Genetic variation and structure of house sparrow populations: is there an island effect?

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Abstract

Population genetic structure and intra-population levels of genetic variation have important implications for population dynamics and evolutionary processes. Habitat fragmentation is one of the major threats to biodiversity. It leads to smaller population sizes and reduced gene flow between populations and will thus also affect genetic structure. We use a natural system of island and mainland populations of house sparrows along the coast of Norway to characterize the different population genetic properties of fragmented populations. We genotyped 636 individuals distributed across 14 populations at 15 microsatellite loci. The level of genetic differentiation was estimated using *F*-statistics and specially designed Mantel tests were conducted to study the influence of population type (i.e. mainland or island) and geographic distance on the genetic population structure. Furthermore, the effects of population type, population size and latitude to the level of genetic variation within populations were examined. Our results suggest that genetic processes on islands and mainland differed in two important ways. Firstly, the intra-population level of genetic variation tended to be lower and the occurrence of population bottlenecks more frequent on islands than the mainland. Secondly, although the general level of genetic differentiation was was low to moderate it was higher between island populations than between mainland populations. However, differentiation increased in mainland populations somewhat faster with geographical distance. These results suggest that population bottleneck events and genetic drift have been more important in shaping the genetic composition of island populations compared to populations on the mainland. Such knowledge is relevant for a better understanding of evolutionary processes and conservation of threatened populations.

Introduction

Genetic variation plays a central role for long term population viability (Lande and Barrowclough 1987), adaptation through natural selection (Willi *et al.* 2006) and speciation (Carson and Templeton 1984). Genetic variation is therefore of paramount importance in order to understand processes that relate to both conservation and evolution (Falconer and Mackay 1996, Storfer 1996). However, because parameters such as population differentiation and genetic diversity may vary between different populations according to their demographic history, the latitude where they are situated, migration and genetic drift, the genetic properties of a given population may not be directly extrapolated to other populations of the same species. For instance, a population bottleneck may have drastic effects on the allele frequencies of a population (Luikart *et al*. 1998). The size of the remaining population after the bottleneck event affects population structure (and viability) as the rate of loss of alleles due to genetic drift is negatively related to population size (Willi *et al*. 2007). Populations that have recently colonized new areas such as the establishment of a new species on islands, share the same genetic properties as bottlenecked populations (see e.g. Nei *et al.* 1975). The number of founding individuals is important under such scenarios, because these individuals form the genetic basis of the new population (Mayr 1942, Slatkin 1996). Additionally, small populations are to a larger extent influenced by demographic stochasticity (random variation among individuals in reproduction and survival) and environmental stochasticity (Kaitala *et al*. 2006, Lande *et al.* 2003). The degree of genetic differentiation between populations generally increases with the distance that separates them (Kimura and Weiss 1964, Wright 1943) due to reduced gene flow between more distant populations (see e.g. Godt *et al*. 2005), and different effects of selection and genetic drift due to the expected decrease in spatial

71 correlation of environmental conditions with increasing distance between populations
72 (Balloux and Lugon-Moulin 2002, Koenig 2002). Genetic differentiation is also affected by
73 landscape resistance (i.e. topography) as geographic barriers reduce gene flow and increase
74 the genetic isolation of the populations (Forman 1995, McRae 2006). Other physical
75 parameters are also important; a reduction in genetic diversity when moving north is a
76 phenomenon that has been established for a number of taxa (review by Martin and McKay
77 2004).

78 Islands create naturally fragmented study systems: isolated islands have discreet
79 boundaries with subsequently reduced migration, and populations on islands can therefore be
80 easily defined. As a consequence, many of the aforementioned population genetic parameters
81 can be known, eliminated or to some degree controlled for. This makes islands suitable for
82 addressing questions on inter- and intra-population genetic diversity and effects of isolation
83 due to distance and topography.

84 The genetic properties of island populations are characterized by reduced gene flow
85 into the population due to lower migration rates, elevated levels of inbreeding (Frankham
86 1997, 1998), and depleted genetic variation as a consequence of the founder effect (Slatkin
87 1996). Correspondingly, islands often have low levels of genetic variation and high
88 probability of loss of alleles due to inbreeding and genetic drift (Eldridge *et al*. 1999,
89 Ellstrand and Elam 1993, Lande 1995). Even island populations that are large often show
90 traces of the low initial genetic variation (Hedrick *et al*. 2001). Island populations that are
91 small are more vulnerable to extinction – a situation similar to a small isolated population in
92 endangered species (see e.g. Pimm *et al.* 1993). Island populations of ubiquitous species may
93 therefore serve as excellent models for threatened species and extinction scenarios (Ringsby
94 *et al.* 2006) which is particularly interesting to conservation scientists and is currently of

95 increasing importance as habitat fragmentation is an escalating problem and a significant
96 threat to biodiversity. With respect to migration, decreasing distance to the mainland and an
97 increasing size of the island are both positively related to colonization rate (MacArthur and
98 Wilson 2001). Intra-specific immigration rates will therefore most likely depend on the same
99 parameters, contributing to increased genetic variation and reduced genetic differentiation on
100 large islands close to the mainland. Moreover, island theory is often applicable or extendable
101 to metapopulation dynamics (e.g. Kaitala *et al.* 2006), as patchy habitats found on the
102 mainland are quite analogous to islands (Whittaker and Fernàndez-Palacios 2007, MacArthur
103 & Wilson 2001). This archipelago-analogy has received some noteworthy criticism (see e.g.
104 Haila 2002) but in general mainland habitats are considered to be often larger and less
105 fragmented than island habitats (Fahrig and Merriam 1985) and mainland populations are thus
106 likely to be less differentiated (Garcia-Ramos and Kirkpatrick 1997) and to carry more
107 genetic variation than island populations. A few recent studies on different taxa have
108 highlighted these facts, such as a study of the the common shrew (*Sorex araneus*) on the
109 Scottish mainland and adjacent offshore islands (White and Searle 2007); South Island robins
110 (*Petroica australis australis*) on the mainland and islands off New Zealand (Boessenkool *et*
111 *al.* 2007), silvereyes (*Zosterops lateralis*) on islands in the southwest Pacific (Clegg *et al.*
112 2002), trumpeter finches (*Bucanetes githagineus*) on the Canary Islands (Barrientos *et al.*
113 2009) and the black-footed rock-wallaby (*Petrogale lateralis lateralis*) in Australia (Mason *et*
114 *al.* 2011).
115 Studying both island and mainland populations of a species in the same geographical
116 area is highly interesting because it increases our understanding of evolutionary and
117 population-dynamic processes in differently constructed habitats. Identifying general rules
118 regarding the structuring of genetic variation among populations with respect to geographic

distance and possible dispersal barriers is in turn applicable to e.g. conservation biology of many species experiencing habitat fragmentation and decreasing connectivity. Evolutionary processes of drift and migration may have different relative importance in island and mainland populations and understanding the mechanisms shaping them will improve our ability to protect many threatened species and populations.

House sparrow populations (*Passer domesticus*) in middle and northern Norway represent an ideal study system for assessment of the above issues. Here, island populations of different sizes and different degrees of isolation can be compared to mainland populations along a 550 km latitudinal gradient. Few similar studies have been carried out on animal species. Specifically, the aims of this study are to examine 1) the intra-population level of genetic variation and occurrence of genetic population bottlenecks in mainland and island populations, 2) characterize the spatial genetic population structure among fourteen house sparrow populations that are situated either on the mainland or on islands over a latitudinal gradient and 3) test if population type (i.e. located on island or on mainland) has an effect on the first two.

Methods

Study area

The study was carried out on island and mainland populations along the coast of Norway, from Gjerøy (66°N, 13°E) in the north to Brattvåg (63°N, 6°E) in the south (see Fig. 1 and Table 1). The range of distances between populations was 6 to 543 km. All island and

mainland localities had a boreal climate. Island populations (n = 9) were (from north to south): Gjerøy, Hestmannøy, Aldra, Løkta, Vega, Leka, Vikna, Storfosna and Harøya. Mainland populations (n = 5) were (from north to south): Helgeland, Leirfjord, Brønnøysund, Ørlandet and Brattvåg. The estimated population sizes (see method in Data collection and sampling) ranged from 34 (Aldra) to 300 (Ørlandet). In this area house sparrow populations have experienced both colonization and extinction events (Billing *et al.* 2012, Ringsby *et al.* 2006). For some of the populations we have detailed data on population demography, dispersal and inbreeding during the last ca. 15 years prior to sampling (Billing *et al.* 2012, Engen *et al.* 2007, Jensen *et al.* 2007, Pärn *et al.* 2012). Geographic population coordinates and specified population data is shown in Table 1. A distance matrix consisting of geographic distances between population centra was calculated using mean coordinates at sub-localities within each main locality (Appendix A, Electronic Supplementary Material). Note that the study area is mostly long and narrow (i.e. one-dimensional), hence $\hat{F}_{ST}$ ($\hat{F}_{ST} = F_{ST} / (1\text{-}F_{ST})$) or $\hat{D}_{ST}$ ($\hat{D}_{ST} = D_{ST} / (1\text{-}D_{ST})$) and untransformed geographic distance were used in the analyses (see Rousset 1997).

Study species

The house sparrow is a small passerine bird widely spread around the whole globe (Blair and Hagemeijer 1997, Summers-Smith 1988, Anderson 2006). It is sexually dimorphic, but the mostly brown and grayish plumage is common for both sexes (Summers-Smith 1988). In northern Norway the breeding period is constrained to the late spring and summer months (generally May to August), and average clutch size is 5 eggs (Husby *et al*. 2006). Each pair lay 1-3 clutches per season (Ringsby *et al.* 2002) and generation time is roughly two years (Jensen *et al.* 2008). The lifespan of this robust passerine is known to be as long as 9 years in

164 northern Norway but in general it is much shorter (Jensen *et al.* 2004). Accordingly, in
165 Norwegian populations only about 15-20% of fledglings recruit into the adult breeding
166 population (Ringsby *et al*. 1999, 2002). Another characteristic feature with the house sparrow
167 is the low dispersal rates. On islands in the northern part of the current study only about 10%
168 of all female and male fledglings, respectively, that recruit into the breeding population are
169 dispersers (Altwegg *et al.* 2000, Pärn *et al.* 2009, 2012). In addition, Tufto *et al*. (2005)
170 estimated relatively short dispersal distances (2-49 km) among island populations of this
171 species, with 60% of dispersers moving shorter than ca. 13 km. Although previous studies of
172 house sparrows in northern Norway have mainly focused on inter-island dispersal,
173 interchange of individuals between island and mainland populations have also been recorded
174 in this area (H. Jensen unpublished results). A study of Finnish house sparrows living in a
175 more continuous suitable habitat suggests however that dispersal rates and dispersal distances
176 are higher in such landscapes (Kekkonen *et al*. 2011a). Only a few of the populations
177 included in this study were thus likely to be within normal dispersal distance from each other,
178 but the presence of house sparrow populations between the sampled ones may nevertheless
179 reduce the probability of genetic isolation between populations. Another practical feature of
180 the study species is its adaptation to human settlement and in particular farming. This restricts
181 the suitable habitat to dairy farms and other human settlements, and increases the efficiency
182 of sampling. The adaptation is strongly reflected in the behavioral ecology and foraging
183 patterns of the species, with diets mainly consisting of seeds from cultivated crops (Blair and
184 Hagemeijer 1997, Summers-Smith 1988). In the summer the house sparrows spend much time
185 outdoors, but when the weather is harsh (especially in the winter) the sheds become critical
186 for survival (Summers-Smith 1988).

