Molecular Ecology

WILEY

MOLECULAR ECOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Host Co-Occurrence and Population Size Explain Genetic Differentiation and Diversity in Seal Lice

Ludmila Sromek[1] | Kevin P. Johnson[2] | Mervi Kunnasranta[3,4] | Aqqalu Rosing-Asvid[5] | Britt-Marie Bäcklin[6] | Aselle Tasmagambetova[7] | Adylkhan Tovassarov[7] | Olga Rusinek[8] | Heather L. Ziel[9] | Ana Rubio-García[10] | Tommi Nyman[11]

[1]Department of Marine Ecosystems Functioning, Faculty of Oceanography and Geography, University of Gdansk, Gdynia, Poland | [2]Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, Illinois, USA | [3]Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland | [4]Natural Resources Institute Finland, Joensuu, Finland | [5]Greenland Institute of Natural Resources, Nuuk, Greenland | [6]Swedish Museum of Natural History, Stockholm, Sweden | [7]Central Asian Institute for Ecological Research, Almaty, Republic of Kazakhstan | [8]Baikal Museum of the Siberian Branch of the Russian Academy of Sciences, Listvyanka, Russia | [9]Marine Mammal Laboratory, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle, Washington, USA | [10]Veterinary, Care & Research Department, Seal Centre Pieterburen Foundation, Lauwersoog, the Netherlands | [11]Department of Ecosystems in the Barents Region, Svanhovd Research Station, Norwegian Institute of Bioeconomy Research, Svanvik, Norway

Correspondence: Tommi Nyman (tommi.nyman@nibio.no)

Received: 31 May 2025 | **Revised:** 11 November 2025 | **Accepted:** 25 November 2025

Handling Editor: Michelle Wille

Keywords: coevolution | genetic diversity | host-associated genetic differentiation | host–parasite interactions | infrapopulation structure

ABSTRACT

We studied the drivers of population-genetic structuring and genetic diversity in specialist parasites based on whole-genome resequencing data from 82 *Echinophthirius horridus* seal louse individuals sampled from 12 ecologically and behaviourally different phocine seal species, subspecies and populations across the Holarctic. We found that the main genetic disjunctions in *E. horridus* lice occur across seal host species and subspecies, with a further level of population subdivision emerging among host individuals within some populations. Endemic and relict landlocked seal (sub)species host the genetically most distinct louse populations, while lice associated with sympatric marine seals show signatures of occasional gene flow across hosts. Within the latter, the most extreme case is seen in the near-panmictic lice associated with northern European grey and harbour seals, which aggregate in shared rookeries and colonies. Although the louse and seal phylogenies were overall statistically significantly congruent, evidence for similar host shifts in the past is reflected in several conflicts in the phylogenetic trees of the lice and their hosts. Population-level mean heterozygosity and theta in seal lice varied considerably, and both measures of genetic variation were statistically significantly related to host population size. Taken together, our results support a non-adaptive model of parasite diversification, in which geographic and behavioural isolation among hosts drives parasite genetic differentiation, and genetic erosion in bottlenecked hosts cascades up to their specialist parasites. Our results provide new insights into processes that generate parasite diversity and trigger parallel losses of genetic diversity in endangered host–parasite systems.

1 | Introduction

Practically every species on Earth is involved in parasitic interactions—either as a host, parasite or both (Price 1980; Lafferty et al. 2008; Jephcott et al. 2016). Because organisms with a parasitic lifestyle constitute a sizeable fraction of global biodiversity (Poulin 2014; Carlson et al. 2020), ecologists and evolutionary biologists have long sought to find the reasons for their extreme

species richness (Nylin et al. 2018; Hay et al. 2020). A potential driver of parasite diversification is specialisation to particular host species or taxa out of the ones that are available in their environment (Abrahamson and Blair 2008; Gómez et al. 2010). For obligate parasites, the host is a source of food as well as a place to live (Paterson and Banks 2001; Desdevises 2007), and many parasites have evolved sophisticated physiological, morphological and behavioural adaptations for overcoming host defences (Hayer et al. 2022; Hernandez-Caballero et al. 2022; Stoldt et al. 2022; Kolencik et al. 2024). If new hosts become colonised, divergent selection pressures between the different environments offered by alternative hosts can lead to the evolution of host-associated genetic differentiation and, eventually, to speciation in the parasite lineages (Stireman et al. 2005; Alcala et al. 2017). The importance of such adaptive processes in the diversification of parasites is suggested by observations that most host switches occur between closely related species (Johnson, Weckstein, et al. 2021; Lei et al. 2024), historical host dispersal often leads to parasite adaptive radiation (Boyd et al. 2022; Benovics et al. 2023), and different morphological traits in parasites influence their likelihood of colonising and establishing on new hosts (Clayton et al. 2003; Sweet, Bush, et al. 2018; Benovics et al. 2023).

However, genetic differentiation and diversification in parasites can also arise through non-adaptive processes. In particular, specialist parasites of widespread hosts could diversify simply through genetic differentiation in geographically isolated host populations (Whiteman et al. 2007; Štefka et al. 2011; Mazé-Guilmo et al. 2016). Over time, successive co-allopatric divergence events can even create parallel phylogenetic patterns in the hosts and parasites in the absence of true antagonistic coevolutionary interactions (Reed and Hafner 1997; Clayton et al. 2004; Desdevises 2007). Making general inferences on the relative frequency of different processes is complicated by the fact that various factors affecting parasite differentiation may act over different spatial and temporal scales (Huyse et al. 2005; Bell et al. 2016, 2018; Sweet, Boyd, et al. 2018) and that the life cycles and dispersal capabilities of parasite lineages may modulate the likelihood of both adaptive and non-adaptive host-associated differentiation (Sasal et al. 1998; Johnson et al. 2002; Sweet and Johnson 2018; Johnson, Calhoun, et al. 2021). In general, highly mobile parasites (e.g., bird louse flies; Janiszewska et al. 2025) and species having complex life histories involving one or more intermediate hosts (e.g., cestodes and acanthocephalans; Wells et al. 2019; Benesh et al. 2022; Nazarizadeh et al. 2023; Sromek et al. 2023) tend to have broader host ranges and show less genetic divergence across hosts than do dispersal-limited parasites that are transmitted directly among host individuals (e.g., amblyceran lice; Grossi et al. 2024). A further level of genetic structuring is found in directly transmitted parasites living on relatively long-lived hosts, such as lice on birds or mammals, in which even infrapopulations on different host individuals may be genetically differentiated (Koop et al. 2014; Nessner et al. 2014; Virrueta Herrera et al. 2022).

A less studied—but increasingly timely—question concerns the determinants and eco-evolutionary significance of genetic variation in host–parasite networks (Ganz and Ebert 2010; Pilosof et al. 2014; Paplauskas et al. 2025). Due to anthropogenic overexploitation and habitat destruction, many previously abundant wildlife species have experienced drastic population collapses across the globe during the last few hundred years (Bar-On et al. 2018; Greenspoon et al. 2023). These population bottlenecks are known to have decimated genetic variation in, for example, many mammals (Hedrick 2009; Hoelzel et al. 2024) and birds (Li et al. 2022). Although parasite conservation has received far less attention than that of charismatic large vertebrates (Brown et al. 2025), it is clear that many specialist parasites have become endangered along with their hosts (Lymbery and Smit 2023; Kwak et al. 2024; Gustafsson et al. 2025) and may also have experienced parallel genetic erosion during host population declines. A direct connection between host census size and parasite genetic diversity seems plausible, yet comparative tests of the hypothesis are rare, and studies done to date have provided evidence both in favour (Leonardi et al. 2019) and against (Doña and Johnson 2023; see also Strobel et al. 2019) the expectation. Understanding how, when and why genetic diversity in parasites responds to reductions in host population size is important because the outcome of coevolutionary interactions may depend on genetic variation present in interacting taxa (Ganz and Ebert 2010; Papkou et al. 2016). If genetic diversity declines at a slower rate in parasites than in hosts, parasitism could pose an additional threat to already endangered host species and populations (Ekroth et al. 2019; Gibson 2022). On the other hand, if parasites become genetically bottlenecked along with their hosts, neither participant would gain an upper hand in the arms race between parasite attack traits and host defences (Hesse and Buckling 2016).

