enhanced the population productivity, leading to an exploding growth (Fig. 2); by the year 1980, the number of moose had taken a leap from less than 20,000 individuals to approximately 100,000 individuals (Nygrén 1987). After a short decrease in the mid-1990s, an all-time record was achieved in the winter of 2002, when approximately 140,000 moose roamed in Finland (Nygrén 2009, Anonymous 2014). Throughout the late 1900s, there has been a trend of increasing population density from the south to the north of the country (Lavsund *et al*. 2003, Nygrén 2009).

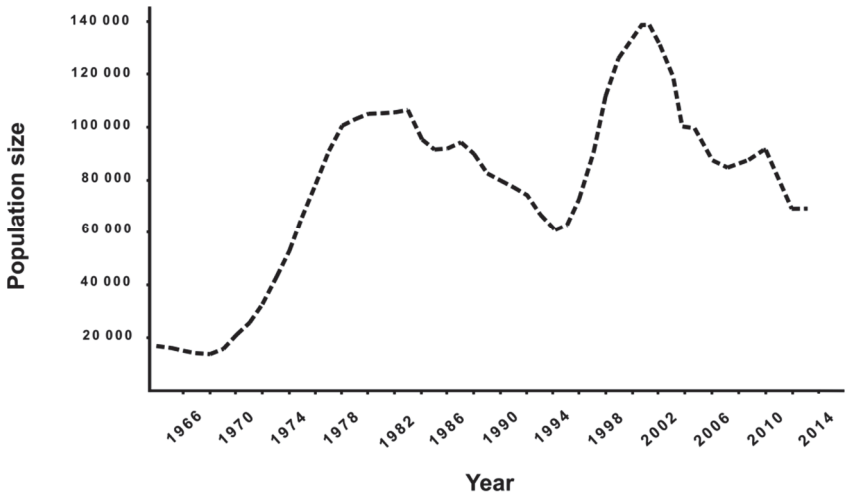

Fig. 2. Population dynamics of the Finnish moose population from 1964 to 2013.

Currently, the Finnish moose population is heavily regulated and structurally modified by management; the goal is to achieve moose densities which decrease moose-inflicted damage to forestry and moose-related traffic accidents, while maintaining good productivity at the same time (Lavsund *et al*. 2003, Nygrén 2009). In contrast, after a peak in the 1970s, moose numbers in Russian Karelia have remained at a clearly lower level due to older age structure of forests, higher predation level and intense, yet less systematic and target-oriented harvesting compared with Finland (Danilov 2005, Danilov & Panchenko, unpublished).

2 Aims of the study

Despite its fairly well-recorded history (Nygrén 1987), only a little is known of the genetic variation and structure of the moose population in Finland and Russian Karelia (e.g. Ryman *et al*. 1980, Hundertmark *et al*. 2002). Even less information exists on how the different potential factors - recolonisation history, consecutive local extinctions and expansions - have in reality affected the population present today, and if their impact is visible in the genetic composition of the moose populations. Accordingly, this thesis presents the first extensive genetic study on the Finnish-Karelian moose using two neutral molecular markers. Furthermore, with the help of geometric morphometrics, patterns of phenotypic variation are investigated using the shape of moose mandible as a model trait. Consisting of three original papers (I–III), this doctoral thesis aims to:

1. Investigate the level of genetic variation and differentiation of moose in Finland and Russian Karelia (I, II)
2. Study the past demography and search for populations bottlenecks (I, II)
3. Evaluate the roles of post-glacial recolonisation and subsequent human exploitation in forming the present genetic composition of moose (I, II)
4. Quantify morphometric variation in the shape of the moose mandible, and to search for possible geographic patterns and association with the genetic structure (III)

3 Materials and methods

This section provides a brief summary of the materials and methods applied. More detailed descriptions can be found in the original papers (I–III).

3.1 Sampling

Sources of DNA for this research included blood (I) and muscle tissue samples of moose (II, III) gathered in Finland and the Republic of Karelia in Russia. The blood samples were obtained from 116 legally hunted (years 2004–2007) and 14 radio-collared (years 2008–2009) Finnish moose. The muscle tissue samples consisted of 583 and 96 legally hunted moose from Finland and the Republic of Karelia, respectively. The Finnish samples were collected during the years 1998 (n = 537) and 2011 (n = 46) and the Karelian samples between 2005 and 2008. The morphometric analyses in subproject III utilised a collection of right side mandibles (n = 179) gathered from the same legally hunted moose in Finland in 1998 (III).

Two different sampling schemes were applied in this study (Fig. 3). For paper I, the samples were gathered using an aggregated sampling scheme in seven areas in Finland: South-Western Finland, Porkkala, Ostrobothnia, Western Lapland, Eastern Lapland, Kainuu and Karelia. Respectively, more spatially continuous schemes were used in papers II and III. The samples were divided into five regional groups for population-level analyses in paper II: Finnish Lapland, Northern Finland, Eastern Finland, Western Finland and Republic of Karelia (Fig. 3).

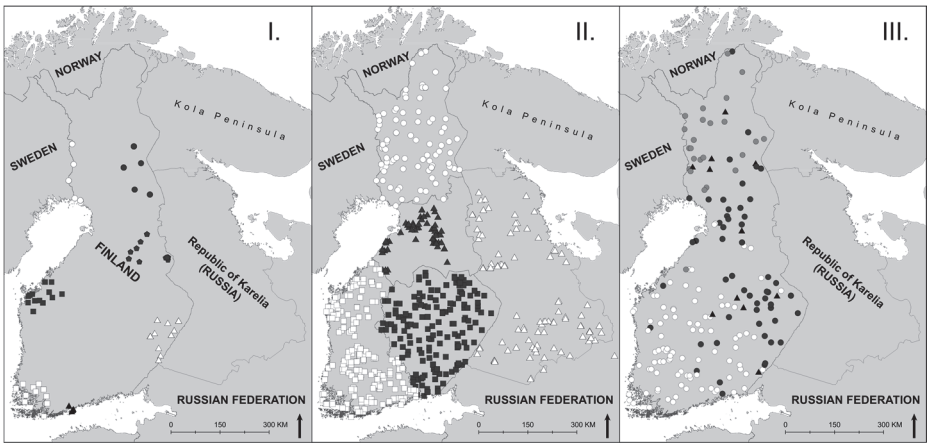

Fig. 3. A map of the sampling schemes of moose applied in the original three (I–III) papers of this study: I) south-western Finland (white squares), Porkkala (black triangles), Ostrobothnia (black squares), western Lapland (white circles), eastern Lapland (black circles), Kainuu (black pentagons) and Finnish Karelia (white triangles); II) western Finland (white squares), eastern Finland (black squares), northern Finland (black triangles), Lapland (white circles) and Russian Karelia (white triangles); III) south-western cluster (white circles), eastern cluster (black circles), northern cluster (grey circles) and un-assigned individuals (black triangles).