187 *Data collection and sampling*

188 Adult house sparrows were caught using mist nets and sampled for blood. Only adults were
189 sampled and sampling was carried out within one year in each population to reduce any bias
190 due to sampling of close relatives (i.e. parents and their nestlings or juveniles). Each
191 individual was assigned unique individual ring codes consisting of a numbered metal ring and
192 three additional plastic color rings; two rings on each tarsus. In this way, re-sampling of the
193 same individuals was omitted, and estimation of population sizes was facilitated. The
194 population size was for most populations (4 and 8-14; Table 1) estimated by counting adult
195 individuals at the time of sampling (Pärn *et al.* 2012, Tufto *et al.* 2005). However, in
196 populations that were part of a long-term house sparrow study where a large proportion (> 90
197 %) of adult birds were ringed (1-3 and 5-6; Table 1) population size was estimated as the
198 number of marked adult individuals present in the population in the year of sampling (Jensen
199 et al. 2006). For one population (7; Table 1) we used the population estimate given in
200 Skjelseth *et al.* (2007). In the long-term house sparrow study there was a strong correlation
201 between counted adult birds and the number of marked adult birds (data from 1993-1999: $N = 37$ island-years, $r = 0.959$, $P < 0.001$); the estimated population size was on average 15%
203 higher when number of marked birds was used than when counts was used (own unpublished
204 results). Adjusting the estimated population sizes in populations that were part of our long-
205 term study accordingly did however not affect our results. When a bird was first ringed, a
206 small blood sample (25µl) was extracted from the underside of the wing where the brachial
207 vein crosses the wing bone. Blood samples were stored in 96% ethanol prior to further
208 laboratory work (Jensen *et al*. 2003). During sampling, the total (local) adult population sizes
209 were estimated, counting males and females (assuming equal sex ratios) at each sub locality
210 (Table 1). The aim was to randomly select at least 40 individuals from each population for

sampling, aiming at an equal sex ratio. This sample size is assumed to be sufficiently large to detect polymorphisms in most of the populations (see e.g. Sjögren and Wyöni 1994). For the two smallest populations (Gjerøy and Aldra), we did not reach the goal of catching >40 individuals. However, approximately 70% of the total population size was sampled, and we assume this sample captured most of the genetic variation present. Most of the house sparrow populations were sampled in the breeding season of 2006, but samples from winter 2002 were used for Vega, Leka and Vikna. On each locality, all samples were collected within the same year (i.e. inter-annual mixing of blood samples does not exist within populations, only among populations), thus minimizing any temporal variation in population substructure. For further details concerning sampling see Table 1.

Laboratory analyses

A Chelex (BioRad, USA) resin-based extraction procedure was carried out, making DNA in the blood samples available for amplification by means of polymerase chain reaction (PCR). The extracted DNA from each individual was used to determine intra-individual genetic variation by genotyping at 21 microsatellite loci: Ase18, Fhu2, HrU5, INDIGO 41, Mcyμ4 (Griffith *et al.* 2007), Pdoμ1, Pdoμ3 (Neumann and Wetton 1996), Pdoμ4, Pdoμ5, Pdoμ6 (Griffith *et al.* 1999), Pdo10, Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo30, Pdo32, Pdo36, Pdo44, Pdo47 (Dawson *et al.* 2012). PCR amplification of the highly polymorphic microsatellite loci was carried out in 10 μL reaction mixture on a "GeneAmp PCR system 9700" (Applied Biosystems, USA). Products were separated by electrophoresis in an automated 16 capillary electrophoretic analysis system: "ABI Prism 3130xl Genetic Analyzer" (Applied Biosystems, USA). To visualise alleles, reverse primers were fluorescently labelled with FAM, NED, VIC or PET (Applied Biosystems, USA). Detailed procedures for genotyping are found in Appendix B, Electronic Supplementary Material.

Genotypes of all individuals on the microsatellite loci were scored using the software package GENEMAPPER 4.0 (Applied Biosystems, USA). Due to problems in scoring alleles at six loci (see Appendix B, Electronic Supplementary Material) the analyses were carried out using information on 15 different microsatellite loci. Allele frequencies for none of the 15 loci used in the analyses deviated significantly from Hardy-Weinberg expectations (see Appendix B, Electronic Supplementary Material).

Software and statistics

The computer program FSTAT v2.9.3.2 (Goudet 1995) was used to estimate gene diversity (i.e. expected heterozygosity) (Nei 1987) and allelic richness within each of the sampled populations. Whether latitude, population size, population type (i.e. island or mainland population), and any interactions between population type and latitude or population size explained any variation in gene diversity or allelic richness was examined running GLMs in the software SPSS (SPSS Inc. 1997).

We used the Wilcoxon test in the program BOTTLENECK to test for genetic signatures of bottlenecks based on heterozygosity excess in the respective populations. We used 70% SMM and 30% IAM in the TPM model, and a TPM variance of 12, as recommended for analysis of microsatellites (Piry *et al.* 1999).

The program STRUCTURE was used to identify genetic clusters without using any prior information of the sampling location of the individuals. Two separate analyses were carried out in STRUCTURE, both times with allele frequencies as correlated and the admixture model. The first analysis was used to infer the most likely range for K. Here, we used a burn-in of 10 000 and a MCMC length of 50 000 iterations and the simulated number of populations from $K = 1 - 14$. The upper limit of 14 was chosen as this corresponds to the number of sampled populations. Twelve independent simulations were performed of each K

to check for consistency across runs. The preliminary results were assessed using the Evanno method where the most likely K was determined by the distribution of ΔK . The second run was then focused on the most likely range of K as inferred by the first step, in this case with K ranging from 2 – 6, this time with a burn-in of 200 000 and 500 000 MCMC iterations. Again we performed 12 independent simulations. We used STRUCTURE HARVESTER and the Evanno method to post-process the final results.

The R package HIERFSTAT (Goudet 2005) was used to estimate pairwise and overall F_{ST} among the sampled populations with 95% confidence intervals (CI); if the 95% CI do not include zero the estimate is regarded as significantly different from zero at P=0.05. A transformation of F_{ST} (i.e. $\hat{F}_{ST} = F_{ST} / (1-F_{ST})$) was used instead of F_{ST} in the analyses including geographic distance. According to Rousset (1997), this transformation is linear with distance in a one-dimensional landscape, which is likely to be a reasonable approximation for the study populations (see Fig. 1). $\hat{F}_{ST}$ was related to factors such as geographic distance, types of populations compared (i.e. mainland-mainland, mainland-island or island-island) using the software R (R Development core team 2006). The global model included pairwise $\hat{F}_{ST}$ as a response variable and geographic distance, types of populations compared and the interaction between the two as explanatory variables. We ran LM (linear models; procedure lm()) in R to obtain parameter estimates for different models nested within the global model. We used the intercepts, slopes, and residuals from these models (in ways described in detail below) to examine the expected level of genetic differentiation at very short distances (i.e. distance ≈ 0 km), the relationship between distance and genetic differentiation (i.e. "isolation by distance"), and to construct significance tests for differences in intercepts and slopes, respectively. Importantly, inter-dependence of data points is an inherent property of analyses of population structure because pairwise estimates are usually obtained, resulting in each

283 population being included x-1 times (where x is the total number of populations) in the
284 analyses. Consequently, the use of tests of significance from traditional LMs was
285 inappropriate as the data violated the basic assumption of independence of data points (see
286 e.g. Underwood 1997). To obtain a significance test of a model allowing for inter-dependence
287 of data points in the analyses we therefore extracted the test-statistic F from the model based
288 on the estimated pairwise $\hat{F}_{ST}$ -matrix, and compared this with the distribution of test-statistics
289 F obtained when rows and columns in this matrix were randomized 5000 times. The level of
290 significance was equal to the number of randomizations giving an F higher than the one
291 estimated from the actual data. Our approach is similar to the procedure used in Mantel tests
292 (Mantel 1967) but has better flexibility in the patterns of genetic differentiation that can be
293 examined.
294 Furthermore, to examine which intercepts and slopes for the relationships between
295 geographic distance and types of populations compared (i.e. mainland-mainland, mainland-
296 island or island-island) were significant and at the same time allow for inter-dependence of
297 data points in the analyses we extracted from the global model either the intercept or slope for
298 each type of populations compared, respectively. The residuals from each of these regression
299 lines were randomized and bootstrapped 10000 times, and for each round of bootstrapping we
300 calculated the difference between groups. If the 95% confidence interval of the distribution of
301 differences generated in this way did not include zero the slopes differed significantly from
302 each other ($P < 0.05$). Similarly, the intercepts for each type of populations compared were
303 tested against each other by calculating the difference in intercepts for the groups obtained in
304 each round of bootstrapping. If the 95% confidence interval of the distribution of differences
305 did not include zero the intercepts were significantly different ($P < 0.05$). The significance of
306 any differences in mean pairwise F_{ST} of different groups of populations was determined in the

same way, by running a LM in R that included only the population type as an explanatory variable. The residuals from each of these intercepts were randomized and bootstrapped 10000 times, and for each round of bootstrapping we calculated the difference in intercept (i.e. mean F_{ST}) between groups to obtain 95% confidence intervals of the distribution of differences. If the 95% confidence interval of the distribution of differences did not include zero the means were significantly different ($P < 0.05$).