Here, we investigated the influence of host-related features such as species identity, geographic range overlap and census population size on population-genetic divergence and diversity in the seal louse *Echinophthirius horridus*, a blood-sucking insect that parasitizes northern-hemisphere seals belonging to the phocid subfamily Phocinae. Phocine seals and their parasites make up a highly suitable system for studies on the ecology and evolution of natural host–parasite networks. Altogether 10 phocine species belonging to seven genera are found across the Holarctic region, with many of the species being further divided into geographically separated subspecies and populations (Ferguson and Higdon 2006; Rosing-Asvid et al. 2023). Marine phocines occur in mixed communities in which species differ in their ecological niches and behavioural traits (Berta et al. 2022; Ferguson et al. 2025). However, the subfamily also comprises six endemic landlocked lineages, of which the Caspian and Baikal seals have been isolated in their respective water bodies for millions of years (Palo and Väinölä 2006; Hassanin et al. 2021), while Saimaa and Ladoga ringed seals and Ungava and Iliamna harbour seals represent younger postglacial isolates (Baird 2001; Kunnasranta et al. 2021; Ferrer et al. 2024; Löytynoja et al. 2025). During the 19th and 20th centuries, many northern-hemisphere seals underwent severe population collapses due to excessive hunting and pollution-related reproductive failure (Harding and Härkönen 1999; Härkönen et al. 2012; Kovacs et al. 2012; Carroll et al. 2024). Due to these bottlenecks and physical limits for population size in landlocked seals, census sizes of phocine (sub)species and populations differ by four orders of magnitude (Kelly et al. 2010), which is largely reflected in their levels of genetic diversity (Stoffel et al. 2018; Peart et al. 2020; Löytynoja et al. 2023).

Like other seals, phocines are parasitized by a rich community of parasites consisting of, for example, nematodes, acanthocephalans, cestodes, mites and lice (Kelly et al. 2010; Walden

et al. 2020). The sucking louse *E. horridus* is an obligate ectoparasite that spends its entire life cycle on the host, feeding exclusively on blood. Like other echinophthiriid lice, its dispersal capacity and life cycle are strongly limited by the haul-out behaviour of its hosts, because transmission from seal to seal requires close contact between hosts (Leonardi et al. 2021). As expected for a parasite with poor dispersal ability, the spatial population-genetic structure of *E. horridus* has been found to reflect host spatial differentiation within the lake-endemic Saimaa ringed seal population (Virrueta Herrera et al. 2022) and among the three subspecies of ringed seal occurring in the Baltic Sea region (Sromek et al. 2024). Given its extremely specialised ecology and life history, *E. horridus* is an archetypal example of a parasite in which genome-level diversity should readily respond to changes in host population size.

To elucidate the drivers of genetic differentiation and genetic diversity in *E. horridus* seal lice, we extended the whole-genome resequencing datasets of Virrueta Herrera et al. (2022) and Sromek et al. (2024) by sequencing altogether 54 louse individuals collected from a substantially expanded set of seal hosts across the Holarctic region. Our combined genome-level dataset includes altogether 82 lice from 12 different seal host species, subspecies and populations (Figure 1). The focal set of hosts includes populations that are distributed in broad sympatry (e.g., Baltic Sea populations of grey, harbour and ringed seals, and Arctic ringed and harp seals), isolated descendants of ancient trans-continental dispersal events (Caspian and Baikal seals), and postglacial landlocked relicts (Saimaa and Ladoga ringed seals). The focal host system also displays extreme variation in population size, from the endangered Saimaa ringed seal numbering only a few hundred individuals (Kunnasranta et al. 2021) to Arctic ringed and harp seals with population sizes ranging in the millions (Laidre et al. 2015). In order to identify the determinants of genetic structuring, we first inferred whether the main clusters and subgroups in our SNP dataset are delimited predominantly according to host (sub)species or by overlaps in host geographic ranges, behavioural traits, or niches. We also tested for the presence of louse infrapopulation structure, that is, genetic differentiation across host individuals within populations. To estimate long-term conservatism in the seal–louse associations, we related phylogenetic relationships and patterns of genetic divergence among the louse lineages to the phylogenetic similarity of their hosts. In our second main line of investigation, we applied phylogenetically controlled regression analyses to test whether genome-wide diversity indices in the main louse genomic clusters are explained by host population size. Our results provide new insights into the forces that create and erode genetic structure and diversity in natural host–parasite systems, and on the consequences of these phenomena on the ecology and evolution of host–parasite relationships in threatened and non-threatened wildlife species.

2 | Material and Methods

2.1 | Sample Collection, DNA Extraction and Sequencing

For this study, we collected and whole-genome sequenced 55 *E. horridus* seal lice, and analysed them together with data from 28 lice previously sequenced by Virrueta Herrera et al. (2022) and Sromek et al. (2024). Because the sequencing of one individual failed, our final dataset comprised a total of 82 seal louse individuals from 49 seal hosts representing 12 different host populations (Figure 1). Our sampling design aimed at maximising the number of host individuals per population, while retaining the ability to test also for the presence of inbreeding within infrapopulations. Therefore, whenever multiple lice were available from a given seal individual, two lice were randomly selected for sequencing. The final set of sequenced lice comprises a total of 10 lice from five Saimaa ringed seals, four lice from four Ladoga ringed seals, five lice from three Baltic ringed seals, three lice from one Arctic ringed seal, seven lice from four harp seals, 12 lice from eight grey seals (six Baltic and two Atlantic grey seals), 23 lice from 14 Atlantic harbour seals (five seals from the Baltic Sea and nine from the North Sea), five lice from three Pacific harbour seals, three lice from one Caspian seal and 11 lice from six Baikal seals (Table S1).

The newly sequenced louse specimens were collected between 2011 and 2021 and originated from necropsies of stranded and by-caught seals (Baltic grey seals and Atlantic harbour seals from the Baltic Sea), seals harvested during the regular hunting season (Baikal seals), seal skins sold to a tannery (harp seal), seals caught for telemetry studies (Pacific harbour seals, permit MMPA 19309) and from adult seals and pups admitted for rehabilitation at the Caspian Seal Research and Rehabilitation Center (Caspian seal), at the Seal Centre Friedrichskoog, Germany (Atlantic grey and Atlantic harbour seals from the North Sea) and at the Seal Centre Pieterburen, the Netherlands (Atlantic harbour seals from the North Sea). Louse specimens were preserved in 99.5% ethanol or RNAlater and stored at −20°C.

Total genomic DNA was extracted from single specimens using either QIAmp DNA Micro Kits (Qiagen) or Xpure Cell&Tissue Micro Kits (A&A Biotechnology). The manufacturers' standard protocols were followed, except that the tissue lysis time was extended to 24–48 h and EB buffer (10 mM Tris-Cl, Ph 8.5) was used for elution. Illumina sequencing libraries were prepared using either KAPA Hyper Prep Kit (Kapa Biosystems) or NEBNext Ultra II DNA Library Prep Kit (New England Biolabs) (Table S1) and sequenced on NovaSeq6000 in 150-bp paired-end mode.