3.2 DNA extraction, genotyping and sequencing

Different DNA extraction methods were applied for the two animal tissue types: DNA from the blood samples was extracted using UltraClean™ BloodSpin™ Kit (MoBio Laboratories), while the muscle tissue samples were treated either with UltraClean® Tissue & Cells DNA Isolation Kit (MoBio Laboratories) or Diatom DNA Prep 200 Kit (IsoGen Ltd). All extractions were performed according to the manufacturers' protocols.

For all the subprojects, moose DNA samples were originally amplified and genotyped at sets of 10 (n = 130; I) and 16 (n = 574; II & III) microsatellite loci, developed for ungulates. Detailed descriptions of the PCR procedures can be found in the original articles. All PCR products were run with an ABI 3730 DNA Analyzer (Applied Biosystems) and alleles were scored using GENEMAPPER 4.0 (Applied Biosystems) software. The data were inspected for possible null alleles, stutter bands and large allele dropouts as well as for deviations from Hardy-Weinberg and linkage equilibrium expectations (I & II). In paper I, significant homozygosity excess ($p <$

0.001), indicating existence of null alleles, was detected at two loci, which were consequently left out from the BOTTLENECK analysis (see 3.3.3). Respectively, in paper II, consistent homozygosity excess was detected at one locus; this locus was therefore discarded from all subsequent analyses.

In subproject II, a 679 base pair part of mitochondrial DNA (mtDNA; including the control region domain I and part of domain II) was amplified using either primers LGL283 and ISM015 (Hundertmark *et al*. 2002) or LmPro and TDKD (Mikko & Andersson 1995). Full description of the PCR procedure can be found in the original article (II). All PCR products were sequenced (ca. 50% in both directions, with consistent results) using their corresponding primers. Sequencing reactions were performed using a BigDye Terminator v.3.1 Kit and run on an ABI 3730 or an ABI 3130 DNA Analyzer (Applied Biosystems). All the mtDNA sequences (n = 224) were aligned manually together with previously published moose mtDNA data (n = 21) from the Republic of Karelia, Kola Peninsula and Leningrad Oblast (Kholodova *et al*. 2005, Rozhkov *et al*. 2009). Those data were included in all of the mitochondrial DNA analyses in subproject II.

3.3 Population genetic analyses

3.3.1 Genetic diversity

Microsatellite genetic diversity can be estimated with several different parameters, the most common being expected heterozygosity *(H_e*; also called gene diversity) and allelic richness (*A*). H_e refers to the expected proportion of heterozygotes over loci under Hardy-Weinberg equilibrium, while *A* is simply the number of alleles averaged across all the studied loci and standardised for sample size. It is possible to calculate these estimates for both individual and population levels. Additionally, one can estimate private allele (i.e., alleles found in only one of the populations) richness (*PA*) to quantify the unique allele diversity within populations. In this study, the microsatellite diversity of east Fennoscandian moose was calculated with several different programs: H_e with ARLEQUIN (Excoffier *et al*. 2005; I) and GENETIX (Belkhir *et al*. 2004; II); *A* (adjusted for sample size by rarefaction) with FSTAT (Goudet 1995; I) and HP-RARE (Kalinowski 2005; II); *PA* (also adjusted for sample size) with HP-RARE (II).

Analogous estimates can be calculated to characterise diversity in the mtDNA sequences; nucleotide diversity (π) and haplotype diversity ($\hat{h}$) describe diversity in

nucleotide and haplotype levels, respectively, while theta (θ) is the function of the effective population size and mutation rate per site per generation, estimated from the number of segregating sites. Furthermore, the number of private haplotypes (i.e., those found in only one sampled individual) can be a highly informative parameter with regards to the history of the population (Avise 2000). Here, all mtDNA diversity estimates for moose were calculated with DNASP 5.0 (Librado & Rozas 2009; II).

3.3.2 Genetic population structure

The genetic population structure of the moose was investigated with several different approaches. Firstly, a haplotype network was drawn combining mitochondrial haplotype data gathered in this study with all published sequence information (at the same mtDNA region) on the Palaearctic moose (II). The time of divergence between the two mtDNA clades detected in the data (see 4.1.1.) was calculated applying divergence rates of 62.8% (domestic cattle, *Bos Taurus*; Bradley *et al*. 1996) and 78.5% per million years (bison, *Bison bonasus*; Burzyńska *et al*. 1999).

With the microsatellite data, the main tools to analyse genetic structure were the Bayesian clustering approaches implemented in the programs STRUCTURE (Pritchard *et al*. 2000, Falush *et al*. 2003); I) and TESS (Chen *et al*. 2007, Durand *et al*. 2009; II), which probabilistically assign individuals to groups (clusters) according to their multilocus genotypes. These programs simultaneously assess the most probable number of clusters and then allocate individuals into them (Guillot *et al*. 2009, François & Durand 2010). Both programs apply admixture models, which suppose the data originate from the admixture of K putative parental populations. Additionally, TESS conducts a spatially explicit analysis, which includes geographic information (based on coordinates of the sampled individuals) to account for clines and spatial autocorrelation (François & Durand 2010).

The spatial principal component analysis (sPCA; Jombart *et al*. 2008) is a multivariate method that investigates spatial genetic patterns by simultaneously taking into account genetic variance and spatial autocorrelation and summarising the data in scores, positive and negative. The positive sPCA scores describe global genetic structures, i.e., clusters and clines, whereas the negative scores account for local patterns. Both structures can be tested statistically using permutations, after which the retained scores are used to assess the spatial genetic patterns visually (Jombart *et al*. 2008). In this study sPCA was applied alongside the Bayesian clustering methods to assess the model's suitability (II). Furthermore, IBD patterns were studied by regressing Loiselle's kinship coefficient (Loiselle *et al*. 1995) against geographic

distances between pairs of moose individuals divided into ten distance classes, as implemented in the spatial autocorrelation analysis in the program SPAGEDI (Hardy & Vekemans 2002; I&II).