There has recently been a discussion about the suitability of using F_{ST} as a measure of genetic population differentiation (e.g. Jost 2008). To examine whether our choice of measure for genetic population differentiation affected our results and conclusions we estimated D_{ST} using the SMOGD software (Crawford 2012) and carried out analyses on genetic structure using D_{ST} instead of F_{ST}. The correlation between F_{ST} and D_{ST} was strongly positive ($r = 0.972$, $P << 0.001$) and results based on D_{ST} were similar to results based on F_{ST}; analyses using D_{ST} as a measure of genetic population differentiation are presented in Appendix E, Electronic Supplementary Material.

Results

Intra-population genetic variation

The level of genetic variation varied within house sparrow populations along the coast of middle- and northern Norway (Table 1). Allelic richness and gene diversity was considerably lower in the Aldra population than in any of the other populations (Table 1). This was probably due to recent colonization and subsequent high level of inbreeding in this island population (see Discussion). In the other populations allelic richness ranged from 7.77 to 9.22, and gene diversity ranged from 0.775 to 0.823 (Table 1).

331 Allelic richness was lower in island populations (mean: 8.15, SD = 1.04, n = 9) than in
332 mainland populations (mean: 8.92, SD = 0.30, n = 5), but due to the large variance in allelic
333 richness among island populations (when Aldra was included) this difference was not
334 significant ($F = 2.546$, df = 1, $P = 0.137$). When pooling all populations, there was a non-
335 significant tendency that allelic richness decreased with increasing latitude ($\beta = -0.270$ (SE =
336 0.168), $F = 2.565$, df = 1, $P = 0.135$) and increased with population size ($\beta = 0.007$ (SE =
337 0.003), $F = 4.182$, df = 1, $P = 0.063$). There were no differences between island and mainland
338 populations in the effects of either latitude (interaction: $F = 0.586$, df = 1, $P = 0.462$) or
339 population size (interaction: $F = 2.208$, df = 1, $P = 0.168$) on allelic richness.
340 Island populations tended to have lower levels of gene diversity compared to mainland
341 populations (Table 1) but this difference was not significant ($F = 1.368$, df = 1, $P = 0.265$). No
342 significant proportion of variation in gene diversity among populations was explained by
343 latitude ($F = 0.964$, df = 1, $P = 0.345$). In contrast, there was a significant positive relationship
344 between population size and gene diversity ($\beta = 2.2*10^{-4}$ (SE = $9.5*10^{-5}$), $F = 5.176$, df = 1, P
345 = 0.042). There were no differences in effects of either latitude (interaction: $F = 0.488$, df =
346 1, $P = 0.501$) or population size (interaction: $F = 2.985$, df = 1, $P = 0.115$) on gene diversity in
347 island and mainland populations.
348 Because of the special demographic history of the Aldra population (Billing et al.
349 2012) this population had considerably lower allelic richness and gene diversity compared to
350 the other populations (Table 1). To examine whether inclusion of this particular population
351 affected our results we re-ran the above analyses after Aldra was excluded. Island populations
352 then had significantly lower allelic richness than mainland populations, but the significant
353 relationship between gene diversity and population size disappeared (see Appendix D,
354 Electronic Supplementary Material). The reason for the counter-intuitive result that allelic

355 richness was significantly different when the population with lowest allelic richness was
356 removed is that inclusion of the Aldra population caused not only a reduction of the mean but
357 also an almost three-fold increase in the standard deviation and standard error of the island
358 populations' mean allelic richness (see Table 1 and Appendix D, Electronic Supplementary
359 Material).
360
361 *Genetic signatures of population bottlenecks*
362 The majority of island populations had a significant heterozygosity excess, which is likely to
363 indicate a previous population bottleneck (Table 1). On the other hand, none of the mainland
364 populations showed significant heterozygosity excess (Table 1), suggesting that none of these
365 had gone through a recent population bottleneck. Accordingly, significantly more island
366 populations had significant signatures of population bottlenecks compared to mainland
367 populations (Fishers's exact test (two-sided): $P = 0.032$).
368
369 *Population structure*
370 The software STRUCTURE was used to examine how the sampled populations clustered
371 based on the genetic data. The preliminary STRUCTURE run indicated that the most likely
372 number of clusters was four; thus the second and more robust simulation was run with $K = 2 –$
373 6. However, in the latter analysis the results suggested that the most likely number of clusters
374 was three (Fig. 2). Both island and mainland populations were included in two of these
375 clusters, whereas the third cluster included only the island population Aldra (Fig. 2). The
376 geographic delimitation of the two large clusters was between Vikna (Pop. nr 7) and
377 Storfosna/Ørlandet (Pop. nr 8 and 13) (see Fig. 1).

Genetic differentiation among populations

The level of genetic differentiation between house sparrow populations along the coast of middle- and northern Norway was low to moderate (Fig. 3; Appendix C, Electronic Supplementary Material), with an overall F_{ST} of 0.0253 (95% CI: [0.0225, 0.0280]). Aldra (Pop. nr 3) and Brattvåg (Pop. nr 14) showed the largest pairwise genetic differentiation (F_{ST} = 0.077), whereas Brattvåg and Harøy (Pop. nr 9) were the two most genetically similar populations (F_{ST} = 0.006). Aldra was characterized by being the most genetically differentiated population compared to all other populations, as shown by the higher mean level of pairwise F_{ST} (mean F_{ST} = 0.068, SD = 0.006) of this population. The remaining 13 populations had generally lower levels of pairwise genetic differentiation (mean F_{ST} = 0.022, SD = 0.008).

There were different levels of genetic differentiation within the three types of population groups (Fig. 3). The mean pairwise F_{ST} of mainland-mainland, mainland-island, and island-island population groups were 0.019 (SD = 0.009), 0.026 (SD = 0.016), and 0.035 (SE = 0.020), respectively. Accordingly, mean F_{ST} of the island-island population group was significantly larger than mean F_{ST} of both mainland-mainland (95% CI for difference: [-0.0294, -0.0035]) and mainland-island (95% CI for difference: [-0.0181, -0.0018] population groups. In contrast, mean F_{ST} of mainland-mainland and mainland-island population groups was not significantly different (95% CI for difference: [-0.0062, 0.0192]).

400 *Relationship between genetic differentiation and geographic distance*

401 In addition to differences in the mean level of genetic differentiation between some of the

402 three types of population groups, plots of pairwise $\hat{F}_{ST}$ against geographic distance suggested

403 also that the three types of population groups had different relationships between genetic

404 differentiation and geographic distance (Fig. 3). Accordingly, the slopes of relationships

405 between $\hat{F}_{ST}$ and geographic distance were significantly positive for mainland-mainland

406 population pairs ($\beta = 5.097*10^{-5}$, 95% CI for slope: [$4.706*10^{-5}$, $6.024*10^{-5}$]) and mainland-

407 island pairs ($\beta = 2.641*10^{-5}$, 95% CI for slope: [$1.642*10^{-5}$, $5.130*10^{-5}$]) (Fig. 3). The slope

408 did however not differ from zero for island-island pairs ($\beta = -1.185*10^{-6}$, 95% CI for slope: [-

409 $1.730*10^{-5}$, $3.866*10^{-5}$]) (Fig. 3).

410 Furthermore, the slopes of relationships between $\hat{F}_{ST}$ and geographic distance was

411 significantly more steep for mainland-mainland population pairs than for island-island pairs

412 (95% CI for difference: [$-6.845*10^{-5}$, $-1.119*10^{-5}$]) (Fig. 3). In addition, the slopes between

413 mainland-mainland populations and mainland-island populations differed significantly (95%

414 CI for difference: [$1.441*10^{-5}$, $4.937*10^{-5}$]) (Fig. 3). On the other hand, the slopes did not

415 differ significantly between mainland-island populations and island-island populations (95%

416 CI for difference: [$-4.612*10^{-5}$, $1.919*10^{-5}$]) (Fig. 3). This suggests that the genetic

417 differentiation between house sparrow populations on the mainland increased more rapidly

418 with geographic distance than the genetic differentiation among island populations.

419 The intercepts for relationships between $\hat{F}_{ST}$ and geographic distance were also

420 significantly different when comparing relationships for mainland-mainland and island-island

421 populations (95% CI for difference: [-0.0522, -0.0049]) and for mainland-island and island-

422 island populations (95% CI for difference: [-0.0289, -0.0026)) (Fig. 3). For mainland-

mainland and mainland-island populations the slopes were not significantly different (95% CI for difference: [-0.0104, 0.0360]). This suggests that despite a steeper increase with distance, the genetic differentiation between mainland populations was smaller than between island populations at short distances.

Similar results were obtained when the island Aldra was excluded from the analyses (Appendix F, Electronic Supplementary Material) and when D_{ST} was used as measure of genetic differentiation instead of F_{ST} (Appendix E, Electronic Supplementary Material).

Discussion

Genetic diversity of house sparrows along a latitudinal gradient of the coast of middle and northern Norway tended to be lower in island populations compared to mainland populations but were not significantly different (Table 1). However, significantly more island than mainland populations showed genetic signatures of population bottlenecks (Table 1). Three genetic clusters were identified, broadly defining a northern and a southern genetic group of house sparrows and one cluster corresponding to the recently colonized island population Aldra (Fig. 2). Island and mainland house sparrow genetics was found to be affected differently by geographic distance, with island populations having significantly higher levels of genetic differentiation than mainland populations especially at shorter distances (Fig. 3). In addition, there was a significantly steeper slope for the relationship between genetic differentiation and geographic distance among mainland populations than among island populations (Fig. 3). These results suggest that different population genetic processes are important on islands compared to the mainland for the northern house sparrow.