2.2 | Nuclear Datasets

Following quality control with FastQC (Andrews 2010), adaptors and low-quality bases were trimmed from raw sequencing reads using BBDuk v. 38.96 (https://sourceforge.net/projects/bbmap/). Resulting clean reads were thereafter mapped on the draft genome of *E. horridus* (Sromek et al. 2024) using Bowtie2 v. 2.4.4 (Langmead and Salzberg 2012) with local alignment mode. After mapping, reads were sorted using SAMtools (Danecek et al. 2021) and marked for duplicates using Picard v.2.27.5 (https://broadinstitute.github.io/picard/). Variant calling was performed using GATK v. 4.3 (Van der Auwera and O'Connor 2020). First, genotype likelihoods were called into GVCF files for each sample separately using GATK HaplotypeCaller, and then samples from the same host population were jointly genotyped using GATK GenotypeGVCF function with the '--include-non-variant-sites' argument. The resulting files were merged and filtered using BCFtools (Danecek

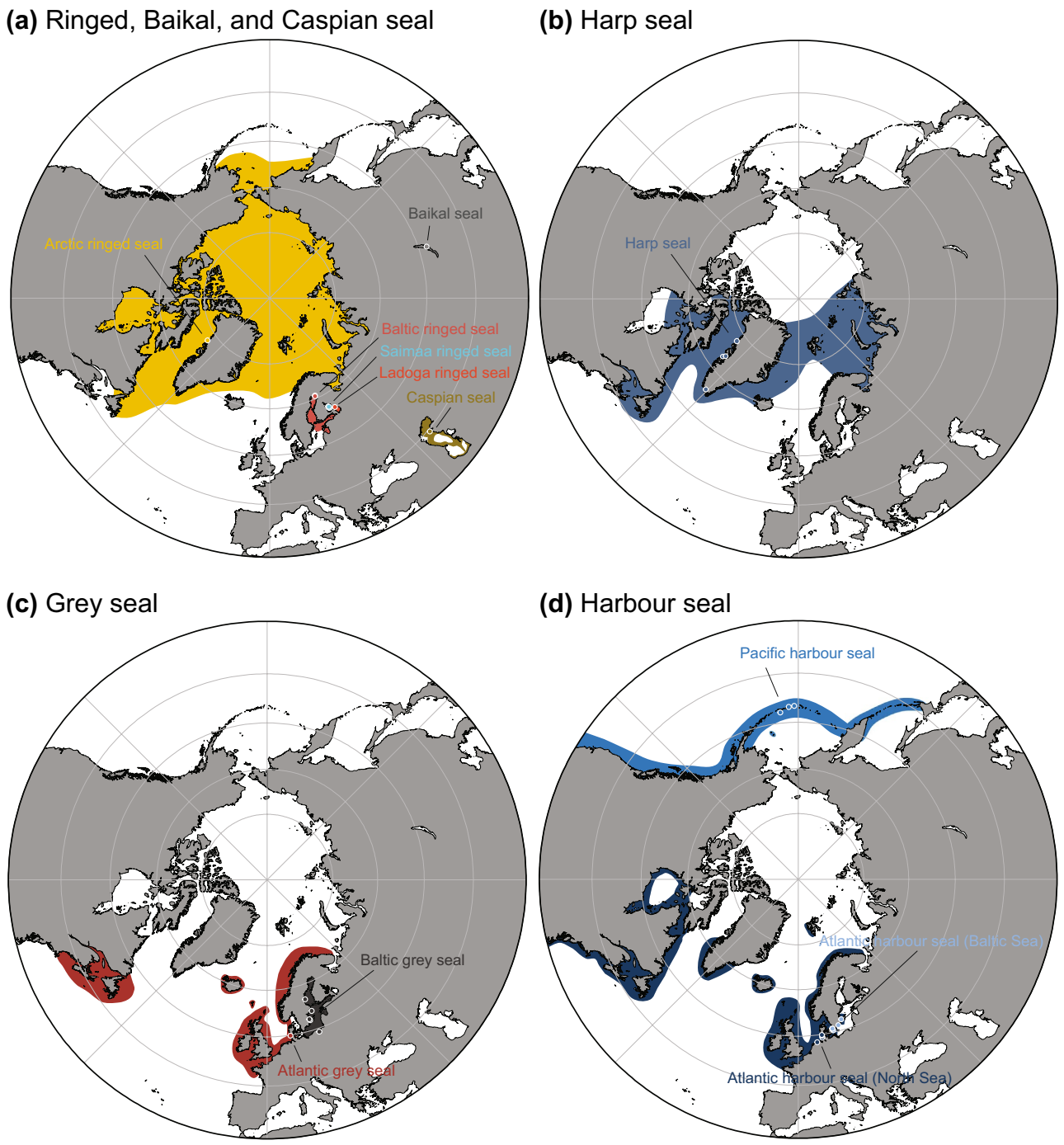

FIGURE 1 | Geographic distributions of the focal seal host species, subspecies and populations. (a) Genus *Pusa*: Baikal seal (*P. sibirica*), Caspian seal (*P. caspica*), and four subspecies of ringed seal (Arctic ringed seal (*P. hispida hispida*), Baltic ringed seal (*P. h. botnica*), Ladoga ringed seal (*P. h. ladogensis*) and Saimaa ringed seal (*P. h. saimensis*)), (b) harp seal (*Pagophilus groenlandicus*), (c) two subspecies of grey seal (Baltic grey seal (*Halichoerus grypus grypus*) and Atlantic grey seal (*H. g. atlantica*)), (d) two subspecies of harbour seal (Pacific harbour seal (*Phoca vitulina richardii*) and North Sea and Baltic Sea populations of Atlantic harbour seal (*P. v. vitulina*)). Dots mark the sampling sites of host individuals. Distributions have been adapted from Jefferson et al. (2015), IUCN-Marine Mammal Protected Areas Task Force (2021) and the North Atlantic Marine Mammal Commission website (https://nammco.no/). Basemaps were drawn using ggOceanMaps (Vihtakari 2024) based on Natural Earth Data distributed under the CC Public Domain licence.

et al. 2021) to exclude uncalled genotypes, indels, non-biallelic variants, and low-confidence variants. Sites were excluded from the final filtered VCF file if they met at least one of the following criteria: (1) Phred quality score < 30, (2) sample-level genotype quality < 30, (3) read depth < 10 or > 5704 (twice the average site read depth), (4) SNP heterozygous in more than 45 individuals.

For phylogeny reconstruction, we split the above mentioned VCF file into 50-kb non-overlapping genomic windows using BCFtools. Of all the resulting windows, 50 were then randomly selected and converted to PHYLIP format with the vcf-2phylip script (Ortiz 2019) for nuclear-gene tree estimation. In order to obtain outgroups for rooting of the trees, we retrieved

from the NCBI SRA database Illumina reads from three Southern Hemisphere seal louse species sequenced by Leonardi et al. (2019): *Antarctophthirus microchir* (SRR5809347) from Australian sea lion, *A. ogmorhini* (SRR5809350) from leopard seal, and *Lepidophthirus macrorhini* (SRR5809351) from southern elephant seal. These outgroup samples were processed in the same way as our samples, but only used in phylogenetic analyses.

2.3 | Mitochondrial Datasets

To gain insights into variation in the mitochondrial genome of lice and its correlation with host divergence, we also used our sequencing outputs for assembling coding sequences of mitochondrial genes of both lice and their seal hosts. Since lice feed on the blood of their hosts and sequencing data come from whole crushed insects, it is possible to retrieve also host DNA from the sequencing reads. This is the case especially for mitochondrial DNA, which is more abundant than nuclear DNA in organisms.

For assembling the louse mitochondrial dataset, we used Bowtie2 for mapping sequencing reads of each individual to sequences of the seven mitochondrial genes of *E. horridus* (COI, COII, COIII, CYTB, ND1, ND4 and ND5) assembled in Sromek et al. (2024). Consensus sequences for each gene were then constructed using BCFtools and SAMtools, and converted to Fasta files using custom scripts by A. Sweet (https://github.com/adsweet/louse_genomes).

To root the louse mitochondrial tree, we used seven outgroup species sequenced by Leonardi et al. (2019): *Antarctophthirus microchir* (SRR5809347) from Australian sea lion, *A. microchir* (SRR5088465) from South American sea lion, *A. ogmorhini* (SRR5809350) from leopard seal, *A. carlini* (SRR5809348) from Weddell seal, *A. lobodontis* (SRR5809349) from crabeater seal, *Proechinophthirus fluctus* (SRR5308138) from northern fur seal, and *Lepidophthirus macrorhini* (SRR5809351) from southern elephant seal. The mitochondrial genes of these species, except *A. ogmorhini* from leopard seal and *A. microchir* from South American sea lion, had already been assembled from the same raw reads in the study of Dong et al. (2022), so they could be directly retrieved from GenBank (MW803074, MW803076–MW803081, MW803106, MW803108, MW803110–MW803114, MW803094, MW803096–MW803098, MW803102–MW803104, MW803082, MW803083, MW803085, MW803088–MW803090, MW803093). To assemble mitochondrial genes of the two missing species, we used mitochondrial gene sequences of *A. carlini* as a target for read mapping for *A. ogmorhini*, and sequences of *A. microchir* from Australian sea lion as a target for *A. microchir* from South American sea lion.