The genetic structure was assessed further with traditional *F*-statistics. In a nutshell, *F*-statistics are based on calculating the summary statistics of variance in allele frequencies to estimate the amount of differentiation and migration rates between pre-defined subpopulations (Wright 1950). The program SAMOVA (Dupanloup *et al*. 2002) was used to search for the best grouping of the studied regions based on their geographical proximity and genetic differentiation (I & II). This grouping was subsequently used in analysis of molecular variance (AMOVA) in the program ARLEQUIN, which was also used to calculate pairwise F_{ST} (microsatellite data; I&II) and φ_{ST} values (mtDNA data; II).

3.3.3 Population history

The genetic imprints of past demographic crashes (population bottlenecks) can be traced with several different methods. The classic heterozygosity excess test implemented by the program BOTTLENECK (Piry *et al*. 1999) relies on the relationship between heterozygosity and allelic diversity. In the course of a population bottleneck, especially rare alleles are lost with only a minor influence on the total heterozygosity. This leads to a transient excess of heterozygosity compared with the observed number of alleles, which can be considered as evidence of a past bottleneck when observed (Cornuet & Luikart 1996). Another method applicable to microsatellite data is based on calculating the ratio of the number of alleles and the range of the allele sizes present in a population. This so-called M-ratio (or G-W index) is expected to decrease during a bottleneck because the random loss of alleles is faster than the decrease in the allele range (Garza & Williamson 2001). Both of these approaches were applied on the microsatellite data to investigate genetic signatures of past population bottlenecks in the Finnish moose population (I).

Many of the more refined methods of inferring the evolutionary histories of populations are based on coalescence theory (Kingman 1982a, Kingman 1982b). In essence, these so-called coalescence approaches trace the alleles of a certain gene in a population back to their most recent common ancestor in order to build gene genealogies representing the inheritance relationships of the alleles, as well as the times of common ancestry (Avise 2000). As the coalescence times are related to the size of the population, the temporal distribution of the common-ancestry times in the built gene genealogy can be used to infer changes in the historical population size. In

this study, the coalescence approach was utilised on the mtDNA data by producing Bayesian skyline plots, i.e., trajectories of the mitochondrial effective population size (mtN_e) of the Finnish and Karelian moose population over time with the program BEAST (II, Drummond *et al*. 2005, Drummond & Rambaut 2007). This approach enables gene genealogy and demographic history to be coestimated simultaneously in a single analysis, providing a plot of the past population size fluctuations with 95% credibility intervals (Drummond *et al*. 2005). In order to assign a time-scale to the population-size estimates, divergence rates for domestic cattle and bison (62.8% and 78.5% per million years, respectively) were applied in the analyses.

Additionally, coalescence methods can be used to test for the most probable historical scenario for the present-day genetic patterns as well as to estimate times of divergence and gene flow between (sub)populations (Kuhner 2009). Here, the program DIYABC2 (Cornuet *et al*. 2014) was used in paper II to estimate times of divergence and effective population sizes in a three-subpopulation scenario (see 4.2.2). Special interest was focused on estimating the time of divergence in order to differentiate between the effects of recolonisation history and more recent events.

3.4 Geometric morphometrics analyses

The mammalian mandible (i.e., the lower jaw) has been studied intensively as a general model for the development and evolution of complex morphological structures (e.g. Atchley & Hall 1991, Atchley 1993, Klingenberg *et al*. 2003, Klingenberg *et al*. 2004). Additionally, due to its fundamentally important role in food selection and mastication, the relationship between the shape and the biomechanical function of the mandible and foraging has been gaining increasing attention in evolutionary morphology (e.g. Young & Badyaev 2010, Zelditch *et al*. 2012, Anderson *et al*. 2014). In deer, remarkable intraspecific variation in the shape of the mandible related to differences in habitat and diet has been reported only in a few species (Aragon *et al*. 1998, Ozaki *et al*. 2007), while the evidence from other taxa is more solid (e.g. Monteiro *et al*. 2003, Renaud & Michaux 2003, Haba *et al*. 2008).

In this study, variation in the shape of moose mandibles was studied using a landmark-based geometric morphometric method (Bookstein 1997, Zelditch *et al*. 2012) as implemented in the TPS software family (Rohlf 2011, 2013a, 2013b, 2013c). Altogether 28 points (10 landmarks and 18 sliding semi-landmarks) were digitised on the standardised photographs of the labial view of each studied mandible (Fig. 4). Generalised Procrustes superimposition of landmark configurations was performed to

remove all non-shape variation as well as to calculate centroid sizes, partial warps scores and the uniform components, respectively (Bookstein 1997, Rohlf 2013b).

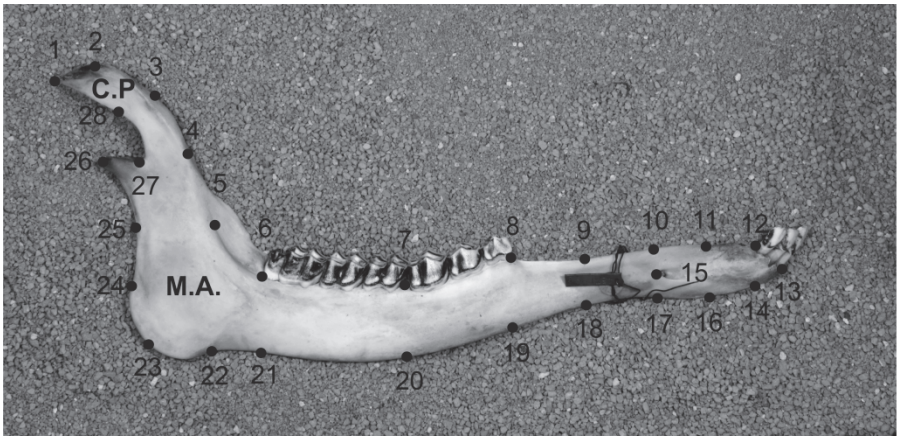

Fig. 4. Mandible of a moose with digitised landmarks 1−28. Points 1, 6, 7, 8, 12, 13, 15, 22, 26 and 27 were defined as fixed landmarks and the rest (2−5, 9−11, 14, 16−21, 23−25 and 28) as sliding landmarks. C.P = coronoid process, M.A. = mandibular angle.

After correction for centroid size, the partial warp scores and the two uniform components were subjected to principal component analysis (PCA). The shape changes summarised by the resulting principal components (PCs) were then visualised by deformation grids (deformation of the consensus configuration of the landmarks corresponding to the PC values; Rohlf 2011) and analysed with linear mixed models (Bates *et al*. 2014). Sex, age, latitude, longitude and their interactions were set as fixed factors while genetic cluster was kept as random factor; the sampled individuals were divided into the three clusters detected with TESS (see 4.2.2; II) according to their membership coefficients. With this division, altogether 91 individuals were assigned to the south-western cluster, 52 to the eastern cluster and 24 to the northern cluster, leaving 12 admixed and un-assigned individuals, which were treated as a group of their own (Fig. 3).

