RESEARCH ARTICLE

Recent large-scale landscape changes, genetic drift and reintroductions characterize the genetic structure of Norwegian wild reindeer

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Received: 22 May 2019 / Accepted: 13 September 2019 / Published online: 21 September 2019 © The Author(s) 2019

Abstract
Landscape changes, such as habitat loss and fragmentation, subdivide wild populations, reduce their size, and limit gene flow. These changes may further lead to depletion of genetic variation within populations as well as accelerating differentiation among populations. As a migratory species requiring large living areas, wild reindeer (Rangifer tarandus) is highly vulnerable to human activity. The number and continued presence of wild reindeer have been significantly reduced due to accelerating anthropogenic habitat modifications, as well as displacement in benefit of domesticated herds of the species. As a basis for future management strategies we assess genetic structure and levels of genetic variation in Norwegian wild reindeer by analysing 12 microsatellite loci and the mitochondrial control region in 21 management units with varying population sizes. Overall, both markers showed highly varying levels of genetic variation, with reduced variation in the smaller and more isolated populations. The microsatellite data indicated a relationship between population size and genetic variation. This relationship was positive and linear until a threshold for population size was reached at approximately 1500 reindeer. We found high levels of differentiation among most populations, indicating low levels of gene flow, but only a weak correlation between geographic and genetic distances. Our results imply that the genetic structure of Norwegian wild reindeer is mainly driven by recent colonization history, population size, as well as human-induced landscape fragmentation, restricting gene flow and leading to high levels of genetic drift. To sustain viable populations, conservation strategies should focus on genetic connectivity between populations.

Keywords Population genetics · Connectivity · Gene flow · Management of large herbivores · Population viability · Human–wildlife interactions

Introduction
Large-scale landscape changes are intimately linked to habitat loss and fragmentation, and pose major threats to biodiversity where many populations are declining, and many species are currently at the brink of extinction (Frankham et al. 2010; Barnosky et al. 2011; Ripple et al. 2017). Whereas habitat loss has large, consistently, negative effects on biodiversity, habitat fragmentation effects may be subtle, scale-dependent, and can be negative or in some cases even positive (review in Fahrig 1997, 2003, 2013; Tischendorf et al. 2005). Among the many possible consequences of fragmentation, is delimited spatial patterns of dispersal and reproduction, which in turn may lead to reduced levels of within-population genetic variation and alterations of spatial genetic structure (Young et al. 1996; Jackson and Fahrig 2016). Population genetic theory

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10592-019-01225-w) contains supplementary material, which is available to authorized users.
predicts that small populations have less variation compared to large populations due to genetic drift and inbreeding (Hartl and Clark 1997). Thus genetic erosion of small populations has become a major conservation concern, as low levels of variation is considered limiting to the ability for populations to respond to changed environmental conditions as well as threats like diseases, parasites and predators (Amos and Harwood 1998). Although the relationship between population size and genetic variability is well-known and supported by empirical data across different taxa (see Frankham 1996 for review), the reality of this relationship may also be questioned (Amos and Harwood 1998; Bazin et al. 2006). For example, Bazin et al. (2006) studied genetic polymorphisms in approximately 3000 animal species. From this comprehensive study they found that nuclear sequence data showed results consistent with the expectation of more genetic variation in abundant species. In contrast, mitochondrial DNA (mtDNA) variation did not reflect population size, probably as an effect of selection acting on mtDNA. This conclusion was, however, based on comparisons of within-species variation among different taxa which probably also differ in other aspects like geographic location, population history, mutation rates and population structure, all of which potentially affect genetic variation (Hague and Routman 2015).

Reindeer (*Rangifer tarandus*), is a circumpolar, free-ranging and migratory herbivore, adapted to harsh alpine and Arctic landscapes. Wild reindeer are in many areas severely affected by human activities and associated landscape changes (Nellemann and Cameron 1998; Nellemann et al. 2010; Wittmer et al. 2010; Skarin and Åhman 2014). The large-scale decline of wild reindeer populations has been particularly dramatic in Western Europe. Today, wild European reindeer is mostly distributed in mountainous areas of variable size in the south-central parts of Norway, and consists of about 40,000 reindeer in total (http://www.villrein.no/om-villreinomrdene). While previously, wild reindeer roamed the entire south-central parts of Norway, landscape changes such as construction of railways, roads, hydropower developments and urbanization during the last 100 years have caused a large-scale, dramatic habitat loss and fragmentation for reindeer (Andersen and Hustad 2004). Over time, large-scale landscape changes have reduced the amount of habitats classified as ‘wilderness areas’ for this part of Norway from approximately 50% around 1900 to 4.9% today (http://www.miljostatus.no) (see also Watson et al. 2016). The wild reindeer are currently managed as 24 separate management units or sub-populations (Fig. 1; http://nvs.villrein.no/). Based on historical documentation, these populations may also be genetically influenced to varying

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**Fig. 1** Map (modified from http://nvs.villrein.no/) of southern parts of Norway showing national wild reindeer areas (green), other wild reindeer areas (orange), areas with domestic reindeer (yellow), and the sampling locations for the 21 wild populations analyzed. Reindeer areas that were not included in the current study are marked with an asterisk. Rondane is divided into Rondane North (1a) and Rondane South (1b) in our analyzes. (Color figure online)
degrees by herds of domestic and mixed origin (Punsvik and Frøstrup 2016; http://www.villrein.no/om-villreinomrdene). Previous studies have only focused on genetic structure of a few larger populations inhabiting areas less affected by human activities, and therefore likely acting as source populations in potential meta-population structures (Røed et al. 2008, 2011, 2014). Genetic structure, origin and gene flow among particularly the small and more isolated populations are thus to a large extent unknown. These populations have probably been more prone to recent landscape fragmentation, but also potentially been more affected by introgression, e.g. from a complex and only in part documented history of straying or (re)introduced domestic reindeer (http://www.villrein.no/om-villreinomrdene).