The seal host mitochondrial dataset was constructed similarly from the louse sequencing reads, but while using coding sequences of the corresponding host species retrieved from GenBank as targets for read mapping (ringed seal—AM181036, Baikal seal—AM181035, harp seal—NC_008429, harbour seal—AM181032, grey seal—X72004, Caspian seal—NC_008431, Australian sea lion—NC_008419, South American sea lion—NC_049152, leopard seal—NC_008425, Weddell seal—MT755639, crabeater seal—NC_008423, northern fur seal—MG916809 and southern elephant seal—NC_008422). For both lice and hosts, resulting gene sequences were aligned in MAFFT v. 7.505 (Katoh and Standley 2013) using a codon-based alignment pipeline (Li et al. 2017). The resulting alignment was then trimmed using trimAl v. 1.2 (Capella-Gutiérrez et al. 2009) with automated selection of trimming parameters (*-automated1*).

2.4 | Estimation of Genetic Differentiation

For analyses of genetic differentiation, we first extracted variable sites from our filtered VCF file based on MAF > 0.01 and presence in at least 95% of individuals using VCFtools (Danecek et al. 2011). The resulting SNP dataset was then imported into R v. 4.2.3 (R Core Team 2023) and pruned for linkage disequilibrium (LD) with a threshold of 0.2 using the package SNPRelate v. 1.30.1 (Zheng et al. 2012).

To determine genetic differentiation between louse individuals, we first used SNPRelate to calculate pairwise dissimilarities (Weir and Goudet 2017) using the snpgdsDiss() function, and then built a hierarchical clustering dendrogram based on the estimates. Subgroups of individuals in the hierarchical clustering analysis were determined using a *Z*-score threshold of 15. To estimate degrees of relatedness within louse populations, we computed identity-by-descent (IBD) values between all pairs of individuals using the KING method of moments.

Next, we estimated genetic structuring within the overall dataset by performing an admixture analysis using the LEA v. 3.10.2 package (Frichot and François 2015), with 30 independent runs for K from 1 to 12. The best *K* value was selected based on the cross-entropy criterion as recommended by Frichot et al. (2014).

To visualise host-associated genetic structure among louse individuals, we conducted discriminant analysis of principal components (DAPC) in the adegenet v. 2.1.10 package (Jombart and Ahmed 2011) using host populations as group priors. To estimate the optimal numbers of principal components (PCs) to retain in DAPC, we used cross-validation with 1000 replicates and retained the number of PCs with the lowest mean squared error. In the same R package, we also performed principal component analyses (PCA) on individual SNP differences with the *dudi.pca* function. Pairwise F_{ST} values (Weir and Cockerham 1984) across louse populations on different hosts were estimated using hierfstat v. 0.5.11 R package (Goudet and Jombart 2022).

We used a randomisation test to determine whether louse individuals collected from the same host individual within a population are genetically more similar to each other than individuals collected from different host individuals. For this analysis, we used all populations that had both within- and between-host louse samples, thus excluding samples from Arctic ringed seal and Caspian seal, where all lice were collected from a single host individual, and samples from Ladoga ringed seal and Atlantic grey seal, where each louse came from a different host. For the test, we firstly calculated individual-based Euclidean genetic distances between louse individuals within host populations using R package adegenet v. 2.1.10. The obtained distance values were then standardised by dividing them by the average

genetic distance of a given population. Then, within each host population, we shuffled whether the pairwise distance values represented a within-host or a between-host comparison. We generated 9999 permuted datasets, each time calculating the average genetic distance for within-host comparisons. Our empirical one-tailed *p*-value was calculated as the percentage of permuted datasets that had a standardised mean equal to or lower than the one seen in the original data.

2.5 | Estimation of Phylogenies and Phylogenetic Congruence

To get an overview of phylogenetic relationships among the sampled seal lice as well as their hosts, we inferred maximum likelihood trees in IQ-TREE v. 2.3.6 (Minh et al. 2020). The nuclear-DNA based tree of lice was estimated from 50 randomly selected 50-kb genomic windows, the louse mitochondrial tree based on the seven mitochondrial genes, and the seal mitochondrial tree from portions of 13 genes assembled from opportunistic host sequencing reads. We used the edge-linked partition model with a separate model selection for each partition. The nuclear dataset was partitioned according to genomic window, and the mitochondrial datasets of lice and seals according to gene and codon position (1 + 2 vs. 3). Branch support was estimated using 1000 ultrafast bootstrapping replicates.

In order to relate the estimated mtDNA divergences to intra- and interspecific estimates from other insect taxa, we used the APE v. 5.7.1 (Paradis and Schliep 2019) R package to estimate percent pairwise sequence divergences (uncorrected p-distances) within and between the nine main clades of the mtDNA phylogeny. These calculations were based solely on sequences (1428 bp) of the COI gene, which has been extensively used for identification and delimitation of species in insects (Hebert et al. 2003; Wilson et al. 2017; Doña and Johnson 2023; Johnson, Weckstein, et al. 2021; Lee et al. 2022).

We estimated the degree of overall congruence between the louse nuclear phylogeny and the seal host mitochondrial tree using the Procrustean Approach to Cophylogeny (Balbuena et al. 2013; Hutchinson et al. 2017) as implemented in the R package PACo v. 0.4.2 (Balbuena et al. 2020). To obtain ultrametric phylogenetic trees for the analysis, we pruned our louse nuclear tree and the seal mitochondrial tree of all but one specimen from each host population, and then transformed branch lengths using penalised likelihood (Sanderson 2002) in the APE package in R. Statistical significance of the observed phylogenetic congruence (measured as the sum of residual sum-of-squares values, m^2_{XY}) was assessed based on 10,000 permutations following the 'r0' null model, that is, assuming that lice track the evolution of their seal hosts.

As an alternative approach for assessing if lice were tracking host divergence, we tested whether the estimated F_{ST} values between louse populations are related to genetic divergence among the seal hosts. The genetic divergence of host populations was estimated based on average Kimura's two-parameter (K2P) distances calculated from our assembled seal mitochondrial genes. For these calculations, we excluded seven individuals that had less than 100 reads aligned to the host's mitochondrial genes. In the case of multiple lice from the same host individual, we took the one that had more host reads successfully mapped. Pairwise K2P distances were calculated in APE with the pairwise deletion option. Finally, we used a Mantel test as implemented in the vegan v. 2.6.4 (Oksanen et al. 2022) R package to test the correlation between mean host genetic distance and F_{ST} estimates across louse populations. We assessed statistical significance with 9999 permutations.

2.6 | Estimation of Genetic Diversity

We estimated genome-wide genetic diversity using two methods. First, we estimated individual-level heterozygosity from the filtered VCF file by calculating the fraction of heterozygous sites over total callable sites using BCFtools. Second, we inferred the population mutation rate theta ($\theta = 4N_e\mu$), which under the infinite-sites model approximates the per-site heterozygosity (Haubold et al. 2010). Sample-specific mean theta was estimated directly from BAM files using the maximum-likelihood estimator implemented in mlRho v. 2.9 (Haubold et al. 2010). These two metrics of genetic diversity are commonly used in conservation genomics (Jeon et al. 2024; Quinn et al. 2024; Solari et al. 2025).