All the models were ranked on the basis of the Akaike information criterion (AIC) for goodness-of-fit (Burnham & Anderson 2002). In case the AIC was not able to rank the models unambiguously ($\Delta AIC < 2$), we utilised information criterion-based model averaging (Bartoń 2012) to acquire the definitive models and then to assess the relative importance of the fixed effects. All the explanatory variables were centred and standardised in the model averaging analyses (Schielzeth 2010). In

further analyses and graphics, we considered those factors that were significant and relatively important (occurred in > 75% of the top models) in the model averaging results (without shrinkage). The effects of the significant fixed factors on the shape were graphically described by plotting the predicted response against the minimum to maximum scale of the explanatory variables, while keeping the other explanatory variables constant. All the statistical analyses on the PCA data were conducted in R (R Core Team 2013).

In order to investigate further the relationship between the morphological and genetic variation among moose, partial Mantel tests (Mantel 1967, Smouse *et al*. 1986) were conducted with the program PASSAGE2 (Rosenberg & Anderson 2011). More particularly, pairwise Procrustes distances calculated from the landmark configurations were compared with pairwise genetic distances computed from the microsatellite data while controlling for the geographic distances among the studied individuals. The analysis was repeated separately for males and females and statistical significances were tested with 10,000 permutations.

4 Results and discussion

4.1 Genetic diversity

Despite the documented historical demographic crashes (Nygrén 1987), the Finnish and especially the Karelian moose population harbour relatively high genetic diversity, yet, with clear regional differences in its spatial distribution (Tables 1 and 2). The number of mitochondrial haplotypes detected in the samples from Russia was 18, 14 of them being private haplotypes, whereas only six haplotypes were found in the Finnish samples. The haplotype diversity and θ values were the lowest in western Finland and the highest in Russian Karelia while the nucleotide diversity was found to be the highest in northern Finland (Table 1). In fact, Russian Karelia seems to be a hotspot for mtDNA diversity of moose in the whole of Europe (Niedziałkowska *et al*. 2014).

Table 1. MtDNA genetic diversity indices of moose in Finland and Russian Karelia (II).

Region	n	*Nh*	$\hat{h}$	π	θ
Finnish Lapland	83	4	0.570	0.958	0.00561
Northern Finland	25	5	0.710	1.022	0.00824
Eastern Finland	50	3	0.358	0.444	0.00371
Western Finland	40	3	0.099	0.073	0.00341
Russian Karelia	47	18	0.819	0.758	0.00878

Sample size (*n*), number of mitochondrial haplotypes (*Nh*), haplotype diversity ($\hat{h}$), nucleotide diversity (π) and theta (θ) values for the five study regions in Finland and Russian Karelia.

The geographic pattern was very similar when estimated with 15 microsatellite loci: Karelia and the northern half of Finland possessed the highest diversity and western Finland the lowest. The regional estimates for H_e and A varied between 0.604–0.684 and 5.53–6.19 in Finland, whereas the corresponding values in the Republic of Karelia were 0.687 and 6.00, respectively (Table 2; II). Excluding western Finland, the heterozygosity estimates surpass the ones reported for Scandinavian (0.630–0.650) and North American moose (0.378–0.616), but are lower compared with the Polish ones (0.720–0.786; Wilson *et al*. 2003, Charlier *et al*. 2008, Schmidt *et al*. 2009, Haanes *et al*. 2011, Świsłocka *et al*. 2015). It must be noted, however, that all the studies have utilised different sets of microsatellites and varying samples sizes, which weakens the straightforwardness and reliability of the comparisons (c.f. Skrbinšek *et al*. 2012). In paper I, the

heterozygosity estimates are somewhat higher than in paper II (Table 2); these figures might possibly have been inflated by the different and smaller set of utilised loci and lower samples size, respectively.

Table 2. Combined results of the microsatellite genetic diversity of Finnish-Karelian moose from papers I and II

Grouping	n	*A*	*PA*	H_e
Finland (10 loci)	130	4.7	n/a	0.740
South-western Finland	20	4.9	n/a	0.728
Porkkala	8	4.3	n/a	0.682
Ostrobothnia	21	4.5	n/a	0.694
Finnish Karelia	22	5.1	n/a	0.747
Kainuu	28	4.9	n/a	0.735
Eastern Lapland	15	4.8	n/a	0.716
Western Lapland	16	4.7	n/a	0.709
Finland-Karelia (15 loci)	574	7.8	n/a	0.671
Lapland	79	6.1	0.16	0.684
Northern Finland	51	6.2	0.19	0.676
Eastern Finland	150	6.0	0.19	0.667
Western Finland	198	5.5	0.07	0.604
Russian Karelia	96	6.0	0.25	0.687

H_e, expected heterozygosity , *A* number of alleles, *PA*, number of private alleles

The observed gradient in the genetic diversity of the moose between Finland and the Republic of Karelia could be partly explained by post-glacial range expansion (Hewitt 2000). Following its more central location, Karelia could have received gene flow from several potential refugia located in the western parts of Russia and the Urals (Kholodova *et al*. 2005, Kholodova *et al*. 2014). Furthermore, the Karelian moose population went through a demographic expansion approximately 3,500 years ago (see 4.3). By contrast, the more peripheral populations, especially in the west of Finland, possess clearly lower genetic diversity. This is possibly a result of leading-edge colonisation, i.e., repeated series of founder effects during spatial expansion following the geological uplifting of land after the Ice Ages (Hewitt 1996, Hewitt 1999). Additionally, the later demographic processes could have promoted the loss of diversity in Finnish moose (see 4.3; Nygrén 1987). However, as an exception, moose occupying the northern half of Finland show elevated genetic diversity as a likely consequence of the secondary contact of the diverged lineages (see 4.2.1; Hewitt 2000).

4.2 Genetic population structure

4.2.1.1. Mitochondrial DNA

During the Ice Age, survival of populations in separate refugia led to development of genetically diverged lineages in several European species. Afterwards, the recolonisation of the previously unoccupied areas brought these lineages together forming secondary contact zones, which are detectable even today (Hewitt 2004). Results presented here indicate similar post-Pleistocene history for the moose: the haplotype network revealed sympatry of two distinct mitochondrial clades (Fig. 5; II), which were estimated to have diverged approximately 21,000 to 26,300 years ago. This estimate overlaps with the last glacial maximum, thus suggesting divergence in allopatric refugia (II; Clark & Mix 2002, Hewitt 2004, Niedziałkowska *et al*. 2014).