Effective conservation of species and populations require knowledge about diversity, connectivity and genetic structure, and the Norwegian wild reindeer areas comprise a valuable opportunity to study the effects of human induced landscape changes. In this study, we use both 12 microsatellite loci and the mitochondrial control region (CR) to calculate levels of genetic variation in 21 wild reindeer populations to evaluate if the central principal of conservation biology, stating that large populations have more genetic variation compared to small populations, applies for Norwegian wild reindeer. Further, we examine the degree of differentiation among sub-populations and describe the genetic structure. To evaluate if isolation by distance (IBD) is the main driver of the structure observed we also test for correlation between genetic- and geographical-distances among populations. On a methodological note, as inappropriate selection of genetic markers may compromise the ability to address specific research objectives, we also evaluate the performance of the microsatellite and mtDNA markers used in this study.

Materials and methods

Study areas

Tissue samples was collected during the hunt from the wild reindeer areas Hardangervidda, Brattefjell-Vindeggen, Blefjell, Nordfjellet, Setesdal Austhe, Lærdal-Ardal, Fjellheimen, Sunnfjord, Førdefjella, Svartebotnen, Skauen Etnefjell and Våmur Roan, in south central parts of Norway, between 2008 and 2014 (Fig. 1). Four areas (Vest-Jotunheimen, Oksenhavoya, Raudafjell and Tolga Østfjell; Fig. 1) did not allow for sampling. Sequence- and microsatellite data from previously published studies from the reindeer areas Hardangervidda (Kvie et al. 2016a), Forollhogna, Reinheimen Breheimen, Norefjell-Reinjofjell (Reimers et al. 2012), Setesdal Rynfylke and five populations from Rondane-Dovre, namely Knusthø, Snøhetta, Solnktetten, Rondane North and Rondane South (Røed et al. 2008), was included for a more complete coverage of the Norwegian wild reindeer populations (Fig. 1). Although, Rondane South and Rondane North is officially a single wild reindeer area, they are managed as separate sub-units and, hence, we decided to separate them in our analyses (referred to as 1a and 1b in the figures). In total, we included 21 wild reindeer management units, which differ in isolation, population size and ancestry, and inhabit areas of greatly varying size (Table 1). The populations in Rondane-Dovre, located in the northern part of the distribution area, is considered to be native wild reindeer, little affected by genetic introgression from other populations. The wild reindeer in the Langfjella Mountain Range comprising Hardangervidda, Nordfjella, Setesdal Ryfylke and Setesdal Austhe are located in the south central parts of the distribution area, and have a mixed origin from both native wild- and domestic reindeer (Røed et al. 2014). Reindeer in Brattefjell-Vindeggen, Lærdal-Ardal and Blefjell are believed to have their origin from Langfjella and/or are considered as extensions of the Langfjella Mountain Range (Andersen and Hustad 2004; Punsvik and Frøstrup 2016). The remaining populations situated north (Forollhogn and Reinheimen-Breheimen), west (Fjellheimen, Sunnfjord, Førdefjella, Svartebotnen, Skauen Etnefjell) and east (Våmur Roan, Norefjell-Reinjofjell) of Langfjella, all have an assumed domestic origin (Andersen and Hustad 2004; Punsvik and Frøstrup 2016; http://www.villrein.no/om-villreinomrdene; Table 1).

DNA extraction and genetic analyses

DNA was extracted using DNAeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, CA) following the manufacturer’s protocol. A subset of 284 samples were analysed for 12 reindeer-specific microsatellites (NVHRT-03, NVHRT-16, NVHRT-73, NVHRT-48, NVHRT-21, NVHRT-01, NVHRT-31 (Røed and Midthjell 1998), RT-1, RT-6, RT-5, RT-9, RT-27 (Wilson et al. 1997). Amplification was performed on a GeneAmp PCR System 9700 (Applied Biosystems) as described by Røed et al. (2002). PCR products were electrophoresed using an ABI Prism 3500xl Genetic Analyzer (Applied Biosystems). We used the MICRO-CHECKER software (Van Oosterhout et al. 2004) to assess the quality of the microsatellite scoring. A total of 315 individuals were sequenced for a 503 base pair (bp) long fragment from the mitochondrial CR using the forward primer RtCRF (5′-AAT AGC CCC ACT ATG AGC ACCC-3′) (Flagstad and Røed 2003) and the reverse primer RtCRI-528 (5′-TAG GTG AGA TGG CCC TGA AGA AA-3′) (Bjørnstad and Røed 2010, but see Kvie et al. 2016b for protocol). The samples were cleaned for unincorporated primers and nucleotides using Illustra ExoStar (GE Healthcare) diluted 10 times. Cycle sequencing was performed in a 10 μl reaction volume, using BigDye v3.1 sequencing kit (Applied
Biosystems) following manufacturer’s recommendations. Purification was carried out using standard EDTA/EtOH precipitation. Capillary electrophoresis and data analysis were performed with an ABI 3130xL- or 3500xL instrument (Applied Biosystems). All sequences were sequenced in both directions, and the consensus sequences were aligned by ClustalW (Thompson et al. 1994) and edited in MEGA v6 (Tamura et al. 2013). The sequences were trimmed down to 467 bp.

**Statistical analyses**

**Genetic variation**

We used GenALEx v.6.5 (Peakall and Smouse 2006, 2012) to calculate microsatellite genetic diversity in terms of number of different alleles (Na), number of effective alleles (Ae), observed heterozygosity (Ho) and unbiased expected heterozygosity (uHe). We estimated deviations from expectations under Hardy–Weinberg equilibrium (HWE) in GENPOP v.4.4 (Rousset 2008) using an exact test based on 10,000 dememorization steps and Markov Chain Monte Carlo (MCMC) length of 5000. Arlequin v.3.5 (Excoffier and Lischer 2010) was used to calculate the proportion of the variance in a sub-population contained in an individual, i.e. the inbreeding coefficient, \( F_{IS} \). After performing a Bonferroni correction, none of these tests were statistically significant (\( p \geq 0.103 \)). Based on the microsatellite data, individual heterozygosity (\( pH_t \)) was estimated as the proportion of heterozygous genotypes for each individual with the R (R Core Team 2018) function “GENHET” (Coulon 2010). Spatial interpolation of genetic diversity was performed by fitting generalized additive models (GAMs), using the mgcv-library in R (Woods 2017), where \( pH_t \) was modelled as a function of geographical coordinates 1