To test for the presence of a relationship between louse genetic diversity and host population size, we fitted phylogenetic generalised least squares (PGLS) models, with the average heterozygosity and theta values of louse populations as a function of host population size. Current seal population sizes (numbers of mature individuals) were collected from the IUCN Red List website (https://www.iucnredlist.org). Based on the results of the genetic differentiation analyses described above, lice from Atlantic and Baltic grey and harbour seals were treated as one population for which the host population size was obtained by summing up the numbers of the Eastern Atlantic populations of grey and harbour seals. Lice from Baltic, Ladoga and Arctic ringed seals were treated as separate populations in the analysis, because these louse populations were separated into monophyletic groups in the nuclear phylogeny, while their clustering together in the LEA results could be caused by bias related to uneven sampling and small numbers of individuals from these populations (Meirmans 2012; Puechmaille 2016). The right-skewed host population size variable was logarithmically (log10) transformed, and PGLS models assuming a Brownian motion model of evolution along the aforementioned ultrametricized louse tree were computed in the nlme v. 3.1.162 (Pinheiro et al. 2023) R package. The predictive power of the models was then extracted using R package rr2 (Ives and Li 2018). For comparison, we also computed ordinary least squares regressions of louse heterozygosity and theta in relation to host population size.

3 | Results

3.1 | Nuclear and Mitochondrial Genomic Datasets

Across the entire dataset including 28 previously sequenced lice from Virrueta Herrera et al. (2022) and Sromek et al. (2024), the number of sequencing reads per sample ranged from 41 to 261 million, with an average of 87 million reads (Table S1).

After removing duplicate reads, mean sequencing depth per individual ranged from 24 to 124, with a mean of 48. A total of 12,674,502 high-quality SNPs over 165,307,860 sites were called in GATK. After filtering for missing data and minor allele frequency, there were 7,304,557 SNPs, of which 171,026 remained after LD-pruning (Sromek et al. 2025).

The phylogenomic nuclear dataset of 50 randomly sampled 50-kb genomic windows had a total alignment length of 2,238,407 bp and contained 77,629 parsimony-informative sites. The louse mitochondrial dataset had an alignment length of 7629 bp. All seven targeted mitochondrial genes were successfully obtained for all individuals, except for the outgroup species *A. microchir* from South American sea lion, for which only an 822 bp long COI fragment was assembled.

The number of sequencing reads that mapped to seal host mitochondrial genes ranged from 5 to 3172 per louse individual. For all individuals, except Echor18 from Saimaa ringed seal with the lowest number of mapped reads, a fragment of at least one of the 13 host mitochondrial genes was obtained. The level of missing data was 13.6% and the total alignment length of the 13 concatenated genes was 9645 bp.

3.2 | Genetic Differentiation

The highest level of hierarchical clustering generally grouped louse individuals according to seal host species (Figure 2a). The only exception to this overall pattern was found in lice collected from grey and harbour seals, in which a distinct group of lice from the Pacific harbour seal was separated from a mixed cluster formed by lice originating from North Sea and Baltic Sea populations of grey and harbour seals. Lice associated with ringed seals were further divided into four subclusters according to host subspecies.

Inspection of cross-entropy values revealed that the optimal number of ancestral populations was 7 (Figure S1). At the optimal $K=7$, the LEA assignment of individuals (Figure 2b) largely reflected the results of the hierarchical clustering analysis. Like the hierarchical clustering tree, LEA assignment indicated that lice from Atlantic and Baltic grey and harbour seals cannot be consistently separated from each other, even in analyses with higher K values (Figure S2). At $K=8$, the louse population from Baltic ringed seal became partly separated from those from Arctic and Ladoga ringed seals. At $K=9$, clustering began to be influenced by close relatedness, distinguishing a pair of individuals from a single harbour seal as a separate cluster (Figure S2). Notably, lice from Baltic ringed seals showed signs of introgression from lice associated with European grey/harbour seal populations (4%–9%), while some of the genetic ancestry of lice from Arctic ringed seal appeared to originate from lice associated with harp seal (12%) and Pacific harbour seal (11%–13%) (Figure 2b).

Results of the DAPC (Figure 2c) and PCA (Figure S3) analyses as well as estimates of F_{ST} values across louse populations (Figure 2d) confirmed these general patterns. In particular, lice from Baikal and Caspian seals and Saimaa ringed seals were separated from lice from other seal hosts; the distinctness of these populations was also evident in the F_{ST} estimates. Among louse populations associated with Atlantic and Baltic grey and Atlantic harbour seals, F_{ST} values were very low (0.01–0.05).

The phylogenetic tree based on concatenated sequences of 50 nuclear 50-kb genomic windows was for the most part strongly supported (Figure S4a). With regard to the grouping of individuals according to seal host (sub)species, the ML tree closely resembled the hierarchical clustering tree. However, the ML phylogeny presented some differences in the order of deeper topological splits: within louse populations associated with ringed seals, the branching order was (Arctic (Saimaa (Baltic, Ladoga))), while lice associated with harp and Caspian seals formed a monophylum subtended by the population associated with Baikal seals.

The louse ML tree based on coding mitochondrial gene sequences (Figure S4b) presented two main differences as compared to the nuclear genomic ML tree (Figure S4a) and the hierarchical clustering tree (Figure 2a). First, lice from Baikal seals were placed as sister to all other louse populations (albeit with low ultrafast bootstrap support). Second, the closely related Baltic and Ladoga ringed seal louse clades each contained one haplotype originating from louse individuals collected from Atlantic and Baltic grey seal, respectively. Mean uncorrected p-distances in the COI gene within the nine main clades ranged from 0.03% to 0.35% (Table S2), with the maximum being 0.63%. Inter-clade mean distances were generally substantially higher, ranging from 0.20%–0.94% between lice associated with different ringed seal subspecies to 2.84%–12.87% between lice from more distantly related hosts (Table S2).

The seal ML phylogeny based on sequences of coding mitochondrial genes of seals assembled from sequencing reads originating from the sampled seal lice (Figure S4c) showed both congruence and conflict with the nuclear and mitochondrial louse phylogenies. Harp seal, harbour seal, grey seal, Caspian seal and Baikal seal sequences formed successive monophyletic sister groups to a clade formed by ringed seal sequences. Within the ringed seal clade, Baltic and Ladoga ringed seal sequences formed a partially intermixed paraphyletic grade with respect to two separate clades formed by Saimaa and Arctic ringed seal sequences.

The PACo analysis indicated statistically significant overall congruence between the louse nuclear phylogeny and the seal mtDNA phylogeny ($m^2_{XY}=2.12$, $p=0.0005$) (Figure S5a). However, clear cases of incongruence were also present, which were manifested as large residuals resulting from the placement of harp seal and their lice, and from the association of lice of Baltic and Atlantic grey seal and Atlantic harbour seal with a set of distantly related hosts (Figure S5a). Along the same vein, no correlation was found between host genetic divergence calculated based on the seal mitochondrial phylogeny and genetic differentiation among the louse populations estimated as interpopulation F_{ST} ($R=-0.02$, $p=0.3$) (Figure S5b).

When considering only those seal host populations that had multiple lice sampled from more than one host individual, louse individuals sampled from the same infrapopulation were on average statistically significantly more closely related than two

individuals sampled at random from the same host population ($p < 0.0001$) (Figure S6a). Genetic structuring based on host individual was particularly evident in that all louse pairs having kinship coefficients corresponding to at least 3rd-degree relationships (> 0.044) originated from the same infrapopulation within host (sub)species (Figure 2a). However, closer examination of genetic distances between lice from the same or different infrapopulation suggested that infrapopulation structuring was present in some, but not necessarily all, of the focal seal louse populations (Figure S6b).