Furthermore, the present genetic structure of the moose population in Fennoscandia is likely to manifest the proposed bidirectional post-glacial recolonisation pattern of Fennoscandia (II; Markgren 1974, Hundertmark *et al*. 2002). Haplotypes dominating in southern parts of Finland and Russian Karelia are allocated to an 'eastern clade' (Fig. 5), common in moose from western Russia and Poland, hence, indicating an eastern origin and recolonisation route (Kholodova *et al*. 2014, Niedziałkowska *et al*. 2014). Haplotype H6 on the other hand, found previously in Scandinavia and now in the north of Finland and Kola Peninsula, belongs to a 'western clade' (Fig. 5). This is thought to reflect an expansion from a close refugium in Central or Western Europe (II, Schmölcke & Zachos 2005, Niedziałkowska *et al*. 2014). The spatial distribution on these two clades was evident in the SAMOVA analysis, as Lapland was clearly separated from the more southern regions (φ_{ST} between the two groups was 0.377, $p < 0.001$; II).

The secondary contact of these two clades in the northern parts of Finland and the Kola Peninsula (Fig. 5) presents a clear deviation from the classic paradigm of central Scandinavian hybrid zone, which was presumably formed as a result of the final melting of the ice sheet separating the eastern and southern colonists of various taxa (e.g. Hewitt 2000, Jaarola & Searle 2002, Knopp & Merilä 2009, Swenson *et al*. 2011). In the moose, however, the southern lineage has reached far into the northeast (II) despite the assumption that it gained access to the area much later than the eastern lineage (Ukkonen 1993, Hewitt 2000, Rankama & Ukkonen 2001). Hence, the genetic pattern is likely to reflect more recent gene flow eastwards from Sweden into Finland, rather than initial secondary contact.

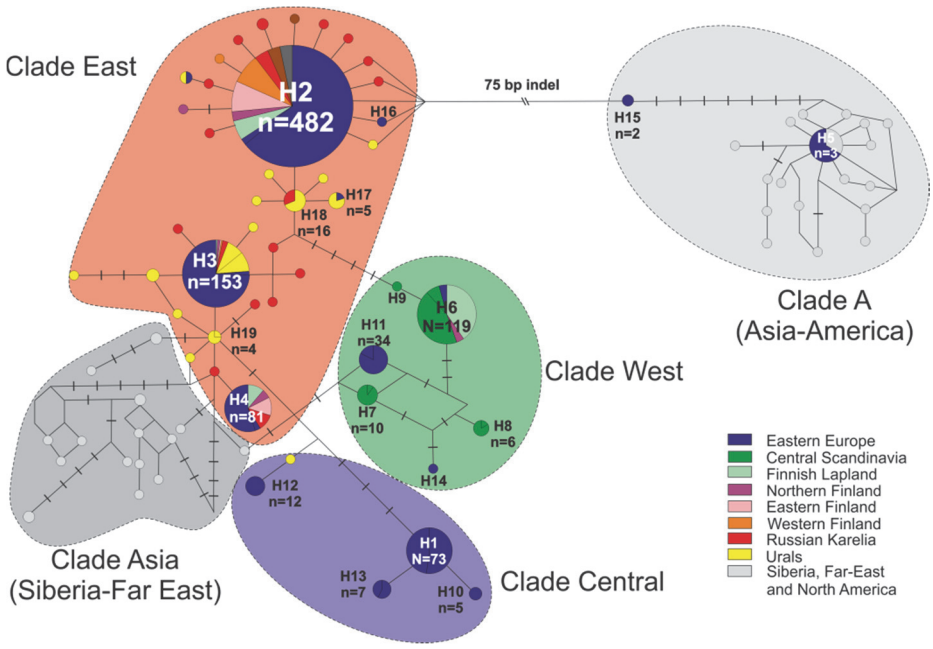

Fig. 5. Haplotype network of mitochondrial sequence variation in the Palaearctic moose. The sizes of the circles are proportional to the number of haplotypes found and the colouring represents the geographical origin of the haplotype (II). Each connecting bar represents one nucleotide substitution.

4.2.2 Microsatellites

Recent microsatellite studies have reported several contemporary European moose populations to be genetically structured in spite of large population sizes and continuous distributions (Charlier *et al*. 2008, Haanes *et al*. 2011, Świsłocka *et al*. 2015). The variety of analyses applied in this thesis undisputedly demonstrated this to be also the case with the Finnish-Karelian moose population (I & II). However, the number of detected genetic clusters varied between different methods and datasets. With 10 loci, SAMOVA advocated two distinct groups: one in Lapland and the other in southern Finland with a total F_{ST} value of 0.064 (see I for details), being more or less congruent with the pattern observed with mtDNA (II). However, in the non-spatial STRUCTURE analysis, the best model ($P \approx 1.000$) to explain the data was the one with four genetic clusters and high levels of admixture (I). Previous studies have shown the Bayesian clustering analyses to overestimate the number of genetic clusters in the

presence of clinal structures, e.g. IBD, especially with aggregated sampling schemes such as the one applied in paper I (Frantz *et al*. 2009, Schwartz & McKelvey 2009). These factors are likely to influence the results acquired with STRUCTURE considering the significant IBD pattern detected with the spatial autocorrelation analysis (regression slope $b = -0.008$, $p < 0.001$; I).

With the four-fold greater and more continuous sampling (II), the spatially explicit model implemented with TESS analysis gave the highest support to three clusters (K = 3) of moose separated by clines: eastern, south-western and northern. (Fig. 6; II). All the three clusters were in HW and linkage equilibrium (II) in addition to being significantly genetically diverged (F_{ST} = 0.049–0.116, $p < 0.001$ in each pairwise comparison). The spatial structure of the three clusters was further supported by the independent sPCA method (II); both significant global and local structures were detected ($p < 0.05$), and the first global sPCA scores clearly separated moose from the south-western parts of Finland from their conspecifics in Karelia and Lapland, whereas the second sPCA scores differentiated between moose from Karelia and those from Lapland (II). Again, significant IBD structure (regression slope $b = -0.019$, $p < 0.001$) was apparent in the pooled data; however, the pattern vanished when the analyses was repeated for each genetic cluster separately (II). All these pieces of evidence suggest that the observed clinal structure is not a result of limited dispersal but rather a secondary contact of diverged three clusters (Guillot *et al*. 2009, Meirmans 2012). Taking into account all the support from different analyses and the increased statistical power following the larger number of utilised samples and loci (Selkoe & Toonen 2006), K = 3 was considered the best model to describe the microsatellite data and the contemporary genetic structure of moose in Finland and Russian Karelia.