Genetic diversity within populations

Even though intra-population allelic richness was not dependent on population size, it was generally lower in the island populations than in mainland populations, probably because bottlenecks were more common on islands (Table 1). The average allelic richness did however not differ significantly between island and mainland populations when all islands were included in the analyses. Interestingly, this seemed to be due to the large variation among islands in allelic richness, which was almost three times the variation among mainland populations. Without the island population Aldra, with a very recent and strong population bottleneck (see below) and hence particularly low allelic richness (Table 1), there was a significant difference in allelic richness between islands and mainland populations (Appendix D, Electronic Supplementary Material). This may suggest that differences between island populations in their recent population history may be a reason for the large inter-island variation in allelic richness (Table 1). In any case, the tendency that allelic richness was lower in island populations compared to mainland populations likely reflects the characteristics of island populations which result from founder effects (effectively a bottleneck event; e.g. Nei *et al.* 1975) and genetic drift and is in concordance with studies of other island populations such as the common shrew (White and Searle 2007). Accordingly, Hartl and Prucek (1994) demonstrated that documented bottlenecked populations had lower proportions of polymorphic loci than populations without such events reported. Depletion of intra-population genetic variation has been found for example in bighorn sheep (*Ovis canadensis mexicana)* after a founder event (Hedrick *et al*. 2001), and in blackspot sea bream *(Pagellus bogaraveo)* after a population bottleneck event (Stockley *et al*. 2005). In birds lower genetic diversity has been found e.g. in island populations of the South Island robins than in mainland populations of the same species (Boessenkool *et al.* 2007). Lower levels of genetic variation on islands is

however not always the case: although trumpeter finch populations on the Canary Islands showed evidence of bottlenecks they did not show lower levels of genetic variation than populations in Africa or on the Iberian Peninsula (Barrientos *et al.* 2009). Furthermore, when studying the species complex of silver-eyes Clegg *et al.* (2002) found that genetic drift was more important in reducing the genetic diversity on island populations than the founding events. These inter-specific differences, and the relatively large intra-specific differences within and between island and mainland populations in our study, suggest that it is important to consider e.g. time since colonization and the effective size of the population after colonization when interpreting differences in levels of genetic variation among populations.

The similar levels of gene diversity in island and mainland populations (Table 1) is to be expected because allelic diversity is a more sensitive indicator of changes in population size than gene diversity (i.e. expected heterozygosity): rare alleles are easily lost during periods of low population size but take a relatively long time to be re-introduced to the population through mutation or gene flow, whereas the level of heterozygosity is less affected by the number of alleles (Nei *et al.* 1975). The only exception to this pattern was the population on the island of Aldra, where also gene diversity was lower than on adjacent islands (Table 1; see also Jensen *et al.* 2007). The house sparrow was extinct on Aldra from the mid 1980's to 1998 when one female and three males re-colonized the island (Billing *et al.* 2012). Subsequent immigration to this island population has been relatively low and the level of inbreeding is high (Billing *et al.* 2012). This island thus provides an example that gives further evidence for the importance of founder effects for the genetics of populations on islands. Similarly, a global study of genetic variation in house sparrows demonstrated lower levels of genetic variation in a recently founded non-insular population in Kenya than in European and American populations (Shrey *et al.* 2011).

These results indicate the vulnerability of island populations or, more generally, isolated and recently founded populations to rapid environmental changes due to the decreased genetic variability. Because genetic variability is the key to long-term population viability, the observed reduced variation may decrease the viability of island populations (Fox and Wolf 2006, Willi *et al.* 2006). Furthermore, reduced variability combined with a higher degree of isolation to adjacent populations can lead to a situation where reduced gene flow does not counteract the effects of genetic drift so that the intra-population genetic diversity is further reduced.

Genetic differentiation between populations

Island populations had higher levels of inter-population genetic differentiation than mainland populations, in particular at short geographic distances (Fig. 3). However, the level of genetic differentiation between mainland populations increased faster with geographic distance than what was observed between island populations (Fig. 3). We suggest that this may reflect the special features of the genetics of island populations, as there is likely to be variation between island and mainland populations in the relative importance of different population genetic processes.

The higher average values of F_{ST} on islands especially at shorter and average distances (Fig. 3) are likely to be a result of the founder effect (see e.g. Louette *et al*. 2007), lower levels of gene flow (White and Searle 2007) and increased genetic drift due to lower population sizes and increased levels of inbreeding (Ellstrand and Elam 1993). Accordingly, genetic signatures of recent population bottlenecks were found for many of the island populations but none of the mainland populations in this study (Table 1). Furthermore, many of the island populations in this study are relatively small and may thus display the combined

519 effects of genetic drift and inbreeding. In accordance with this, relatively high levels of
520 inbreeding (Billing *et al.* 2012, Jensen *et al*. 2007) and low effective population sizes (Engen
521 *et al.* 2007) were found in some of the insular house sparrow populations included in this
522 study. In addition, the effects of isolation may be enhanced by a strong barrier to gene flow,
523 like water (Hayes and Sewlal 2004). Previous studies of house sparrow populations in the
524 same area have shown that there are low levels of dispersal between the island populations;
525 natal dispersal predominates and only approx. 10% of all recruits are dispersers (Altwegg *et*
526 *al.* 2000, Pärn *et al.* 2009, 2012). Dispersal distances are also short, with approx. 60% of
527 dispersers moving less than ca. 13 km (Tufto *et al.* 2005). In accordance with this the results
528 of Kekkonen *et al.* (2011a) who studied the genetic structure of house sparrows in mainland
529 Finland, which represent a comparably continuous suitable habitat, showed much lower levels
530 of genetic differentiation than we found in mid- and northern Norway. It is thus likely that the
531 impact of geographic barriers represented by open water overrule the effect of geographic
532 distance, resulting in a reduced slope among island populations despite the overall higher
533 divergence. Previous studies on house sparrows in northern Norway also suggest the
534 existence of an interaction between dispersal rate and population size which result in lower
535 levels of gene flow when populations are small (Pärn *et al.* 2012). Accordingly, the level of
536 genetic differentiation among Finnish house sparrow populations increased three-fold after
537 strong declines in abundance from the 1980s to 2009, probably because reduced population
538 sizes resulted in fewer migrants (Kekkonen *et al.* 2011b). Genetic drift (Engen *et al.* 2007)
539 and inbreeding (Jensen *et al.* 2007) increase in small insular house sparrow populations in
540 northern Norway. In combination, these results may indicate that the effects of gene flow,
541 bottleneck events, genetic drift and inbreeding may be more conspicuous on islands than on
542 the mainland.

543 The island of Aldra stood out also in the analysis of population differentiation. It
544 differed markedly from all other populations included in this study (Fig. 2, 3; Appendix E,
545 Electronic Supplementary Material). This relatively extreme genetic differentiation compared
546 to the other populations (identified as a separate genetic cluster; mean pairwise F_{ST} = 0.068
547 between Aldra and other populations) can be explained by the founder effect, as only four
548 individuals formed the genetic basis for the current population in 1998 (Billing *et al.* 2012).
549 Similarly, a global study of genetic variation in house sparrows demonstrated a particularly
550 high level of genetic differentiation between a recently founded population in Kenya and
551 European and American populations (Shrey *et al.* 2011). A newly founded population
552 represents a random sample of the source population (Slatkin 1996) and especially if it is
553 colonized by a few individuals it should have relatively high levels of F_{ST} when compared to
554 other populations. Despite some immigration to the island after the colonization event (Billing
555 *et al.* 2012) the levels of inbreeding (Billing *et al.* 2012) and genetic drift (Engen *et al.* 2007)
556 in this population were high and sufficient to maintain a high level of genetic differentiation.
557 Available evidence from local contacts at many of the sample localities indicate that house
558 sparrows have been present for many years prior to sampling, but with varying population
559 sizes. Furthermore, the population sizes on two of the other relatively small island populations
560 (Hestmannøy and Gjerøy) have fluctuated between approx. 35 and 145 individuals since 1993
561 (Jensen *et al.* 2007, Jensen *et al.* unpublished results, Sæther *et al.* 1999,). Although our
562 analyses indicate that many of the other island populations have gone through population
563 bottlenecks (Table 1), the genetic clustering analyses (Fig. 2) and estimates of pairwise
564 genetic differentiation (Fig. 3) suggest that they were not as recent and extreme as the one on
565 Aldra.

566 The mainland is in general considered to provide more continuous favorable habitat or
567 corridors (Chetkiewicz *et al.* 2006), which facilitates migration. Consequently, higher levels
568 of gene flow can homogenize genetic variation among populations (Aars and Ims 1999,
569 Ellstrand and Elam 1993, Kekkonen *et al.* 2011a). This can result in a steeper slope among
570 mainland populations with geographical distance whereas in islands other factors (like genetic
571 drift) are more important in creating structure. However, topography may create natural
572 geographical barriers to migration on the mainland (Forman 1995) and especially in modern
573 times the mainland habitats are constantly being fragmented due to human activities (Fischer
574 and Lindenmayer 2007, Vellend *et al*. 2006). Humans may cause increased fragmentation of
575 house sparrow populations because the size and distance between high-quality habitat pathces
576 (i.e. dairy farms) increase as small farms close down and agricultural practices are intensified
577 (Hole *et al.* 2002, Kekkonen *et al.* 2011b, von Post et al. 2012). As a consequence of such
578 human-caused habitat loss and fragmentation, mainland habitats have been suggested to start
579 to resemble archipelagos more than large, continuous habitats (MacArthur and Wilson 2001,
580 but see e.g. Haila 2002). The landscape along the Norwegian coast mainly consists of
581 mountains and fjords, which provide natural barriers to gene flow. For example, some sort of
582 barrier seems to exist between the populations Stofosna/Ørlandet and Vikna (Fig. 1) as
583 populations north and south of this area cluster together genetically (Fig. 2). The landscape
584 corresponding to the division between these clusters is characterized by barren mountainous
585 country with little human habitation, likely providing a strong barrier to gene flow. The higher
586 level of differentiation among island populations than among mainland populations
587 nevertheless suggests that the open stretches of water are in general stronger barriers to gene
588 flow than topography on mainland (see e.g. Hayes and Sewlal 2004). This is in accordance
589 with theories in the field of island biogeography, which predict lower colonization rates of

590 new species to true islands than to empty patches on the mainland (MacArthur and Wilson
591 2001).
592
593 *Implications to conservation biology*
594 Increased levels of genetic structuring between island compared to mainland populations on
595 relatively short spatial and temporal scales has been demonstrated in mammals (e.g. Naitoh
596 and Ohdachi 2006; White and Searle 2007), plants (e.g. Yeh and Hu 2005), threatened birds
597 (Boessenkool *et al.* 2007) and now the widespread house sparrow (current study), suggesting
598 that this may be a general pattern, and consequently that short-term evolutionary processes
599 may be faster on islands. Importantly, we have shown that geographic distance may affect
600 genetic differentiation among island populations differently than genetic differentiation
601 among mainland populations. Showing how population genetic processes act to shape genetic
602 variability on an ecological time scale in different types of populations is important because
603 we need to know to what extent small and fragmented populations are able to cope with
604 environmental stochasticity and evolve in response to changes in the environment (Frankham
605 1996, 2005, Parmesan 2006, Willi *et al.* 2006, 2007). A better understanding of the distinct
606 genetic characteristics of island populations and how these affect population viability will for
607 example help us to better manage threatened populations, which are often fragmented and
608 isolated.
609

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847 Data accessibility

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849 The microsatellite genotype data for individual birds in the different populations are deposited
850 in the Dryad depository: doi: 10.5061/dryad.jt85h. A matrix consisting of geographic
851 distances between populations can be found in Appendix A, Electronic Supplementary
852 Material.