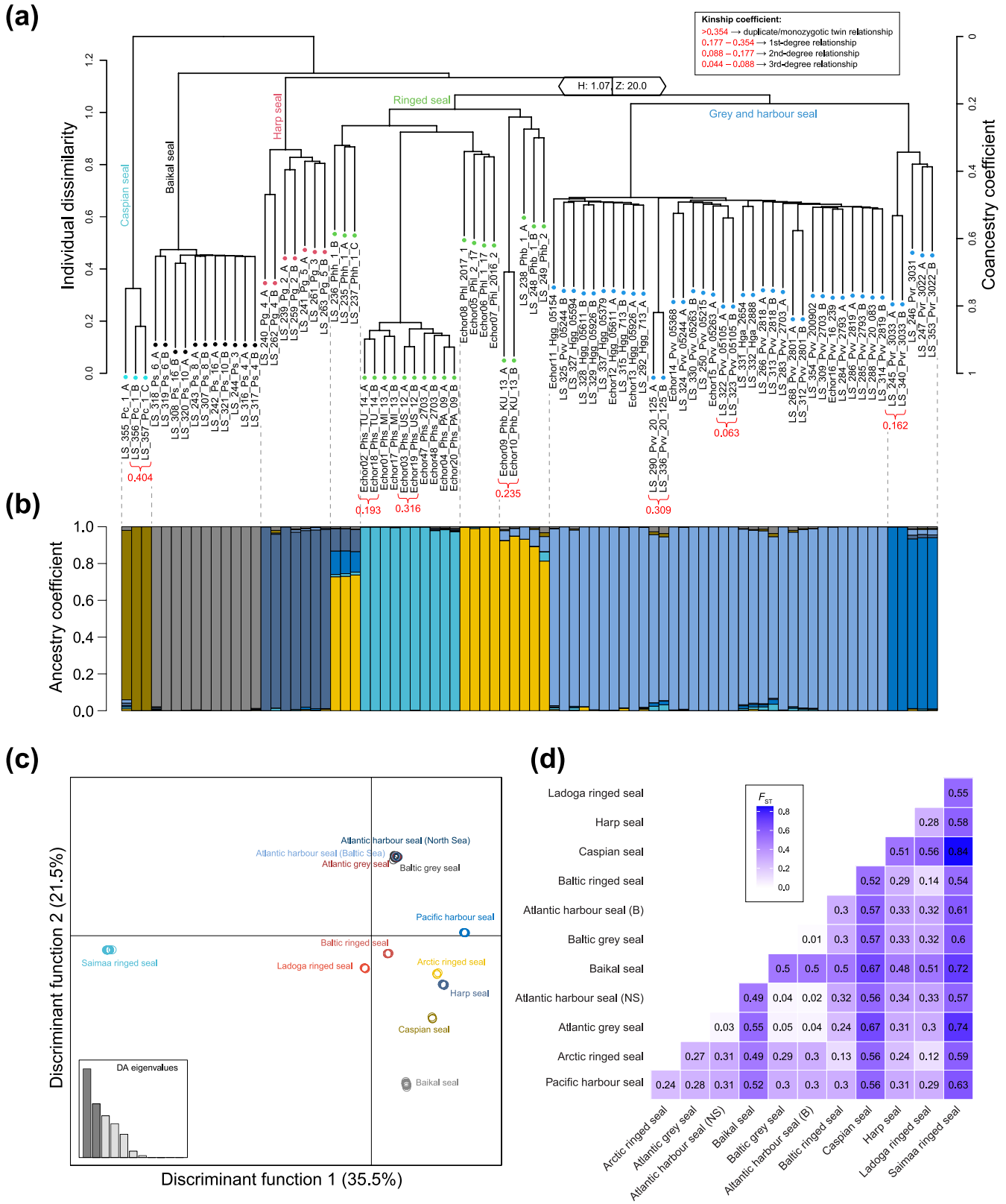

FIGURE 2 | Legend on next page.

FIGURE 2 | Genetic structure and differentiation of *E. horridus* seal louse populations from different seal host species and subspecies. (a) Hierarchical clustering dendrogram based on a dissimilarity matrix among individuals, (b) LEA admixture plot for $K=7$, (c) Discriminant Analysis of Principal Components (DAPC) plot and (d) F_{ST} estimates between population pairs. In (a), letters (A/B/C) after louse specimen and host individual codes denote lice sampled from the same seal host individual, while red numbers below the labels indicate close relatedness based on estimated kinship coefficients (see legend). In (b), bar sections show the estimated ancestry proportions for each louse individual ($N=82$), which are sorted in the same order as in the hierarchical clustering dendrogram above. The result is shown for $K=7$, which had the lowest value of cross entropy (Figure S1); see Figure S2 for results based on $K=2$ to $K=9$ ancestral groups. In the DAPC plot (c), each circle represents an individual louse and is coloured according to the seal host sub(species). Letters in parentheses after Atlantic harbour seal in (d) refer to the Baltic Sea (B) and North Sea (NS) populations of the subspecies.

3.3 | Genetic Diversity

We found wide variation in genome-wide heterozygosity (H) and theta (θ) across louse populations associated with different seal (sub)species (Figure 3, Table S3). The lowest median estimates were found in lice on Saimaa ringed seals ($H=0.00063$, $\theta=0.00447$). The highest estimates were found in lice of harp seals, in which the median of heterozygosity was over nine times as high ($H=0.00589$) and the median of theta over three times as high ($\theta=0.01410$). The estimates for the other louse populations fell between these extremes, but, notably, the variation appeared to be more related to seal populations and subspecies rather than species. High theta values corresponded to high heterozygosity values, except for the louse population from the Caspian seal. In this population, heterozygosity was possibly underestimated because all three individuals originated from the same host individual and two of them were closely related (Figure 2a).

Phylogenetic generalised least squares models revealed that log-transformed host population size is a significant predictor of mean heterozygosity ($R^2_{pred}=0.441$, $p=0.0114$) and theta ($R^2_{pred}=0.505$, $p=0.0097$) within seal louse populations (Figure 4). The non-phylogenetic models were likewise significant for both heterozygosity ($R^2=0.579$, $p=0.017$) and theta ($R^2=0.682$, $p=0.006$).

4 | Discussion

Genetic differentiation in parasitic organisms associated with different hosts could arise and be maintained through adaptive as well as non-adaptive processes. These two types of processes can be distinguished by examining closely related parasite lineages on increasingly distantly related hosts with and without overlapping geographic ranges (Brooks et al. 2006; Bell et al. 2021). If adaptive processes predominate, we expect host-associated genetic differentiation to be present between related parasite populations also when their hosts occur in sympatry. However, if non-adaptive processes prevail, genetic differentiation between parasite populations from different hosts is expected to occur mainly among hosts that are allopatrically distributed (Clay 1949; Huyse et al. 2005; Althoff et al. 2014). We used genome-level data from *E. horridus* seal lice collected from 12 differentially isolated seal species, subspecies and populations across the Holarctic to tease apart the roles of geographic range overlap and host relatedness on the genetic structuring of the lice. The fact that the population sizes of the focal hosts differ by four orders of magnitude also allowed us to test whether genome-level diversity in the lice is connected to host population size. We discuss our results in relation to factors that shape genetic variation in specialist parasites and the maintenance of genetic variability in parasites reliant on threatened and near-threatened wildlife species.

4.1 | Host Isolation Drives Genetic Differentiation in Seal Lice

Our different statistical analyses of the nuclear genomic dataset consistently revealed clear genetic differences in *E. horridus* lice sampled from different seal hosts (Figure 2, Figures S2–S4a). With the exception of a mixed genetic cluster comprised of lice originating from northern European grey and harbour seals, the main groups were defined by seal host species, with further differentiation among lice associated with the four ringed seal subspecies. Variation in mitogenomic coding sequences (Figure S4b) was for the most part consistent with the structuring observed in the nuclear dataset, but also revealed indications of lability in associations as well as gene flow across louse lineages (see below). *Echinophthirius horridus* on northern phocid seals has traditionally been treated as a single widespread generalist species (Leidenberger et al. 2007; Preuss et al. 2024), with a few subspecies proposed for, for example, the lineage in Lake Baikal (Ass 1935) and the Caspian Sea (Kurochkin and Badamshin 1968). According to our results, however, uncorrected COI p-distances between the main clades of the mtDNA tree (Table S2) exceed the 5% limit for intraspecific variation in lice proposed by Johnson, Weckstein, et al. (2021) and Doña and Johnson (2023). Together with the consistent pattern of genetic differentiation in the nuclear genomes, the deep splits in mtDNA sequences indicate that *E. horridus* represents a complex of cryptic species rather than a single lineage (see also Sromek et al. 2024). In addition to detailed studies on potential morphological differences among the genetically defined clusters revealed by our study, artificial breeding experiments aimed at estimating the actual degree of reproductive isolation among the lineages are clearly warranted.