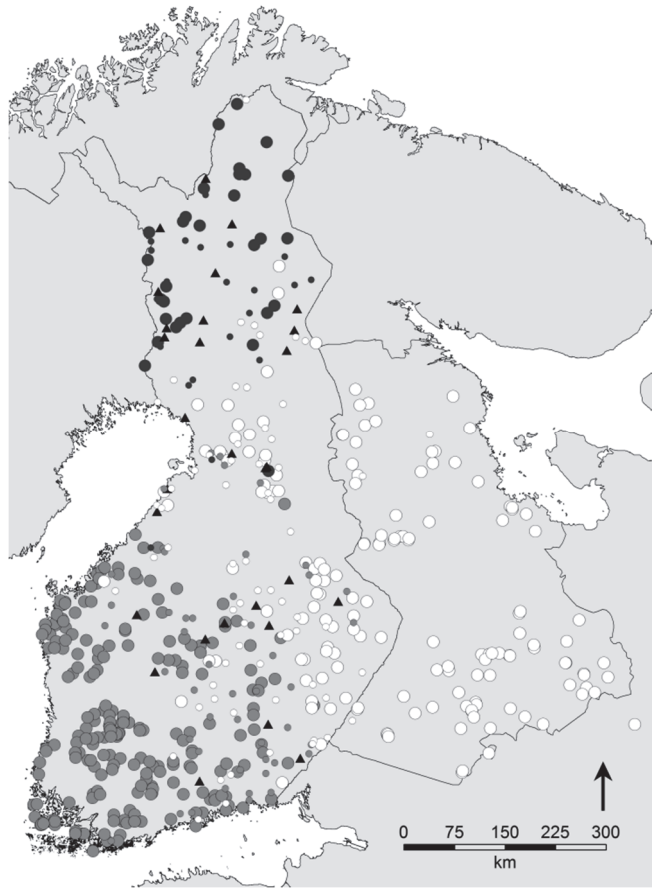

Fig. 6. The geographic distribution of the three genetic clusters of the Finnish-Karelian moose population (II). Grey circle = south-western cluster, white circles = eastern cluster, black circle = northern cluster. Large circles represent membership coefficients greater than 0.7, small circles coefficient greater than 0.5, and triangles coefficients below 0.5 (highly admixed).

One feasible historical explanation for this trichotomous structure would be re-colonisation in three colonisation waves: south-eastern, eastern and northern (*sensu* Ukkonen 1993). However, according to the best of the four historical models in the coalescence analysis in DIYABC2 (posterior probabilities: 0.926 and 0.910 with the direct and logistic regression approaches, respectively), all the clusters diverged simultaneously 628 generations ago (95% HPD 158–1,310; II),

which equals to 4,521 years using a generation time of 7.2 years (a mean calculated from several moose populations; Gaillard 2007). Fossil evidence indicates that moose were present in Fennoscandia already at 9,000–8,000 years before present (BP; Ukkonen 1993), which would imply that the observed genetic structure has been developed thousands of years after the re-colonisation (II). A potential alternative explanation for the emergence of the three clusters would include population fragmentation, including genetic drift and subsequent range expansion, and/or secondary recolonisation from different founding populations (II). Interestingly, the estimate of 4,521 years matches fairly well with the population declines inferred from moose fossil data between 5800 and 3000 BP (Ukkonen 1993, Oinonen *et al*. 2014), suggesting a possible connection between population fragmentation and the combined effects of environmental change and human exploitation (II). The later population declines during the last few centuries (Nygrén 1987) could have promoted genetic divergence, representing an explanation why this trichotomy has persisted until today (II).

In addition, the more contemporary patterns of gene flow could have played their part in forming the current genetic structure. In the north of Fennoscandia, the population densities of moose are not as high as in the south (Lavsund *et al*. 2003, Nygrén 2009) and at present, reindeer fences on the northern part of the border between Finland and Russia may prevent migration to some extent. As a consequence, migration of moose is likely to be lower between north-eastern Finland and Russia than across the same border more southwards. On the contrary, migration rates between Swedish and Finnish Lapland in the north-west have possibly been rather high, as suggested by high densities of moose in south-western Lapland, where there are no fences on the border. Higher densities in Sweden than in Finland during the recent decades indicate also that the migration might have been stronger towards Finland than vice versa (Nygrén 1990, Nygrén, unpublished data from years 1975–1996). These migration patterns could have led to a high gene flow from the Swedish population to the population in Finnish Lapland and from the Karelian population to eastern Finland, and these patterns of gene flow are now reflected in the spatial distribution of the three clusters (Fig. 6).

4.3 Past population demography

Over the last few centuries, the history of moose in Finland and Russian Karelia has been characterised by consecutive population crashes (Nygrén 1987, Danilov 2005). This has not come without genetic consequences: the Bayesian skyline plots revealed

that moose from Lapland and Northern Finland experienced considerable reductions in mtN_e approximately 190–230 (mtN_e ~4,700–5,800) and 110–136 years ago (mtN_e ~8,400–10,500), respectively (Fig. 7). These dates coincide with the documented declines in moose numbers in Finland in the 18th and 19th centuries (Nygrén 1987). Subsequently, the populations have started to increase in both regions. In previous studies, evidence of past genetic bottlenecks of moose has been reported in Sweden and Poland, where the history of the species is congruent with that in Finland and Karelia (Charlier *et al*. 2008, Świsłocka *et al*. 2015).