Figure legends

Figure 1. Map showing the sampled house sparrow populations along the coast of Norway. Open circles show the mainland populations (n = 5), whereas arrows point to island populations (n = 9). Populations are numbered from north to south within each type (see Table 1). Inter-population distances range from 6 to 543 km.

Figure 2. Estimated population structure in house sparrow along the coast of Norway. Each sampled individual is represented by a thin vertical line, which is partitioned into three segments (black, grey and white) representing the individual's relative membership in the three genetic clusters defined by STRUCTURE. Numbers correspond to populations as defined in Table 1 and are ordered from north to south.

Figure 3. The relationships between genetic differentiation ($\hat{F}_{ST} = F_{ST}/(1-F_{ST})$) and geographic distance (km) for house sparrow populations along the coast of middle- and northern Norway accounting for types of population groups (data from Aldra was excluded, see text for details). Black dots show estimated $\hat{F}_{ST}$ for pairwise mainland-mainland populations, open circles show the $\hat{F}_{ST}$-values for mainland-island populations, and black triangles show $\hat{F}_{ST}$-values for island-island populations. Lines indicate linear regression lines for the three different population groups. Note the steeper slope for mainland populations (solid line; $y = 0.005 + x * 5.097*10^{-5}$), and the relatively high general level of $\hat{F}_{ST}$ for island

874 populations (dashed line; $y = 0.037 + x * -1.185*10^{-6}$). The dotted line shows the regression

875 for island-mainland populations ($y = 0.021 + x * 2.641*10^{-5}$).

876 **Table 1.** Name and number of the different house sparrow populations. The numbers correspond to numbers in Fig. 1. Coordinates are
877 given as mean coordinates of all sub-coordinates within each main locality as degrees north (North) and east (East). Population type
878 indicates whether the population is located on the mainland or on an island. The number of sampled individuals from each population
879 is given by Sampled n. The estimated adult population size (Estimated N) and the proportion sampled (Prop. sampled) were estimated
880 based on the following methods indicated by superscripts: 1) Capture, re-capture and re-sighting of previously ringed individuals, 2)
881 Observation during sampling, 3) Estimate from Skjelseth *et al.* 2007. Allelic richness and gene diversity (i.e. expected heterozygosity)
882 was calculated using FSTAT. Allelic richness was calculated as the mean across loci where locus-specific allelic richness was
883 calculated using rarefaction and n=23 as minimum sample size. P-values for genetic signatures of bottlenecks based on heterozygote
884 excess are also provided; $P < 0.05$ in bold. (§ Sampled in February-March, * Sampled in May-July.)

Pop. Nr	Pop. name	Pop. type	North	East	Sampled n	Estimated N		Prop. sampled	Allelic richness	Gene diversity	Bottle-neck
1	Gjerøy	Island	66.622	13.02	32	46	1*	0.70	8.20	0.789	0.068
2	Hestmannøy	Island	66.545	12.846	43	114	1*	0.38	8.39	0.793	**0.021**
3	Aldra	Island	66.401	13.108	23	34	1*	0.68	5.53	0.708	**0.001**
4	Løkta	Island	66.167	12.732	48	145	2*	0.33	8.51	0.800	0.151
5	Vega	Island	65.655	11.963	48	146	1§	0.33	7.77	0.793	**0.000**
6	Leka	Island	65.088	11.675	49	114	1§	0.43	8.75	0.823	**0.000**
7	Vikna	Island	64.913	11.001	49	244	3§	0.20	8.83	0.814	**0.009**
8	Storfosna	Island	63.67	9.407	49	92	2*	0.53	8.50	0.775	0.555
9	Harøya	Island	62.764	6.459	49	152	2*	0.32	8.85	0.807	**0.021**
10	Helgeland	Mainland	66.454	13.086	54	74	2*	0.73	9.09	0.805	0.281
11	Leirfjord	Mainland	66.085	12.96	50	134	2*	0.37	8.69	0.811	0.054
12	Brønnøysund	Mainland	65.531	12.285	45	200	2*	0.23	8.51	0.801	0.094
13	Ørlandet	Mainland	63.716	9.658	48	300	2*	0.16	9.22	0.813	0.533
14	Brattvåg	Mainland	62.599	6.555	49	150	2*	0.33	9.08	0.802	0.281
				Total	636	2245					

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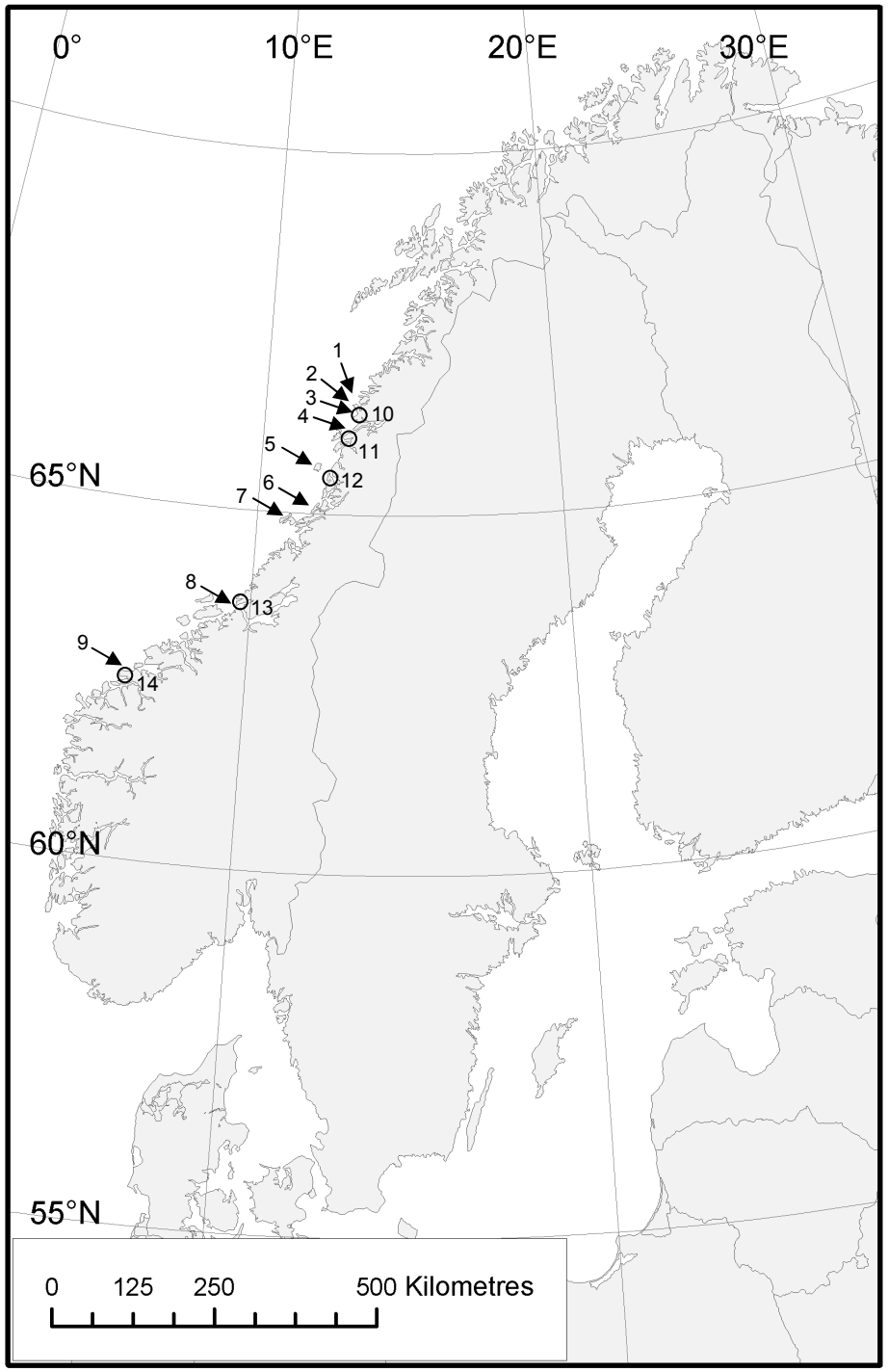
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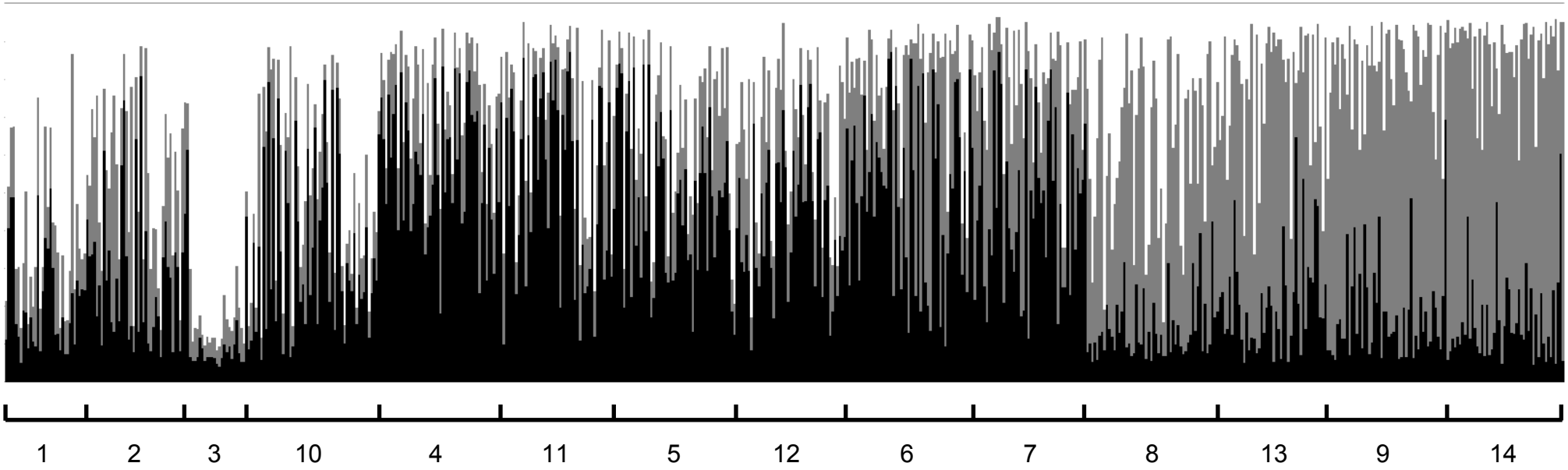
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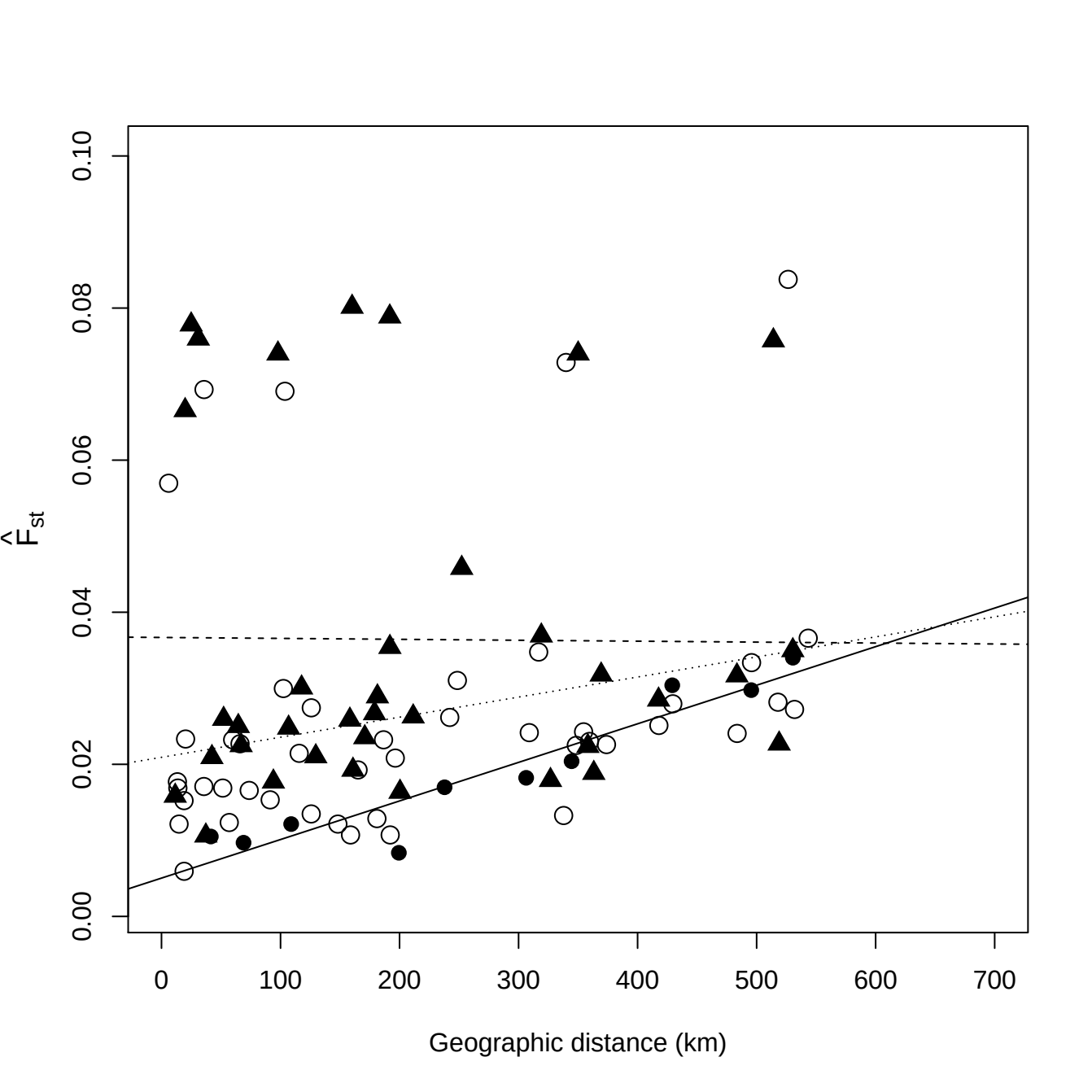
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Geographic distance (km)