As such, the overall pattern of our results conforms to host-associated genetic divergence frequently observed in parasitic organisms (Dietrich et al. 2013; Booth et al. 2015; Hood et al. 2015; Stefan et al. 2018; Harrison et al. 2022; Tietjen et al. 2022). However, several lines of evidence suggest that the differentiation is driven by co-allopatry (geographic isolation of parasites along with their hosts) rather than by coevolutionary interactions or louse adaptation to host species-specific morphological characteristics or physiological defences.

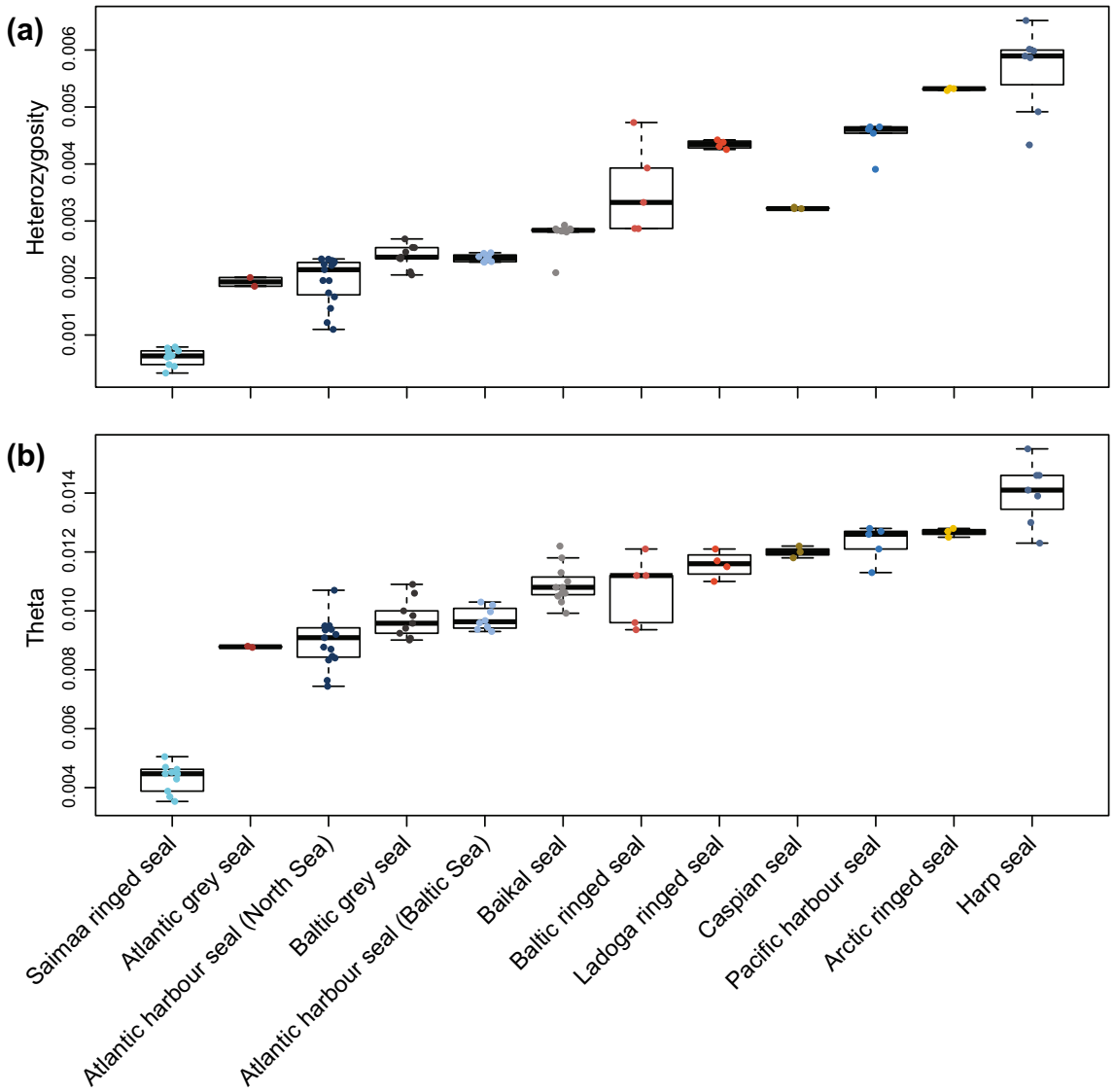

FIGURE 3 | Genetic diversity in seal louse populations from different seal host species and subspecies, estimated as (a) heterozygosity and (b) theta (θ). In the boxplots, coloured points represent individuals, vertical lines show medians and boxes and whiskers represent first and third quartiles and extremes that are not outliers, respectively.

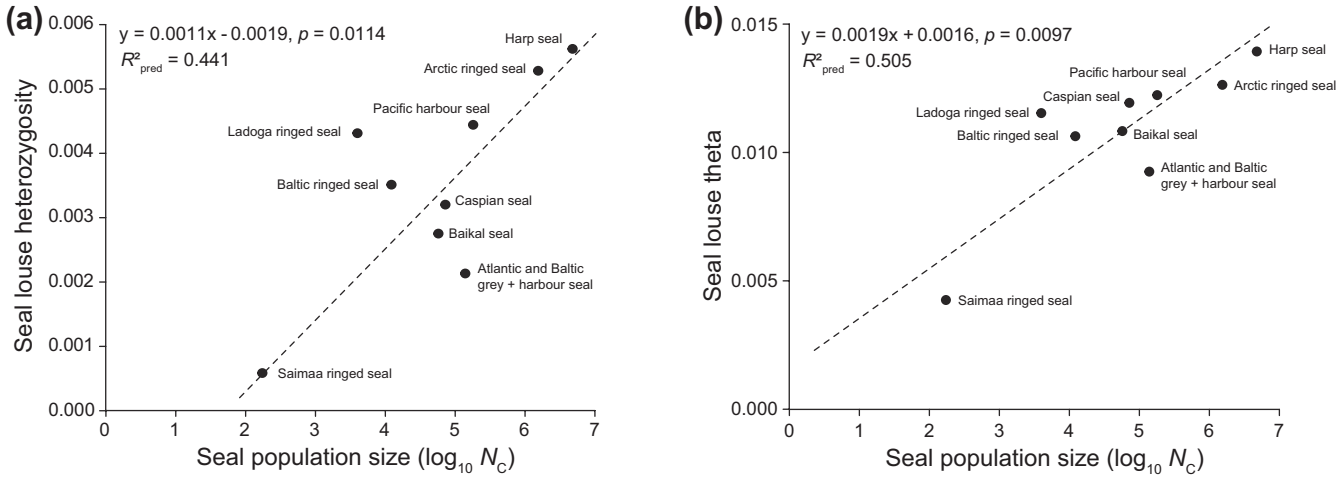

FIGURE 4 | Relationships between genetic diversity measured as (a) heterozygosity and (b) theta (θ) in louse populations and log-transformed population sizes of their seal host (sub)species. Lines show estimated phylogenetic generalised least squares (PGLS) regressions, with regression coefficients and R^2 and p values shown next to the plots.

First, most notably louse populations associated with the landlocked hosts (Caspian and Baikal seals and Ladoga and Saimaa ringed seals) are differentiated and distinguishable based on both nuclear and mtDNA data. Caspian and Baikal seals derive from ancient colonisation events, and were most likely separated from their marine ancestors more than 1.5 million years ago (Hassanin et al. 2021; Nebenführ et al. 2024; Park et al. 2024). In comparison to these old lineages, Ladoga and Saimaa ringed seals are substantially younger, as their respective lakes emerged from the Baltic basin less than 10,000 years ago, after the deglaciation of Northern Europe (Ukkonen 2002; Sromek et al. 2024; Löytynoja et al. 2025).