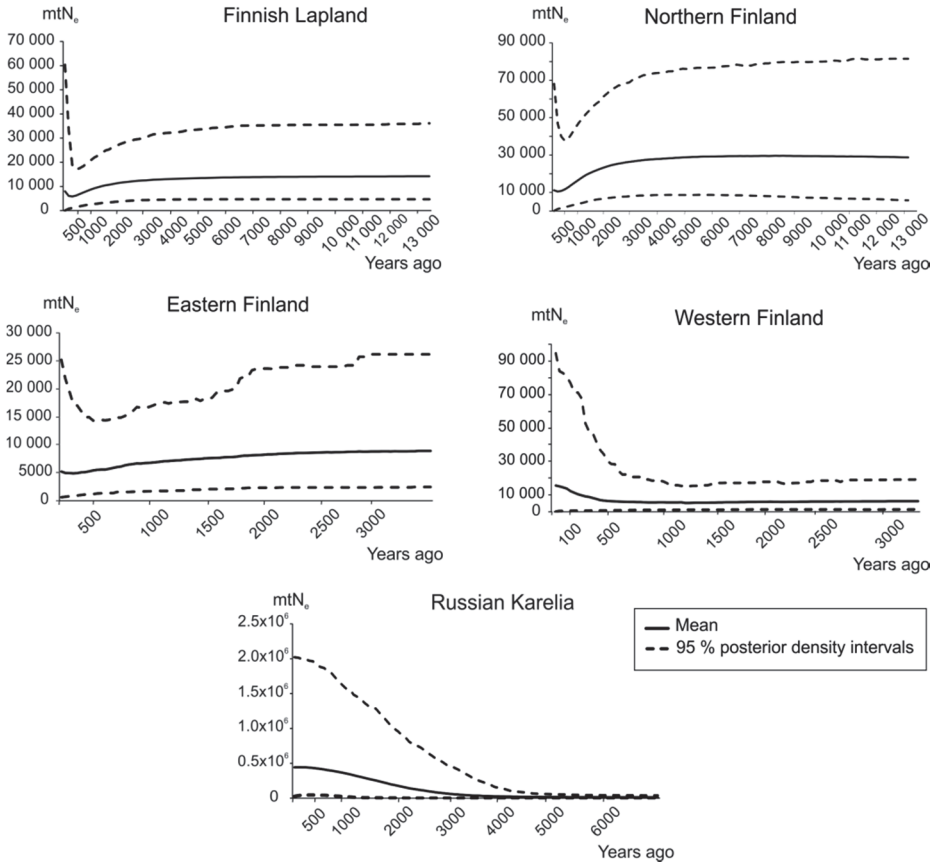

Fig. 7. Bayesian skyline plots of mitochondrial effective population size (mtN_e) trends over time for the moose in Finland and Russian Karelia (II).

In contrast, strong and steady population growth throughout the Holocene was observed in Russian Karelia, where the mtN_e was only 13,900 ca. 7,000 years ago, while the present-day estimate is as high as 443,000 (Fig. 7; II). This demographic expansion is also visible in the haplotype network exhibited by the star-shape phylogeny of the Karelian haplotypes (Fig. 5). Similarly, yet in lower magnitude, the moose population in western Finland has experienced demographic expansion during the last 500 years (Fig. 7). This is rather surprising, since moose in this very region have likely gone through a very narrow bottleneck in the early 20th century (Nygrén 1987). Regardless of this, the low genetic diversity in this region is indicative of a small number of founding individuals of the current population in western parts of Finland (Tables 1 and 2; II).

In comparison, the two bottleneck tests applied did not find any support for past population bottlenecks: there was no heterozygote excess in any of the sites studied (*p*-values 0.097-0.875, I) and the G-W index values were between 0.68–0.72; above the directive threshold of 0.68 below which values would be indicative of a bottleneck (Garza & Williamson 2001). The only exception was the Porkkala sample with a value of 0.58, most likely resulting from the small sample size (I). According to Hundertmark & Van Daele (2010), rapid population growth right after the bottleneck can impede the loss of alleles. The Finnish moose population has indeed expanded fast after the known bottlenecks (Nygrén 1987, Lavsund *et al*. 2003), which together with gene flow from Russia and Scandinavia to Finland (II) could at least give a partial explanation for the results obtained. Furthermore, a recent study showed that both the heterozygosity excess method and the G-W index tests have very limited power to detect population bottlenecks even in cases where the bottleneck has been severe (Peery *et al*. 2012).

4.4 Mandible shape variation

Latitudinal phenotypic variation is probably one of the most commonly investigated patterns in ungulates; e.g. the moose in Fennoscandia have in several studies (Herfindal *et al*. 2006, Nygrén *et al*. 2007, Lundmark 2008) been shown to follow Bergmann's rule of increasing body size towards the north (Bergmann 1848, Mayr 1963). Respectively, this study provided the first evidence of a significant latitudinal, yet sexually determined trend in the mandible shape of the moose (III). Furthermore, more subtle, yet statistically significant age-related variation was discovered. The changes described by the main shape variable PC1 (variance proportion = 0.409)

occur in the mandibular angle and the coronoid process, which are the attachment points of the temporalis and the masseter/pterygoid group muscles, crucially important in grinding and chewing of food (Pérez-Barbería & Gordon 1999). The best linear mixed models explaining this variable included the significant effects of latitude (z = 2.936, P = 0.003) and sex (z = 2.058, P = 0.0401); PC1 increased alongside with latitude, while females had a higher intercept than males (Fig. 8).

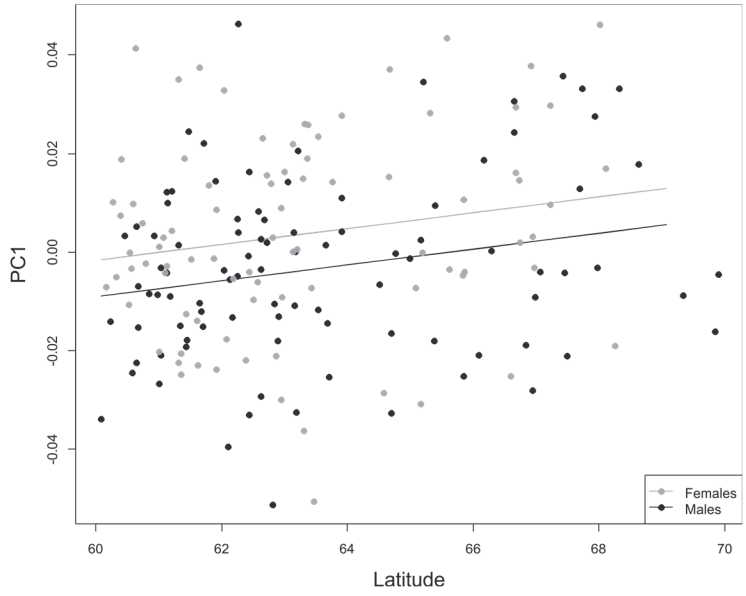

Fig. 8. Latitudinal change in the mandible shape (described by the variable principal component 1, PC1) of male and female moose (III).