### Table 1

| Abbr. | Area (ancestry) | AS | N   | n   | Microsatellites | \( F_{IS} \) | n   | MtDNA | Na  | Ae  | Ho  | uHe  | Nh  | Hd  | π   |
|-------|----------------|----|-----|-----|----------------|-------------|-----|-------|-----|-----|-----|------|-----|-----|-----|
| HV    | Hardangervidda (M) | 8136 | 10,500 | 29 | 7.167 | 4.307 | 0.696 | 0.750 | 0.059 | 32 | 10 | 0.760 | 0.016 |
| BV    | Brattefjell-Vindeggen (M) | 357 | 500 | 25 | 6.083 | 3.990 | 0.690 | 0.733 | 0.050 | 25 | 4  | 0.597 | 0.017 |
| BF    | Blefjell (M) | 186 | 140 | 24 | 5.250 | 3.209 | 0.631 | 0.676 | 0.042 | 19 | 3  | 0.556 | 0.014 |
| NE    | Norefjell-Reinsjøfjell (D) | 314 | 700 | 32 | 4.417 | 2.755 | 0.581 | 0.625 | 0.072 | 21 | 2  | 0.324 | 0.010 |
| NF    | Nordfjella (M) | 3004 | 2100 | 32 | 7.000 | 4.226 | 0.746 | 0.760 | 0.015 | 38 | 5  | 0.656 | 0.016 |
| LÅ    | Lærdal-Årdal (M) | 488 | 120 | 31 | 6.250 | 4.276 | 0.754 | 0.754 | −0.003 | 31 | 3  | 0.617 | 0.015 |
| FH    | Fjellheimen (D) | 1705 | 440 | 31 | 4.917 | 2.928 | 0.624 | 0.648 | 0.038 | 38 | 4  | 0.508 | 0.014 |
| SF    | Sunnfjord (D) | 700 | 125 | 14 | 4.833 | 3.200 | 0.629 | 0.683 | 0.079 | 14 | 3  | 0.560 | 0.011 |
| FF    | Fordejella (D) | 700 | 100 | 9  | 3.833 | 3.021 | 0.704 | 0.667 | −0.058 | 9  | 3  | 0.556 | 0.011 |
| SB    | Svartebotnen (D) | 99 | 55  | 8  | 3.167 | 2.446 | 0.594 | 0.592 | −0.003 | 8  | 3  | 0.464 | 0.008 |
| SE    | Skauen Etnefjell (D) | 486 | 60  | 18 | 4.750 | 2.937 | 0.581 | 0.611 | 0.031 | 18 | 4  | 0.669 | 0.016 |
| SR    | Setesdal Ryfylke (M) | 6154 | 3500 | 23 | 6.667 | 4.307 | 0.675 | 0.754 | 0.088 | 18 | 10 | 0.876 | 0.018 |
| SA    | Setesdal Austhei (M) | 2400 | 2000 | 32 | 7.083 | 4.431 | 0.736 | 0.757 | 0.024 | 33 | 9  | 0.777 | 0.019 |
| VÅ    | Våmur Roan (D) | 406 | 240 | 32 | 5.750 | 3.750 | 0.724 | 0.720 | −0.016 | 48 | 4  | 0.334 | 0.007 |
| RB    | Reinheimen-Breheimen (D) | 4551 | 2900 | 30 | 6.500 | 3.561 | 0.636 | 0.700 | 0.078 | 17 | 3  | 0.544 | 0.014 |
| FO    | Forollhogna (D) | 1843 | 2900 | 30 | 5.417 | 3.108 | 0.648 | 0.662 | −0.021 | 17 | 5  | 0.625 | 0.015 |
| SN    | Snesøta (W) | 3345 | 2700 | 25 | 5.917 | 3.716 | 0.665 | 0.735 | 0.086 | 21 | 7  | 0.690 | 0.010 |
| RN    | Rondane North (W) | 1200 | 1600 | 28 | 6.750 | 3.902 | 0.730 | 0.720 | −0.018 | 15 | 2  | 0.133 | 0.002 |
| RS    | Rondane South (W) | 2100 | 2300 | 30 | 6.000 | 3.532 | 0.652 | 0.680 | 0.026 | 10 | 1  | 0.000 | 0.000 |
| KN    | Knutshe (W) | 1776 | 1500 | 30 | 6.500 | 3.988 | 0.689 | 0.724 | 0.033 | 11 | 8  | 0.945 | 0.016 |
| SL    | Solnkletten (W) | 1330 | 800  | 27 | 5.667 | 3.473 | 0.622 | 0.682 | 0.051 | 13 | 3  | 0.410 | 0.001 |
| Total | –   | –   | 540 | 5.710 | 3.574 | 0.667 | 0.697 | 0.031 | 456 | 37 | 0.742 | 0.018 |

Genetic variation is given as number of different alleles (Na), number of effective alleles (Ae), observed heterozygosity (Ho) and unbiased expected heterozygosity (uHe) for the microsatellites, and as number of haplotypes (Nh), haplotype diversity (Hd) and nucleotide diversity (π) for the control region. Inbreeding coefficient, \( F_{IS} \) was calculated for the microsatellite markers (Bonferroni corrected 0.05/19 = 0.0026) and show no significant values.

*Numbers from https://villrein-no.squarespace.com/rondane-1/

1 Using the following projection: +proj = longlat + ellps = WGS84.
we rescaled and ranked each candidate model relative to that only included the linear effect of each genetic variability measure as the response: (1) a model which only included X, one only including Y, one with X and Y separately (i.e. no interaction between them), and the selected model where the interaction between X and Y was included (i.e. the model specified above). The predictions from the GAM was plotted as contours on a map where random noise was induced to the geographical position values by using the built-in jitter function in R (with a factor of 80) in order to break ties. mtDNA polymorphism calculations in terms of number of haplotypes (Nb), haplotype diversity (Hd) and nucleotide diversity (π) was performed in DnaSP (Librado and Rozas 2009) for each population.