Electronic Supplementary Material

Appendix A

Geographic distance matrix

Table S1. Semi matrix consisting of distances (km) between the study populations. The distance matrix was calculated using mean coordinates at sub-localities within each main locality. Population numbers refer to Fig. 1 and Table 1. The distance between populations ranged from 6 km to 543 km.

	1	2	3	4	5	6	7	8	9	10	11	12	13
2	12												
3	25	20											
4	52	42	31										
5	118	107	98	67									
6	181	171	160	130	65								
7	211	200	192	161	94	37							
8	369	358	350	319	252	192	158						
9	530	519	514	483	418	363	327	179					
10	19	15	6	36	102	165	196	355	518				
11	60	51	36	14	66	126	159	317	484	41			
12	126	116	104	74	20	57	91	249	418	109	69		
13	360	348	340	309	242	181	148	13	192	345	306	238	
14	543	532	526	496	430	374	338	187	19	530	495	429	199

Appendix B

Details concerning microsatellite genotyping

Each sampled individual was genotyped at 21 microsatellite loci by PCR amplification. PCR was carried out separately for each locus. Each reaction mixture (10 μL) included approximately 20 mM $(NH_4)_2SO_4$, 75 mM Tris-HCl (pH 8.8), 0.15 mg mL^{-1} DNAse free BSA, 10mM β-mercaptoethanol, 2.5 mM $MgCl_2$, 0.6 μM of each primer, and approximately 20 ng of genomic DNA. In addition, each PCR mixture contained 0.14mM dNTPs (Promega, USA) and 0.5 units of GoTaq polymerase (Promega, USA). Cocktails of 6 to 8 PCR-products were made (***Mix1:*** Ase18, HrU5, Pdoμ1, Pdoμ5, Pdoμ6, Pdo10, Pdo30. ***Mix2:*** Fhu2, INDIGO41, Mcyμ4, Pdoμ3, Pdoμ4, Pdo36. ***Mix3:*** Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo44, Pdo47). To each cocktail a size ladder (GeneScan LIZ 600, Applied Biosystems, USA) and a Hi-Di Formamide solution were added (Applied Biosystems, USA). Products were separated by electrophoresis in an automated 16 capillary electrophoretic analysis system: "ABI Prism 3130xl Genetic Analyzer" (Applied Biosystems, USA). To visualise alleles, reverse primers were fluorescently labelled with either FAM (Fhu2, Pdoμ1, Pdoμ5, Pdoμ6, Pdo19, Pdo22, Pdo36 and Pdo44), NED (Ase18, HrU5, Pdoμ3, Pdoμ4, Pdo16 and Pdo27), VIC (INDIGO41, Mcyμ4, Pdo10, Pdo30, Pdo32 and Pdo47) or PET (Pdo17).

After the scoring of alleles for the 21 loci in GENEMAPPER 4.0 (Applied Biosystems, USA) it was found that Pdoμ6 was extremely polymorphic (having 137 alleles). Because some of the programs can not handle markers with more than 99 different alleles this locus was excluded. Furthermore, HrU5 and Mcyμ4 gave low quality genotypes, and genotypes on these loci were thus only available for a small proportion of individuals. Moreover, the Pdoμ4-alleles were especially difficult to define and score due to a complex repeat structure (Griffith *et al.* 1999). These 3 loci were therefore also excluded prior to any

analyses. Two of the loci (Fhu2 and Pdo32) had relatively high frequency of null alleles (0.14 – 0.16) and allele frequencies deviated significantly from H-W equilibrium ($P < 0.001$). Because the inclusion of loci with null alleles in the analyses might have major effects on the results (see e.g. Lugon-Moulin *et al*. 1999), we carried out the analyses after excluding also Fhu2 and Pdo32. Hence, the analyses were carried out using information on 15 different microsatellite loci.

Table S2. Information on the 15 different microsatellite loci utilized in the analyses and the number of different alleles found at each locus is given in Table S2. N denotes the total sample size. Observed (HObs) and expected (HExp) heterozygosity were calculated using CERVUS 3.0 (Kalinowski *et al*. 2007). F(Null) denotes the expected frequency of null alleles associated with the deviation from Hardy-Weinberg equilibrium (HW) estimated using CERVUS 3.0 (Kalinowski *et al*. 2007). Significance levels: NS: No Significant deviation from HW.

Locus	Number of alleles	N	HObs	HExp	HW	F(Null)
Ase18	24	636	0.877	0.897	NS	0.011
INDIGO41	12	636	0.786	0.830	NS	0.026
Pdoμ1	17	636	0.852	0.857	NS	0.003
Pdoμ3	18	636	0.854	0.871	NS	0.009
Pdoμ5	18	636	0.877	0.875	NS	-0.001
Pdo10	16	636	0.830	0.848	NS	0.010
Pdo16	12	636	0.810	0.858	NS	0.029
Pdo17	21	636	0.885	0.893	NS	0.004
Pdo19	6	636	0.530	0.554	NS	0.027
Pdo22	13	636	0.717	0.742	NS	0.019
Pdo27	11	636	0.832	0.835	NS	0.002
Pdo30	11	636	0.676	0.690	NS	0.012
Pdo36	17	636	0.819	0.829	NS	0.006
Pdo44	15	636	0.852	0.872	NS	0.011
Pdo47	16	636	0.810	0.816	NS	0.005

Appendix C

Genetic differentiation: F_{ST} matrix

Table S3. Semi matrix consisting of genetic differentiation (F_{ST}) between all study populations (see Table 1, Fig. 1 and Fig. 2). Pairwise F_{ST} values and their 95% confidene intervals (in brackets) were calculated using the R-package HIERFSTAT (Goudet 2005).