Interestingly, as the PC1 value increases along with latitude, the mandibular angle widens (Fig. 9), implying enlarging masseter and pterygoid muscles and hence, a stronger bite towards the north (Greaves 1991). This makes sense, because moose inhabiting the northern latitudes are more dependent on dormant woody plants throughout the year compared with their southern conspecifics, due to the significantly shorter annual growing period (Swihart & Bryant 2001, Karlsen *et al*. 2006). Thus, higher bite force would be beneficial in the north, and in this sense the observed shape shift could be plausibly adaptive in the mechanical function of the jaw (III).

The significance of the genetic clusters on the mandible shape variation as a random effect was very low in the linear mixed models applied; e.g., the marginal

variance component of this factor on PC1 was only 3.594^{-20} with a standard deviation of 1.896^{-10} (III). In addition, only a weak correlation between the morphometric and genetic distances was discovered in female moose but not in males (females: r = 0.140, two tailed p = 0.020; males: r = 0.036, two-tailed p = 0.477). Thus, the revealed geographic pattern was considered independent of the genetic population structure of the Finnish moose, indicating a more prominent role of other factors, such as differential selection or environmentally driven plastic response (III). In fact, previous studies on mice and shrews have shown diet-induced plasticity in the mandible development to be connected with the formation of shape variation and local ecological adaptations (Renaud *et al*. 2010, Young & Badyaev 2010, Anderson *et al*. 2014). In this sense, the latitudinal shape trend observed in the moose could possibly reflect a similar plastic response to a gradient in the diet. Geographic and diet-related variation in mandible morphology has previously been reported e.g. in the European roe deer (*Capreolus capreolus*; Aragon *et al*. 1998), the wood mouse *(Apodemus sylvaticus*; Renaud & Michaux 2003) and the punaré rat (*Thrichomys apereoides*; Monteiro *et al*. 2003). The fact that the mandibles of female moose differed significantly from those of males (Fig. 8) possibly reflects their different dietary optimum and foraging behaviour (Barboza & Bowyer 2000).

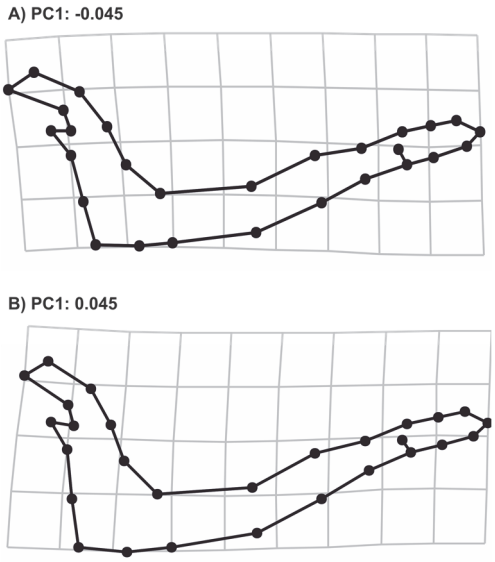

Fig. 9. Mandible shape deformation grids at the negative (A) and positive extreme scores (B) of the principal component 1 (III).

5 Conclusions and future perspectives

This study revealed significant spatial variation in the genetic and phenotypic make-up of the Finnish-Karelian moose population, providing new information on the recolonisation of Fennoscandia. The findings of this thesis support the existence of separate refugia for the European moose during the Last Glacial Maximum and the subsequent bi-directional recolonisation of Fennoscandia. Yet, the moose clearly deviates from the classic secondary contact paradigm reported in other species in Northern Europe. Moreover, the results presented here showed that the past population crashes during the 18th and 19th centuries left genetic imprints on the current moose population. In conclusion, the genetic composition of moose in Finland and Karelia has indeed been affected both by ancient and more recent, likely human-mediated processes. In order to disentangle the more specific effects of particular historical events, DNA extracted from moose fossils and museum samples from different eras is required (c.f. Pääbo *et al*. 2004). Evidently, this approach would also bring long-awaited knowledge on the locations of the glacial refugia and recolonisation routes of the moose, especially in Central and Western Europe, where the species is currently extinct.

The present study provided the first piece of evidence of a latitudinal trend in the mandible shape of the moose (III). However, more extensive studies are required to confirm if the shape shift is truly adaptive (biomechanically and evolutionary), as well as to separate the total contributions of genetic and environmental components to the mandible shape. Herfindal *et al*. (2014) suggested that the genetic structure might play an important role in the distribution of phenotypic variation in the moose, whereas the discovery made in this study proved otherwise. Hence, the questions of whether the mandible shape presents only an exception, and whether the three genetic clusters detected exhibit any distinct phenotypic differences, require further attention. However, it is very likely that we have managed only to scratch the surface of the true morphological variation and the adaptive potential possessed by this species.

The early genetic inquiries suggested a very low genetic diversity in the moose (e.g. Ryman *et al*. 1980), but as shown in this thesis, the current Finnish and especially Karelian moose harbour relatively high diversity (I, II). However, it must be kept in mind that genetic diversity is not a static, but a dynamic phenomenon. All over Northern Europe, the moose populations are heavily exploited, holding a risk of reducing the genetic variation and thus compromising the long-term evolutionary potential of this species under changing climatic conditions (Allendorf *et al*. 2008, Sæther *et al*. 2009, Mysterud & Sæther 2010). Therefore, more attention on the

genetic and evolutionary effects of harvesting is warranted in order to prevent further negative consequences. More particularly, strong reductions in the population size and biases in the sex ratio should be avoided to reduce the probability of losing the unique genetic diversity especially in areas such as Karelia and northern parts of Finland. The good news is the inclusion of maintenance of genetic diversity as a management objective in the new management action plan for the Finnish moose population (Anonymous 2014). This is significant progress as genetics has long been scorned and neglected in wildlife management in Finland (Nygrén 2009). However, there is still room for improvement as the plan does not include any mention of practical measures for maintaining the genetic diversity. Additionally, although this study provides the first basis for 'genetically enlightened management' of moose, continuous monitoring is a necessary action to detect possible temporal changes in the genetic diversity in the future (Schwartz *et al*. 2007).

A further major concern is brought about by the selective nature of the harvest, which may cause possible adaptive genetic changes that are hard to detect with neutral molecular markers (Allendorf & Hard 2009). In fact, such effects have likely already occurred during the last 40 years of intense hunting, as shown by recent changes detected in the life history traits of the Finnish moose (Tiilikainen 2010). Undoubtedly, the novel genome-wide molecular approaches will provide help in unravelling the true extent of anthropogenic impact on wildlife, and hopefully in minimising them as well (Allendorf *et al*. 2008, Ellegren 2014).

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