Population size and genetic variation

Population genetic theory states that genetic variation depends on effective population size (Ne) (Kimura 1983). However, for these analyses we were constrained to use consensus population size (N) as a proxy for Ne. We thus considered N as our primary predictor of interest, and we ran separate analyses on each measurement of genetic variation. Visual expectation of standard diagnostics tools revealed deviations from the underlying distributional assumptions for linear models. Thus, we chose to loge-transforming N, and this resulted in residuals that approximated a normal distribution. Initially, we also considered area size (AS) as an alternative predictor, but as AS explained 53% of the variance in N (Fig. SI1.2), we excluded AS from the remaining analyses. All the responses measuring genetic variation were also highly correlated to each other (SI1). Na was the response best explained by N. Consequently, we ended up showing only the result from this analysis in the main text (but see SI2 for results for all the other predictors).

Further, we performed statistical analyses in several steps. First, we fitted linear models (e.g. Zuur et al. 2009) using each genetic variability measure as the response: (1) a model that only included the linear effect of N, and (2) a model that in addition to the linear effect also included a second-order polynomial (i.e. $N^2$). For these two candidate models, we rescaled and ranked each candidate model relative to the model with the lowest second-order AIC (AICc; e.g. Burnham and Anderson 2002; Zuur et al. 2009) values - $\Delta_j$ denotes this difference for model (i) and we selected the simplest model with a $\Delta_j \leq 1.5$ (we also provide Akaike’s weights; Table SI3.1). This part of the analyses was performed using the AICcmodavg library in R (Mazerolle 2013).

The relationship between Na and N, when back-transformed from loge to normal scale, showed evidence of a marginal diminishing return—where an increase in N did not translate into an increase in Na after reaching a certain value for N. Based on this, we fitted a plateau model where we estimate a linear increase in Na as a function of N up to a given threshold (Threshold$_N$) for population size. After this threshold, we assume a flat relationship between the response and the predictor. We fitted this model in R using the nls-function in the stats package (see Table SI3.3 for details). We estimated 95% confidence intervals (CIs) for the predictions using the nls2-package (Grothendieck 2013), whereas 95% CIs for the estimates were calculated using the nlstools-package (Baty et al. 2015).

Finally, we were concerned that our measures of genetic variability were biased due to different sample size (n) across the populations. We thus plotted these relationships and fitted linear regression models where we predicted each response separately as a function of sample size relative to population size [$\log_e(nN^{-1})$; Fig. SI3.2]. None of these relationships were significant, even though two of them were close to significant (Fig. SI3.2), so we conclude that our measures of genetic variability were not highly biased.

Genetic differentiation and structure

$\text{F}_{\text{ST}}$ values among all 21 populations was calculated in Arlequin to examine population differentiation, for both the microsatellite- and the CR-dataset. For the microsatellite data we also calculated $R_{\text{ST}}$ values (Slatkin 1995) assuming a stepwise mutation model (SMM), as microsatellites often mutate through stepwise changes in allele size (Levinson and Gutman 1987). For the mtDNA data, pairwise $F_{\text{ST}}$ genetic distances was calculated based on the number of pairwise differences between sequences and the Tamura–Nei model of nucleotide substitutions (1993), as inferred from Modeltest in MEGA version 6 (Tamura et al. 2013) and the AIC. The statistical significance of $F_{\text{ST}}$ and $R_{\text{ST}}$ values were estimated using 10,000 permutations.

We used Bayesian assignment as implemented in the program Structure 2.3.4 (Pritchard et al. 2000a, b) to investigate population structure in the microsatellite data. Structure assumes no a priori group membership to identify groups of individuals, and the analysis was based on the admixture model, correlated allele frequencies, a burn-in of 20,000 and 200,000 MCMC iterations. We tested for up to 12 populations (K=1–12) and repeated this procedure 10 times. For each K-value, average posterior probability among runs and standard deviation (SD) was calculated. We used Structure Harvester (Earl and vonHoldt 2012) and Evanno’s Delta K ($\Delta K$) (Evanno et al. 2005) method to estimate a possible main structure that can describe the system under study. However, while $\Delta K$ helps identify the
main structure, it should not be used exclusively (Evanno et al. 2005). Therefore, we also considered mean posterior probability \( \text{LnP}(D) \) to determine the number of clusters within the dataset. We used CLUMPP version 1.1.2 (Jakobsson and Rosenberg 2007) with the FullSearch algorithm and 1000 repeats, to find the optimal alignment of clusters across all 10 runs for the selected number of K’s. For the graphical display of genetic structure, we used the program Distruct (Rosenberg 2004). A neighbor joining tree based on CR genetic distances among populations was constructed in MEGA v6 (Tamura et al. 2013) using the Tamura 3-parameter substitution model (Tamura 1992) with all sites included, the complete deletion option, assuming homogenous pattern among lineages and uniform substitution rates among sites.

**Isolation by distance (IBD)**

Arlequin was used to perform a Mantel test (1000 iterations), on both the microsatellite and mtDNA data sets, to examine if there was an association between genetic distances \( F_{ST} \) and geographical distances (loge-transformation of the geographical distance in kilometer) for the 21 sub-populations.

**Results**

**Genetic variation**

Levels of genetic variation for the microsatellite loci, analysed for a total of 540 individuals, varied substantially among the 21 sampled populations (Fig. 2; Table 1). The highest levels of variation were found in the larger, central wild reindeer areas in the Langfjella Mountain Range (Nordfjella, Hardangervidda, Setesdal Ryfylke and Setesdal Austhei, Fig. 1). Mean number of alleles \( (N_a) \) was 5.71, ranging from 3.167 (Svartebotnen) to 7.167 (Hardangervidda), and unbiased expected heterozygosity \( (uHe) \) ranged from 0.592 (Svartebotnen) to 0.760 (Nordfjella). Assessing HWE for 12 loci across 21 populations resulted in 252 statistical tests. After performing Bonferroni correction, 3.57% of these tests deviated from HWE \( (p \leq 0.05) \). Among these significant tests, we found 5 loci (Re16, Re31, Re73, Rt1 and Rt9) in 8 populations. Moreover, only Knutshø showed evidence of deviation for more than one locus (Rt9 and Re31), and only two loci were statistically significant in more than one population (Re31 and Rt1). As the majority of these tests were non-significant (>96%), and as no locus or population were over-represented among these tests, we conclude that our data do not show any major deviation from HWE. All loci were thus included in the analyses. Varying levels of genetic variation among the 21 populations was also found for the 467 bp long CR fragment assessed for 456 individuals (see Table SI5.1 for GenBank accession numbers). In total, 37 haplotypes, haplotype diversity \( (Hd) \) equal to 0.742 and nucleotide diversity \( (\pi) \) equal to 0.018 were found. \( Hd \) ranged between 0.000 (Rondane South) and 0.945 (Knutshø), while \( \pi \) ranged between 0.000 (Rondane South) and 0.019 (Setesdal Austhei; Table 1).