	1	2	3	4	5	6	7	8	9	10	11	12	13
2	0.0155 (0.0083-0.0245)												
3	0.0723 (0.0521-0.0915)	0.0621 (0.0435-0.0827)											
4	0.0253 (0.0144-0.0366)	0.0204 (0.0124-0.0291)	0.0707 (0.0500-0.0909)										
5	0.0293 (0.0176-0.0419)	0.0242 (0.0160-0.0343)	0.0687 (0.0406-0.1012)	0.0219 (0.0139-0.0319)									
6	0.0280 (0.0157-0.0418)	0.0230 (0.0127-0.0356)	0.0741 (0.0534-0.0958)	0.0206 (0.0141-0.0278)	0.0245 (0.0155-0.0336)								
7	0.0255 (0.0156-0.0364)	0.0160 (0.0102-0.0226)	0.0729 (0.0504-0.0969)	0.0191 (0.0097-0.0298)	0.0175 (0.0103-0.0254)	0.0105 (0.0070-0.0136)							
8	0.0308 (0.0213-0.0420)	0.0219 (0.0156-0.0287)	0.0691 (0.0441-0.0998)	0.0356 (0.0232-0.0509)	0.0438 (0.0304-0.0595)	0.0343 (0.0234-0.0462)	0.0254 (0.0168-0.0349)						
9	0.0338 (0.0206-0.0483)	0.0222 (0.0142-0.0297)	0.0706 (0.0538-0.0886)	0.0307 (0.0191-0.0435)	0.0277 (0.0202-0.0346)	0.0186 (0.0134-0.0243)	0.0177 (0.0108-0.0254)	0.0260 (0.0177-0.0341)					
10	0.0150 (0.0088-0.0220)	0.0119 (0.0077-0.0172)	0.0536 (0.0384-0.0695)	0.0168 (0.0096-0.0245)	0.0292 (0.0191-0.0414)	0.0190 (0.0121-0.0260)	0.0203 (0.0130-0.0285)	0.0239 (0.0140-0.0349)	0.0274 (0.0200-0.0350)				
11	0.0227 (0.0149-0.0324)	0.0165 (0.0094-0.0288)	0.0651 (0.0399-0.0922)	0.0166 (0.0099-0.0257)	0.0223 (0.0148-0.0299)	0.0132 (0.0083-0.0184)	0.0107 (0.0058-0.0157)	0.0334 (0.0232-0.0482)	0.0234 (0.0157-0.0332)	0.0104 (0.0064-0.0149)			
12	0.0266 (0.0180-0.0359)	0.0210 (0.0136-0.0312)	0.0646 (0.0441-0.0884)	0.0162 (0.0101-0.0232)	0.0228 (0.0136-0.0322)	0.0123 (0.0067-0.0181)	0.0151 (0.0086-0.0209)	0.0303 (0.0173-0.0446)	0.0245 (0.0149-0.0349)	0.0119 (0.0073-0.0174)	0.0096 (0.0044-0.0155)		
13	0.0225 (0.0113-0.0352)	0.0221 (0.0130-0.0316)	0.0679 (0.0478-0.0895)	0.0236 (0.0154-0.0332)	0.0256 (0.0173-0.0344)	0.0127 (0.0082-0.0177)	0.0120 (0.0064-0.0182)	0.0175 (0.0089-0.0268)	0.0106 (0.0050-0.0193)	0.0200 (0.0109-0.0307)	0.0179 (0.0120-0.0256)	0.0167 (0.0108-0.0227)	
14	0.0352 (0.0218-0.0476)	0.0265 (0.0147-0.0387)	0.0770 (0.0565-0.0985)	0.0323 (0.0195-0.0463)	0.0271 (0.0187-0.0356)	0.0223 (0.0148-0.0332)	0.0131 (0.0086-0.0182)	0.0228 (0.0158-0.0299)	0.0059 (0.0018-0.0104)	0.0329 (0.0222-0.0444)	0.0291 (0.0167-0.0464)	0.0297 (0.0192-0.0431)	0.0084 (0.0022-0.0156)

Appendix D

Intra-population levels of genetic variation – Aldra excluded

When the Aldra population was excluded from the analyses allelic richness was lower in island populations (mean: 8.48 ± 0.36, n = 8) than in mainland populations (mean: 8.92 ± 0.30, n = 5) and this difference was significant ($F = 5.144$, $df = 1$, $P = 0.044$; model $r^2 = 0.319$). Accounting for the effect of population type there was also a tendency that allelic richness decreased with increasing latitude ($\beta = -0.117$ (SE = 0.063), $F = 3.513$, $df = 1$, $P = 0.090$). In total, population type and latitude explained 49.6% of the variance in allelic richness among populations ($r^2 = 0.496$). The non-significant decrease with latitude in allelic richness was similar for island and mainland populations (interaction: $F = 0.163$, $df = 1$, $P = 0.696$). Population size did not have any effect on allelic richness either when accounting for the effect of population type ($F = 0.808$, $df = 1$, $P = 0.390$) or not ($F = 1.817$, $df = 1$, $P = 0.205$).

When Aldra was excluded no significant proportion of variation in gene diversity among populations was explained by either latitude ($F = 0.143$, $df = 1$, $P = 0.713$) or population size ($F = 3.135$, $df = 1$, $P = 0.104$). Neither was there any significant difference in level of gene diversity in island and mainland populations ($F = 1.202$, $df = 1$, $P = 0.296$), or differences in effects of either latitude (interaction: $F = 0.058$, $df = 1$, $P = 0.815$) or population size (interaction: $F = 1.098$, $df = 1$, $P = 0.322$) in island and mainland populations.

Appendix E

Genetic differentiation among populations – analyses based on D_{ST}

Pairwise D_{ST}-values were low to moderate (Table S4), with a mean D_{ST} of 0.078 (SD = 0.048). In accordance with results for F_{ST} Aldra (Pop. nr 3) and Brattvåg (Pop. nr 14) showed the largest pairwise genetic differentiation also for D_{ST} (D_{ST} = 0.226), whereas Brattvåg and Ørlandet (Pop. nr 13) were the two most genetically similar populations (D_{ST} = 0.011). Aldra was characterized by being the most genetically differentiated population compared to all other populations, as shown by the higher mean level of pairwise D_{ST} (mean D_{ST} = 0.177, SD = 0.030) of this population compared to the remaining 13 populations (mean D_{ST} = 0.061, SD = 0.024).

D_{ST} also showed different levels of genetic differentiation within the three types of population groups. Accordingly, mean pairwise D_{ST} of mainland-mainland, mainland-island, and island-island population groups were 0.053 (SD = 0.032), 0.070 (SD = 0.044), and 0.094 (SE = 0.052), respectively. Two of these differences were significant: mean D_{ST} of the island-island population group was significantly larger than mean D_{ST} of both mainland-mainland (95% CI for difference: [-0.1611, -0.0162]) and mainland-island (95% CI for difference: [-0.0887, -0.0086] population groups. In contrast, mean D_{ST} of mainland-mainland and mainland-island population groups was not significantly different (95% CI for difference: [-0.0304, 0.1112]).

Table S4. Semi matrix showing genetic differentiation (D_{ST}) between all study populations. Pairwise D_{ST} values were calculated using the software SMOGD (Crawford 2010).

	1	2	3	4	5	6	7	8	9	10	11	12	13
2	0.037												
3	0.189	0.166											
4	0.062	0.055	0.183										
5	0.077	0.068	0.138	0.066									
6	0.069	0.050	0.214	0.059	0.072								
7	0.074	0.048	0.193	0.044	0.048	0.036							
8	0.080	0.068	0.149	0.094	0.125	0.099	0.067						
9	0.094	0.070	0.212	0.095	0.095	0.065	0.053	0.080					
10	0.036	0.035	0.138	0.035	0.081	0.056	0.062	0.054	0.099				
11	0.068	0.047	0.147	0.048	0.063	0.040	0.024	0.112	0.081	0.029			
12	0.071	0.058	0.161	0.046	0.052	0.028	0.041	0.072	0.073	0.030	0.021		
13	0.052	0.059	0.182	0.068	0.081	0.034	0.028	0.034	0.022	0.053	0.054	0.047	
14	0.098	0.072	0.226	0.095	0.082	0.077	0.037	0.076	0.012	0.105	0.082	0.097	0.011

Relationship between genetic differentiation and geographic distance

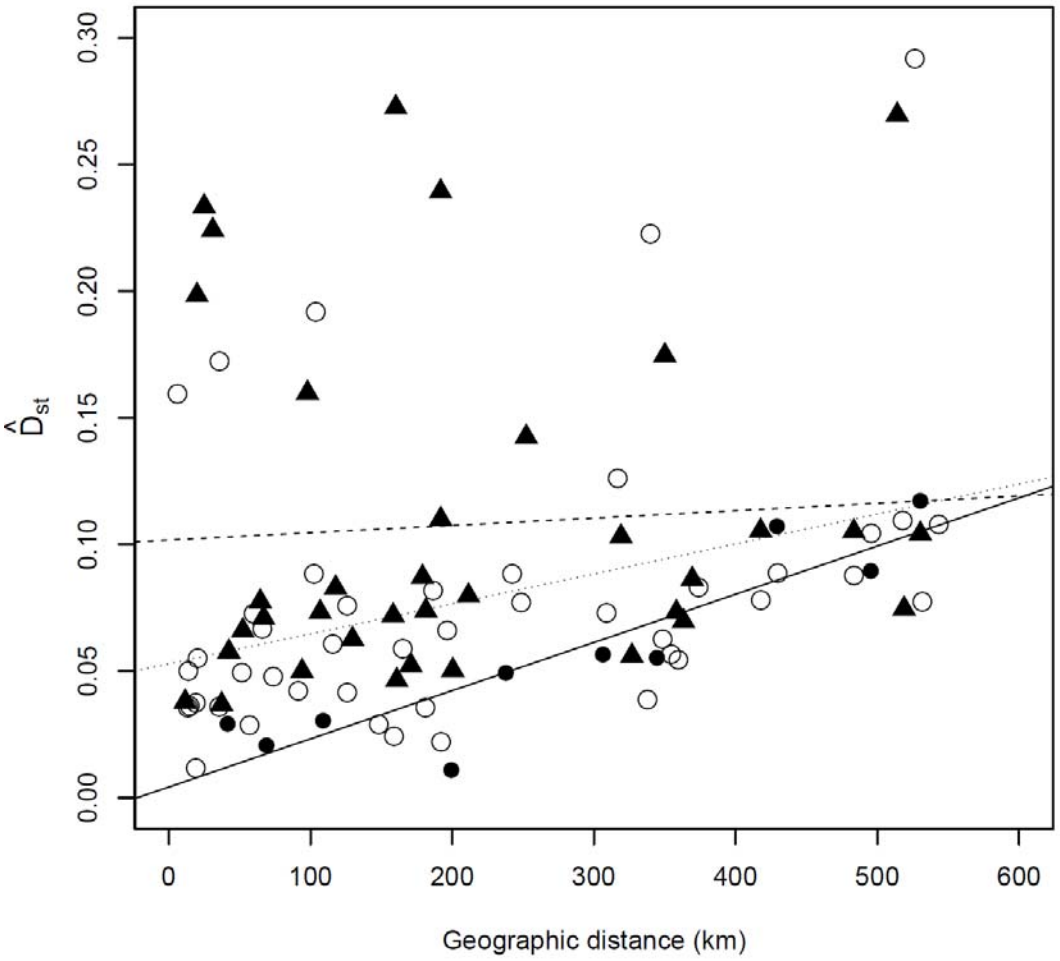
The slopes of relationships between $\hat{D}_{ST}$ and geographic distance were significantly positive for mainland-mainland population pairs ($\beta = 1.901*10^{-4}$, 95% CI for slope: [$1.710*10^{-4}$, $2.366*10^{-4}$]) and mainland-island pairs ($\beta = 1.182*10^{-4}$, 95% CI for slope: [$8.801*10^{-5}$, $1.922*10^{-4}$]) (Fig. S1). The slope did however not differ from zero for island-island pairs ($\beta = 2.902*10^{-5}$, 95% CI for slope: [$-2.015*10^{-5}$, $1.510*10^{-4}$]) (Fig. S1). Furthermore, the slopes of relationships between $\hat{D}_{ST}$ and geographic distance was significantly more steep for mainland-mainland population pairs than for island-island pairs (95% CI for difference: [$-2.143*10^{-4}$, $-2.936*10^{-5}$]) (Fig. S1). In addition, the slopes between mainland-mainland populations and mainland-island populations differed significantly (95% CI for difference: [$3.740*10^{-5}$, $1.572*10^{-4}$]) (Fig. S1). On the other hand, the slopes did not differ significantly between mainland-island populations and island-island populations (95% CI for difference: [$-1.465*10^{-4}$, $5.218*10^{-5}$]) (Fig. S1).