**Population size and genetic variation**

In all analyses, we selected a model where each measure of genetic variability was predicted solely based on the main effect of population size \( (N, \text{log}_e\text{-scale}; \text{Appendix SI3}) \), which explained a large proportion of the variance of \( Na \) \( (R^2 = 0.58) \): a relationship that was positive and linear (Fig. 3a): \( \beta = 0.55 \pm 0.11 \) SE \( (p < 0.01, \text{Table SI3.2}) \). For the other measurements of microsatellite variation, \( N \) only had a significant positive effect on \( Ae \) and \( uHe \), but not on \( Ho \) (Table SI3.2; Fig. SI3.1). In the analyses based on the CR, \( N \) only had a significant and positive effect on the number of haplotypes \( (Nh) \) \( (R^2 = 0.29, F_{1,17} = 7.81, p = 0.01; \text{detailed results not shown}) \). Moreover, the results from these separate analyses were not independent as the pairwise Pearson’s...
The product moment correlation ($r$) between the original variables were 0.65–0.97 and 0.62–0.85 for the microsatellite and the mitochondrial measures of genetic variability, respectively (Fig. SI2.1). The plateau model indicated that $N_a$ did not increase after reaching a threshold value for $N$ of 1561 animals (95% CIs = 279–2844). 12 of the 21 sampled populations had population sizes below the estimated threshold, 7 populations fell below the lower 95% CI of the threshold, and 12 fell below the upper 95% CI (Fig. 3b).

**Genetic differentiation and structure**

The $F_{ST}$ matrix based on the microsatellite data indicated a high degree of divergence, notably that all areas are genetically significantly different from each other, except Hardangervidda and the neighboring Nordfjella area (Table SI4.1). The $R_{ST}$ matrix tended to group areas into fewer, larger units, i.e. showed a less fragmented pattern (Table 2). There was no differentiation among the central Langfjella areas, or among some of these and the adjacent populations from Lærdal-Ardal, Brattefjell-Vindeggen and Blefjell. In the Rondane-Dovre area, the $F_{ST}$ analysis grouped Knutshst and Rondane North, and Snøhetta and Rondane North. Moreover, the smaller areas to the west were also grouped, as there was no significant differentiation between between Sunnfjord and Fjellheime, Sunnfjord and Reinheimen-Breheimen, Lærdal-Ardal and Førdefjalla or between Våmur Roan and Blefjell (Table 2). $F_{ST}$ calculations based on the CR show less divergence than found in the microsatellite data (Table 3). However, the Rondane-Dovre populations, Norefjell-Reinsjøfjell, Reinheimen-Breheimen as well as Våmur Roan were identified as significantly different from most other sampled areas.

Based on the Bayesian assignment analysis and Evanno’s $\Delta K$, the microsatellite data showed a main structure of two genetic clusters with a division between the native wild populations from Rondane-Dovre (population 1–4) and the remaining sampled areas (population 5–20, Figs. 4a, 5). Further sub-structure was apparent as the LnP(D) showed a relatively high increase up to $K = 3$ (Fig. 4b), where Rondane-Dovre still comprise a separate group, but the remaining populations were divided into two groups. The first group includes populations from the large, central areas in Langfjella (Nordfjella, Hardangervidda and Setesdal) in addition to five adjacent populations, with a mixed wild-domestic origin (5–11) or domestic origin (12 and 13). The second group comprise the remaining populations situated west-, north- and east-of Langfjella, all with an assumed domestic origin (14–20, Fig. 5). The structure result at $K = 2$ was corroborated by the neighbor-joining tree constructed from CR genetic distances. Here it is again mainly Rondane-Dovre that differentiate from the other populations (Fig. 6). However, the CR data showed minimal sub-structure within these two clusters.

**Isolation by distance (IBD)**

The Mantel test, including the 21 management units, indicated a weak, but significant correlation between pairwise geographical distances and microsatellite genetic distances ($p < 0.001$, $r = 0.322$, $R^2 = 0.104$). A similar correlation was found also for the mtDNA data ($p \leq 0.001$, $r = 0.296$, $R^2 = 0.088$).

**Discussion**

Our results on the genetic effects of the substantial landscape changes that has occurred in south-Norway during the last 100 years show highly varying levels of genetic variation among areas, and that levels of genetic variation is strongly...
Table 2  \( R_{ST} \) values among all 21 populations, based on 12 microsatellite markers, calculated in Arlequin