The intercepts for relationships between $\hat{D}_{ST}$ and geographic distance were also significantly different when comparing relationships for mainland-mainland and island-island populations (95% CI for difference: [-0.0884, -0.0071]) and for mainland-island and island-island populations (95% CI for difference: [-0.0559, -0.0051)) (Fig. S1). For mainland-

mainland and mainland-island populations the slopes were not significantly different (95% CI for difference: [-0.0222, 0.0574]).

These results are fully in accordance with results based on F_{ST} and suggest that the genetic differentiation between house sparrow populations on the mainland increased more rapidly with geographic distance than the genetic differentiation among island populations. Furthermore, the results show that the genetic differentiation between mainland populations was smaller than between island populations at short distances.

Figure S1. The relationships between genetic differentiation ($\hat{D}_{ST} = D_{ST}/(1-D_{ST})$) and geographic distance (km) for house sparrow populations along the coast of middle- and northern Norway accounting for types of population groups. Black dots show estimated $\hat{D}_{ST}$ for pairwise mainland-mainland populations, open circles show the $\hat{D}_{ST}$ -values for mainland-island populations, and black triangles show $\hat{D}_{ST}$ -values for island-island populations. Lines indicate linear regression lines for the three different population groups. Note the steeper slope for mainland populations (solid line), and the relatively high general level of $\hat{D}_{ST}$ for island populations (dashed line). The dotted line shows the regression for island-mainland populations.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$\hat{D}_{st}$
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100
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500
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Geographic distance (km)

Appendix F

Genetic population differentiation among mainland and island populations based on F_{ST} – Aldra excluded

In the following analyses, Aldra was excluded due to its extraordinary colonization history and resulting high genetic differentiation from the other populations (see Discussion). After exclusion of this population there were different levels of genetic differentiation within the three types of population groups (see Fig. S1). The mean pairwise F_{ST} of mainland-mainland, mainland-island, and island-island population groups were 0.019 (SD = 0.009), 0.021 (SD = 0.007), and 0.025 (SE = 0.007), respectively. Accordingly, mean F_{ST} of the island-island population group was significantly larger than mean F_{ST} of both mainland-mainland (95% CI for difference: (-0.0111, -0.0008)) and mainland-island (95% CI for difference: (-0.0075, -0.0006)) population groups. Mean F_{ST} of mainland-mainland and mainland-island population groups was however not significantly different (95% CI for difference: (-0.0032, 0.0068)).

Relationship between genetic differentiation and geographic distance

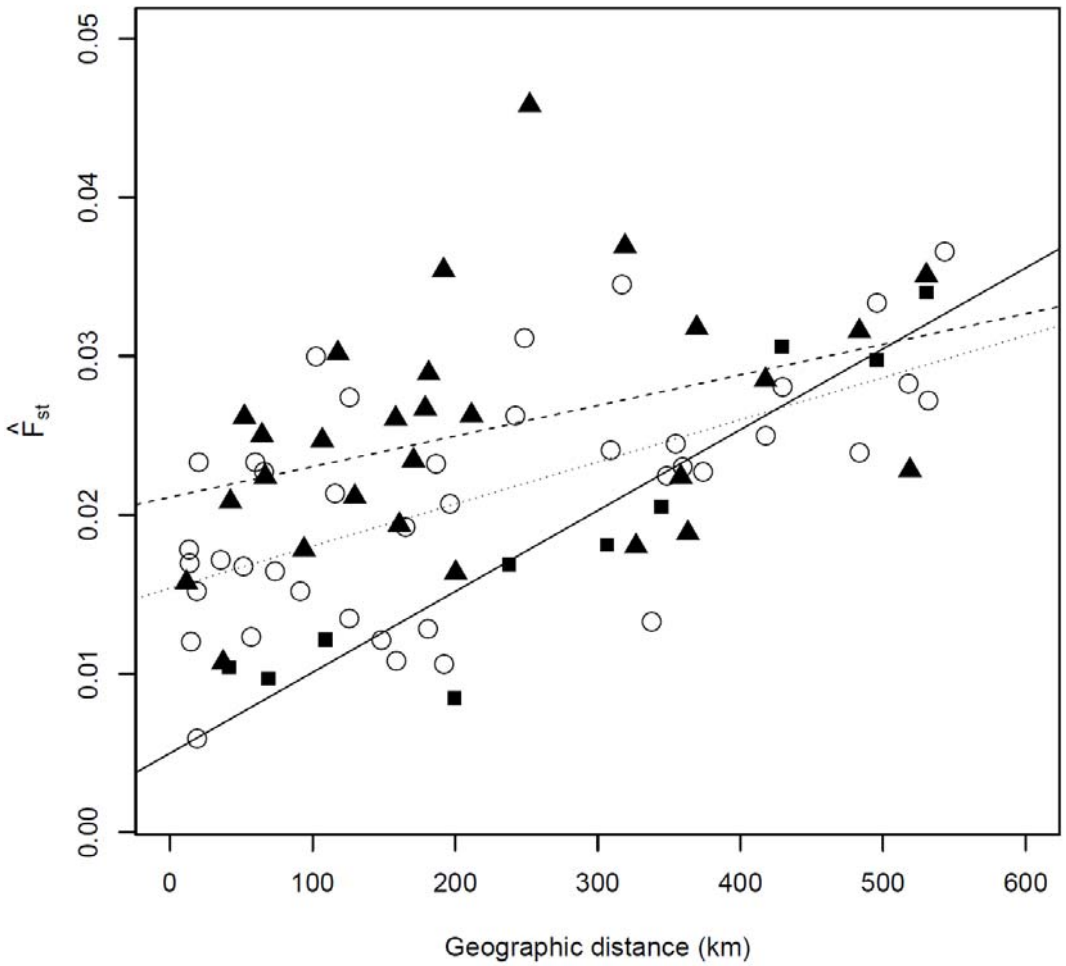
In addition to differences in the mean level of genetic differentiation between some of the three types of population groups, plots of pairwise $\hat{F}_{ST}$ against geographic distance suggested also that the three types of population groups had different relationships between genetic differentiation and geographic distance (Fig. S2).

Accordingly, the slopes of relationships between $\hat{F}_{ST}$ and geographic distance was significantly more steep for mainland-mainland population pairs than for island-island pairs (95% CI for difference: ($-5.115*10^{-5}$, $-1.067*10^{-5}$)) (Fig. S2). In addition, the slopes between mainland-mainland populations and mainland-island populations differed significantly (95% CI for difference: ($9.058*10^{-6}$, $4.005*10^{-5}$)) (Fig. S2). On the other hand, the slopes did not

differ significantly between mainland-island populations and island-island populations (95% CI for difference: ($-2.687*10^{-5}$, $1.266*10^{-5}$)) (Fig. S2). This suggests that the genetic differentiation between house sparrow populations on the mainland increased more rapidly with geographic distance than the genetic differentiation among island populations.

Furthermore, the intercepts for relationships between $\hat{F}_{ST}$ and geographic distance were significantly different when comparing relationships for mainland-mainland and island-island populations (95% CI for difference: (-0.0238, -0.0080)), for mainland-mainland and mainland-island populations (95% CI for difference: (0.0028, 0.0180)), as well as for mainland-island and island-island populations (95% CI for difference: (-0.0105, -0.0009)) (Fig. S2). This suggests that despite a steeper increase with distance, the genetic differentiation between mainland populations was smaller than between island populations at short distances.

Figure S2. The relationships between genetic differentiation ($\hat{F}_{ST} = F_{ST}/(1-F_{ST})$) and geographic distance (km) for house sparrow populations along the coast of middle- and northern Norway accounting for types of population groups (data from Aldra was excluded, see text for details). Black squares show estimated $\hat{F}_{ST}$ for pairwise mainland-mainland populations, open circles show the $\hat{F}_{ST}$-values for mainland-island populations, and black triangles show $\hat{F}_{ST}$-values for island-island populations. Lines indicate linear regression lines for the three different population groups. Note the steeper slope for mainland populations (solid line), and the relatively high general level of $\hat{F}_{ST}$ for island populations (dashed line). The dotted line shows the regression for island-mainland populations.


0.00
0.01
0.02
0.03
0.04
0.05
$\hat{F}_{st}$
0
100
200
300
400
500
600
Geographic distance (km)

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