|     | HV   | LÅ   | SR   | SA   | NF   | BV   | BF   | RB   | FO   | NE   | RS   | RN   | KN   | SN   | FH   | VR   | SE   | SF   | FF   |
|-----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| HV  | 0.011|      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| LÅ  |      | 0.009| 0.049**| |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| SA  | 0.030| 0.020*| 0.025**| |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| NF  | −0.005| 0.017|      | 0.001| 0.009| |      |      |      |      |      |      |      |      |      |      |      |      |      |
| BV  | 0.006| 0.040**| −0.008| 0.014| 0.000| |      |      |      |      |      |      |      |      |      |      |      |      |      |
| BF  | 0.008| 0.023|      | 0.007| 0.018| 0.015| −0.002| |      |      |      |      |      |      |      |      |      |      |      |
| RB  | 0.084***| 0.056***| 0.112***| 0.049***| 0.078***| 0.087***| 0.083***| |      |      |      |      |      |      |      |      |      |      |
| FO  | 0.157***| 0.143***| 0.170***| 0.115***| 0.147***| 0.146***| 0.107***| 0.051***| |      |      |      |      |      |      |      |      |      |      |
| NE  | 0.140***| 0.091***| 0.132***| 0.103***| 0.109***| 0.114***| 0.090***| 0.050***| 0.069***| |      |      |      |      |      |      |      |      |      |
| RS  | 0.126***| 0.216***| 0.131***| 0.212***| 0.169***| 0.129***| 0.134***| 0.312***| 0.325***| 0.330***| |      |      |      |      |      |      |      |      |
| RN  | 0.084***| 0.177***| 0.077***| 0.157***| 0.120***| 0.076***| 0.092***| 0.256***| 0.275***| 0.282***| −0.001| |      |      |      |      |      |      |      |
| SL  | 0.099***| 0.195***| 0.152***| 0.199***| 0.168***| 0.141***| 0.155***| 0.291***| 0.337***| 0.351***| 0.026**| 0.038**| |      |      |      |      |      |      |
| KN  | 0.073***| 0.124***| 0.055***| 0.137***| 0.085***| 0.060***| 0.067***| 0.215***| 0.239***| 0.216***| 0.027*| 0.018| 0.054***| |      |      |      |      |      |
| SN  | 0.097***| 0.205***| 0.099***| 0.191***| 0.138***| 0.108***| 0.146***| 0.307***| 0.362***| 0.354***| 0.032**| 0.004| 0.046**| 0.041**| |      |      |      |      |
| FH  | 0.151***| 0.091***| 0.227***| 0.144***| 0.171***| 0.211***| 0.188***| 0.066***| 0.192***| 0.141***| 0.398***| 0.361***| 0.357***| 0.304***| 0.407***| |      |
| VR  | 0.048***| 0.027**| 0.056***| 0.022*| 0.033***| 0.041**| 0.016| 0.049***| 0.089***| 0.043***| 0.257***| 0.208***| 0.272***| 0.168***| 0.271***| 0.144***| |      |
| SE  | 0.114***| 0.118***| 0.114***| 0.163***| 0.134***| 0.113***| 0.110***| 0.164***| 0.222***| 0.207***| 0.145***| 0.120***| 0.123***| 0.062***| 0.154***| 0.239***| 0.198***| |      |
| SF  | 0.088***| 0.047**| 0.148***| 0.085***| 0.101***| 0.137***| 0.133***| 0.018| 0.164***| 0.127***| 0.333***| 0.282***| 0.296***| 0.242***| 0.331***| 0.000| 0.109***| 0.176***| |      |
| FF  | 0.067***| 0.033| 0.077***| 0.039**| 0.052*| 0.079***| 0.082*| 0.046*| 0.151***| 0.050***| 0.273***| 0.221***| 0.275***| 0.171***| 0.278***| 0.087***| 0.055*| 0.172**| 0.065*| |      |
| SB  | 0.180***| 0.183***| 0.207***| 0.167***| 0.210***| 0.220***| 0.235***| 0.147***| 0.288***| 0.214***| 0.348***| 0.294***| 0.338***| 0.263***| 0.361***| 0.186***| 0.244***| 0.200**| 0.168***| 0.128***| |

The level of statistical significance for these values are marked with asterisks (given as \( ^{**} p > 0.05, ^{*} p < 0.05, ^{**} p < 0.01, \) and \( ^{***} p < 0.001 \)) and abbreviations for the areas are as in Table 1.
Table 3  \( F_{ST} \) values among all 21 populations, based on the mitochondrial control region, calculated in Arlequin

|     | HV  | LÅ  | FH  | VR  | SA  | NF  | BV  | SE  | SF  | FF  | SB  | BF  | RB  | FO  | NE  | SR  | RS  | RN  | SL  | KN  |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| HV  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| LÅ  | 0.017 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| FH  | 0.199** | 0.139** |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| VR  | 0.002 | −0.004 | 0.030 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| SA  | −0.018 | 0.013 | 0.142** | −0.008 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| NF  | 0.071* | 0.058 | 0.046 | 0.339*** | 0.010 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| BV  | 0.050 | 0.057 | 0.012 | 0.308*** | 0.017 | 0.041 | −0.025 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| SE  | 0.017 | 0.033 | −0.010 | 0.015 | 0.071 | 0.032 | 0.137* | 0.093 |     |     |     |     |     |     |     |     |     |     |     |     |     |
| FF  | −0.006 | 0.014 | −0.024 | −0.003 | 0.047 | 0.014 | 0.125 | 0.083 | −0.083 |     |     |     |     |     |     |     |     |     |     |     |     |
| SB  | 0.030 | 0.057 | 0.023 | −0.058 | 0.103 | 0.057 | 0.199 | 0.158 | −0.077 | −0.095 |     |     |     |     |     |     |     |     |     |     |     |
| BF  | −0.003 | −0.004 | −0.019 | 0.180** | −0.004 | −0.009 | 0.021 | 0.005 | 0.020 | −0.015 | 0.063 |     |     |     |     |     |     |     |     |     |     |
| RB  | 0.187** | 0.172* | 0.149* | 0.504*** | 0.088* | 0.153* | −0.016 | 0.017 | 0.280* | 0.275* | 0.364* | 0.123 |     |     |     |     |     |     |     |     |     |
| FO  | 0.005 | 0.004 | −0.037 | 0.175** | 0.008 | −0.003 | 0.009 | −0.022 | −0.002 | −0.013 | 0.044 | −0.031 | 0.103 |     |     |     |     |     |     |     |     |
| NE  | 0.713*** | 0.357*** | 0.342*** | 0.115*** | 0.657*** | 0.234*** | 0.333* | 0.318* | 0.196*** | 0.492*** | 0.502** | 0.264*** | 0.010*** | 0.305*** |     |     |     |     |     |     |
| SR  | 0.000 | −0.008 | 0.059 | 0.269** | −0.032 | −0.010 | 0.020 | 0.038 | 0.108 | 0.082 | 0.147 | 0.013 | 0.105 | 0.035 | 0.264** |     |     |     |     |     |     |
| RS  | 0.574*** | 0.604*** | 0.644*** | 0.825*** | 0.516*** | 0.582*** | 0.566*** | 0.636*** | 0.779*** | 0.815*** | 0.885*** | 0.650*** | 0.639*** | 0.671*** | 0.713*** | 0.547*** |     |     |     |     |     |
| RN  | 0.574*** | 0.602*** | 0.643*** | 0.817*** | 0.515*** | 0.579*** | 0.568*** | 0.639*** | 0.776*** | 0.805*** | 0.864*** | 0.652*** | 0.638*** | 0.674*** | 0.705*** | 0.549*** | −0.029 |     |     |     |     |
| SL  | 0.857*** | 0.617*** | 0.653*** | 0.826*** | 0.531*** | 0.593*** | 0.582*** | 0.652*** | 0.787*** | 0.821*** | 0.882*** | 0.665*** | 0.653*** | 0.685*** | 0.722*** | 0.568*** | 0.029 | 0.014 |     |     |     |
| KN  | 0.206* | 0.221* | 0.289* | 0.569*** | 0.142* | 0.208* | 0.152* | 0.198* | 0.380*** | 0.358*** | 0.440* | 0.225* | 0.186* | 0.239* | 0.294*** | 0.113* | 0.356*** | 0.337*** | 0.80*** |     |     |
| SN  | 0.430*** | 0.453*** | 0.517*** | 0.710*** | 0.369*** | 0.437*** | 0.411*** | 0.468*** | 0.666*** | 0.602*** | 0.658*** | 0.481*** | 0.455*** | 0.505*** | 0.523*** | 0.361*** | 0.122* | 0.077 | 0.143* | 0.084 |     |     |

The level of statistical significance for these values are marked with asterisks (given as \( p > 0.05 \), \( *p < 0.05 \), \( **p < 0.01 \), and \( ***p < 0.001 \)) and abbreviations for the areas are as in Table 1
linked to population size. The high levels of differentiation among most sampled areas suggest low levels of gene flow, especially among the smaller and probably more isolated populations. The effect of geographic distance on spatial genetic structure was significant, but explained only approximately 10% of the genetic differentiation among populations.

**Genetic variation and population size**

Levels of genetic variation varied substantially among the populations under study, in both the microsatellite loci and in the CR. We found high levels of variation in the relatively large populations within the Central Langfjella Mountain Range, and reduced levels of variation in the smaller populations, e.g. Svartebotnen, Fordeljella, Sunnfjord, Blefjell and Våmur Roan, implying a relationship between population size and genetic variation. Based on the microsatellite data, this relationship was positive and linear, until reaching a plateau at approximately 1500 animals even though the precision for this estimate was poor (95% CIs = 279–2844 animals). Although a general relationship between population size and genetic variation was apparent, we also found exceptions where it is likely that population history rather than population size have affected the current levels of
genetic variation. For example, Lærdal-Årdal, with a population size of approximately 120 reindeer, show moderate to high levels of genetic variation. This population has its origin from the Nordfjella area, but appear to have been recently re-established or ‘reinforced’ (during the 1990s) through two re-introductions (Punsvik and Frøstrup 2016). Thus, high variability in this population may be the result of two different founding events, as well as possible gene flow between this population and the adjacent Nordfjella area. In contrast, Norefjell-Reinsjøfjell is a population counting 700 animals, which shows reduced levels of genetic variation. Historically, the Norefjell-Reinsjøfjell population appears to originate from a single founder event of approximately 32–35 straying domestic reindeer that escaped slaughter in 1968 (Reimers et al. 2009), which likely explain the low levels of genetic variation. The three native populations from Rondane South, Rondane North and Solnkletten also showed highly reduced levels of genetic variation, despite relatively large population sizes. Interestingly, this is only apparent from the CR data, whereas moderate to high levels of variation is evident from the microsatellite data. This discrepancy probably reflects previous bottlenecks in these populations (Røed et al. 2014), but also the fact that mtDNA is maternally inherited, resulting in an effective population size that is only one-quarter of the biparently inherited microsatellite markers. Consequently, mtDNA is more exposed to genetic drift, resulting in fixation and reduced genetic variation, compared to nuclear DNA (Birky et al. 1983). Higher variability in the microsatellites compared to the mitochondrial CR might also indicate some gene flow due to male movement among populations within the Rondane-Dovre region.

Genetic differentiation and structure

Overall, a high degree of differentiation in the microsatellite data was evident from the population-based analysis ($R_{ST}/F_{ST}$), suggesting a main pattern of fragmentation congruent with the current pattern of 24 wild reindeer areas, with limited levels of gene flow especially among the smaller populations. However, reindeer inhabiting Langfjella, including the by far largest population, Hardangervidda, as well as some adjacent populations with an assumed origin from Langfjella, showed less differentiation. This imply common origin and possibly some level of genetic exchange among these areas. On the contrary, the mtDNA dataset showed little differentiation and that it is mainly the native, wild populations in Rondane-Dovre and three populations of domestic ancestry (Norefjell-Reinsjøfjell, Vamur Roan and Reinheimen-Breheimen) that is significantly differentiated from most other populations. This discrepancy between the levels of differentiation between the two markers was somewhat surprising, as reindeer show strong female philopatry—implying that males migrate among populations more frequently than females. Hence, under temporally relatively stable environmental conditions, we would expect the biparently inherited microsatellite markers to show a more homogeneous genetic structure compared to the mtDNA markers (Roffler et al. 2012). The general pattern of less genetic differentiation in mtDNA as compared to microsatellites may likely be the result of recent habitat alterations by human infrastructure (e.g. intensified development of railways and roads), and relatively recent origin of several of the populations—combined with lower mutation rate in the mtDNA marker.

The individual assignments analysis and the neighbor-joining analysis both show a main structure of two clusters, separating between native Rondane-Dovre reindeer and the remaining areas with mixed or domestic origins. This structure is in accordance with Røed et al. (2008, 2014) who studied the few, larger wild populations. However, by also including the many small additional Norwegian populations, we document further sub-structuring with at least three clusters. These three clusters comprise the sub-populations within the Rondane-Dovre region, within the Langfjella region together with five adjacent populations, and a third cluster comprising the remaining populations—all with an assumed domestic origin. While reindeer in Rondane-Dovre seem to be little affected by introgression from domestic reindeer, wild reindeer in Langfjella have experienced...
considerable admixture with domestic reindeer during the last two centuries (Røed et al. 2014; Punsvik and Frøstrup 2016). Hence, the mixed group differentiates from most of the populations of wild or domestic origin due to introgression, but also because the ancient wild reindeer in Hardangervidda and in Rondane-Dovre appear to comprise different genetic lineages (Røed et al. 2014). The fact that two populations with assumed domestic origin (Våmur Roan and Skauen Etnefjell) cluster with the mixed group may be explained by some level of gene flow among populations. The third group show little geographical structure and includes populations situated both north, west and east in the distribution area. Hence, they appear to be similar by common descent, rather than through homogenization by gene flow.

Geographic distance and spatial structure

The geographic distribution of species is generally wider than individual dispersal capacity, and functional landscape connectivity may be limited, which may lead to natural differentiation through IBD (Wright 1943; Balloux and Lugon-Moulin 2002). We did not, however, find compelling evidence of IBD being the main driver of the observed genetic structure. Both markers indicate that only a small fraction of the variation (−10%) is explained by geographic distance. Genetic differentiation could also reflect founder effects and selection. Natural selection can alter allele frequencies in several different ways, e.g. by divergent selection, which will cause populations to evolve traits that gives a fitness advantage under local conditions (e.g. Kawecki and Ebert 2004). However, the studied reindeer populations all live in similar mountainous, alpine areas with no obvious habitat differences, except for a wetter, more oceanic climate in the western regions. Conversely, selection and possible local adaptation may be hindered by gene flow, lack of genetic variation, and genetic drift (Freeland 2005). Several of the Norwegian reindeer populations is probably prone to high levels of genetic drift, because of small population sizes and low inter-fragment functional connectivity, independent of geographic distance. Also, considering the timeframe since these populations were founded (mainly during the 1960–1970s), genetic drift seems to be a main driver of differentiation, rather than selection resulting in local adaptations. Nevertheless, within small and fragmented populations, local processes like founder effects, expansion rate, as well as historical sex ratios and reproduction success (Holand et al. 2007), are all local population-ecological uncertainties that potentially can affect genetic structure.

The genetic markers used in this study gave congruent results in the sense that they both showed varying levels of variation, a clear separation between Rondane-Dovre and the other populations, and that geographic distance explains little of the variation. However, we also found that the resolution of the microsatellite markers is higher than for the CR, as we found more differentiation and structure in the microsatellite dataset. The microsatellite markers also revealed a clear relationship between genetic variation and population size, a relationship that was not as evident from the CR data. From this, we conclude that microsatellites is a more appropriate marker to monitor genetic variation and to identify genetic structure in Norwegian wild reindeer.

Management implications

Analysing intraspecific genetic variation across wild Norwegian reindeer populations showed a clear and positive relationship between population size and genetic variation. However, in the linear model this relationship was curved (due to our log₁₀-transformation of the predictor), and showed evidence of a marginal diminishing return as the increase in variation per se decreased with increasing population size (Fig. 3a). This motivated us to fit the plateau model to these data, and the results showed that several of the Norwegian wild reindeer populations have population sizes well below our estimated threshold (Fig. 3b). This finding is important and has strong management implications as it shows that the smaller populations are vulnerable for demographic effects, which further questions the long-term viability for some of the populations under study. Svartebotnen, Førdefjella and Sunnfjord, are examples of this as they stand out as having low-levels of genetic variation in combination with small population size. Moreover, the population-based analyses show low-levels of gene flow, especially among the smaller populations, which is unexpected for a mobile and large-bodied species such as reindeer (Miguet et al. 2016). In sum, the genetic structure found within Norwegian wild reindeer, particularly in the smaller fragmented areas, seems to be highly influenced by colonization history, bottlenecks and current isolation due to fragmentation, in the sense that strongly human-reduced or non-existent functional connectivity limits gene flow.

From a research perspective, an important implication of our study is that landscape characteristics seems to interact with anthropogenic impacts (e.g. management decisions related to harvest and land-use issues related to increasing tourism) in affecting both the genetic structure and variation within Norwegian wild reindeer. Future studies should thus apply a multiple stressor approach (e.g. Munns Jr 2006; Bårdsen et al. 2018) to population genetics. The point being that landscape changes, such as habitat loss and fragmentation, might mitigate or aggravate the effect of other on-going stressors affecting Norwegian wild reindeer. We believe that these are interesting and necessary perspectives for current wild reindeer management as ecological studies have shown
the effects of multiple stressors on body mass, reproduction and population dynamics for this species. The strength of negative climatic effects is, for example, dependent on population size as harsh winters have a much greater negative impact at high- compared to low-density of animals (e.g. Bårdsen et al. 2010; Bårdsen and Tveraa 2012).

The level of genetic differentiation and genetic drift (i.e. loss of genetic variation), and how they relate to population size, have clear management implications. To achieve a long-term preservation of wild reindeer in Norway, management efforts with focus on increasing population sizes and genetic connectivity among populations should be prioritized—especially for the smaller and more isolated populations, provided that conservation of genetic variation is an objective (as documented for other Rangifer sub-species in North America; e.g. Courtois et al. 2003; Gubili et al. 2017). This is important considering the fact that several studies have documented negative effects of landscape changes, such as habitat loss and fragmentation, which is expected to co-occur with increasing levels of impacts from other stressors (such as, but not limited to, climate; e.g. Bårdsen et al. 2017). This is particularly important for the populations in the present study since the last remaining wild tundra reindeer in Western Europe are located in Norway.

Acknowledgements This study, which in its original form was a part of KSK’s PhD, was supported by the University College of Southeast Norway, Bø in Telemark and the Norwegian Wild Reindeer Centre. Further development has been supported by the Project “Reindeer Husbandry in a Globalizing North – Resilience, Adaptations and Pathways for Actions (ReiGN)”, which is a Nordforsk-funded “Nordic Centre of Excellence” (Project Number 76915). We would like to thank Liv Midthjell for assistance in the laboratory.

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