Second, lice from Pacific harbour seals are clearly differentiated from lice on Atlantic harbour seals in the North Sea and the Baltic Sea, while the latter are indistinguishable from lice occurring on sympatric grey seals (Figure 2, Figures S2 and S3). In both the nuclear (Figure S4a) and mitochondrial (Figure S4b) phylogenetic trees, Pacific harbour seal lice are placed as sister to a mixed clade of lice from Atlantic harbour and grey seals and Baltic grey seals. These results are consistent with the proposed origin of harbour seals in the Pacific Ocean (Liu et al. 2022), and suggest that there was an incomplete host switch (i.e., expansion of host range while maintaining gene flow; Johnson et al. 2003) to grey seals after harbour seals colonised the Atlantic in the Late Pleistocene. Such a scenario would fit the suggestion of Herzog, Wohlsein, et al. (2024), that the greater prevalence and intensity of infections in grey seals as compared to harbour seals is explained by grey seals being a susceptible naïve host for seal lice. Sharing of lice in sympatric grey and harbour seal populations is likely facilitated by the fact that, during and outside the breeding season, both grey and harbour seals aggregate in colonies that frequently contain both species (Härkönen et al. 2006; Hoekendijk et al. 2023; Herzog, Siebert, and Lehnert 2024). A similar situation has been found in the southern-hemisphere seal louse genus *Antarctophthirus*, where little genetic divergence is present between *A. carlinii*, *A. ogmorhini* and *A. lobodontis* (Leonardi et al. 2019; see also Dong et al. 2022; Soto et al. 2023). Their seal hosts (Weddell, leopard and crabeater seals, respectively) have widely overlapping distributions and partially share fast and pack ice habitats (Laws 1981; Southwell et al. 2012). A relatively high rate of transmission and gene flow is also suggested by the fact that we found no signs of differentiation between grey and harbour seal lice originating from the North Sea and the Baltic Sea, despite the fact that harbour seals tend to be strongly philopatric (Andersen and Olsen 2010; Liu et al. 2022) and Atlantic and Baltic grey seals constitute two genetically distinct subspecies (Galatius et al. 2024). However, the two grey seal subspecies meet and probably hybridise in the western Baltic Sea (Fietz et al. 2016; Galatius et al. 2024), and particularly young grey seals can disperse (and hence transport lice) over long distances (Brasseur 2017; Peschko et al. 2020).

The clearest cases resembling a pattern of sympatric host-associated genetic differentiation are found in lice associated with Arctic and Baltic ringed seals, both of which are distinct from lice on co-occurring seal species: harp seal in the Arctic Ocean and grey and harbour seals in the Baltic Sea (Figures 1 and 2, Figures S2–S4). However, also in these cases the genetic differentiation seems to be driven by the limited dispersal capability of seal lice rather than by adaptations to specific alternative hosts. The distinctness of lice on marine ringed seals appears to be connected to the solitary breeding and moulting behaviour (Smith et al. 1991; Krafft et al. 2007) and distinct habitat and niche preferences (Ferguson et al. 2025) of ringed seals, which would tend to restrict louse transmission to occur only within host species. Notably, however, it seems that in neither of these cases is the reproductive isolation from co-occurring louse populations complete. Hence, and in direct contrast to lice on the two landlocked ringed seal subspecies, both of the marine ringed seal louse populations show signatures of introgression from lice associated with other seal species having overlapping geographic ranges: a total of 23%–25% of the genetic ancestry of lice on Arctic ringed seals appears to derive from lice on harp and Pacific harbour seals, while all analysed Baltic ringed seal lice have 4%–9% ancestry from the louse population associated with the co-occurring grey and harbour seals (Figure 2a). Our finding of two grey seal lice with mitochondrial haplotypes typical of ringed seals (Figure S4b) is consistent with the inference of ancient asymmetric gene flow from ringed seal lice to grey seal lice within the Baltic Sea postulated by Sromek et al. (2024) on the basis of ABBA-BABA tests and demographic simulations. One of the grey seal louse haplotypes is placed as sister to the Ladoga ringed seal louse clade (Figure S4b), which could reflect gene flow prior to the separation of Lake Ladoga, or the underestimation of variation in Baltic ringed seal lice due to low sample size in this population. Topological differences in the placement of lice from Baikal, Caspian, and harp seals in the mitochondrial (Figure S4b) and nuclear (Figure S4a) phylogenomic trees reveal another putative case of mitonuclear discordance. However, this apparent incongruence may be caused by weak support for the exact placement of Baikal seal lice near the root of the mtDNA tree.

4.2 | Louse and Seal Phylogenies Show Both Congruence and Conflict

On a broader scale, the parallel genetic differentiation of geographically isolated seals and their associated lice results in statistically significant congruence between the seal and seal louse phylogenies (Figure S5a). Examination of PACo residuals shows that the cophylogenetic signal is largely driven by concordant patterns in the divergences of landlocked ringed, Baikal and Caspian seals and their lice. In fact, the similarity of the phylogenetic trees of phocid seals and their *Echinophthirius* lice appears more extreme than in the classic case of allopatrically distributed North American pocket gophers and their strongly dispersal-limited chewing lice (Hafner et al. 1994; Reed and Hafner 1997), although the mechanism of co-divergence is evidently the same in both host–parasite systems.

Despite the statistically significant overall congruence, both the mitochondrial and nuclear louse phylogenies also show strongly supported conflict with phylogenetic relationships among their host seals (Figure S4c; see also Hassanin et al. 2021; Park et al. 2024). A reflection of this conflict is seen in that genetic differentiation among louse populations is not related to host mitochondrial divergence (Figure S5). In addition to the aforementioned relatively recent host-range

expansion from harbour to grey seals, the clearest case of phylogenetic incongruence involves the deepest splits within the nuclear clade consisting of Baikal, Caspian and harp seal (Figures S4a and S5a). Harp seal is a distant relative of the other seals in our study, suggesting that its lice were retrieved through a host shift from the ancestor of Caspian seals. Considering the need for close contact for louse transmission and that harp seal is a strict high-Arctic specialist, the result supports the hypothesis that the Caspian seal originated through colonisation via the north (Davies 1958; Palo and Väinölä 2006) rather than that the species is a relic descended from seals that inhabited the Ponto-Caspian region during the Miocene (Árnason et al. 1995; Artamonova et al. 2021). This inference is consistent with recent geological studies, which have increasingly revealed evidence for a direct but transient connection between the Arctic Ocean and the Caspian Sea during the Plio-Pleistocene transition about 2.5 million years ago (Bista 2019; Lazarev et al. 2021; Trifonov et al. 2024).

4.3 | Seal Lice on the Same Host Individual Are Genetically More Similar

While our study was focused mainly on genetic differentiation in seal lice across host (sub)species and geographic space, we also found clear evidence of structuring on the basis of host individuals within seal populations (Figure S6a). Close first- and second-degree relatives inhabiting the same infrapopulation were found in half of the studied populations (Figure 2a) regardless of the genetic diversity of the overall population (Figure 3). These findings were, as such, expected, because genetic structuring by infrapopulation is a frequent phenomenon in many parasitic taxa (Guzinski et al. 2009; Koop et al. 2014; Cole and Viney 2018; DiBlasi et al. 2018; Gustafson et al. 2018; Virrueta Herrera et al. 2022).

Intriguingly, however, closer inspection of pairwise genetic distances within and between infrapopulations suggests that the strength of infrapopulation structuring varies across host (sub)species, ranging from very strong in lice of Saimaa ringed seals to weak in lice of grey and harbour seals and near-absent in lice of Baikal seals (Figure S6b). Although more thorough sampling from additional seal host species will be needed for a formal statistical test of the apparent pattern, we hypothesise that variation in the strength of infrapopulation structure is driven by host behavioural traits that influence the rate at which lice can disperse among host individuals. Because transmission of seal lice requires close contact between host individuals (Leonardi et al. 2013; Soto et al. 2023), infrapopulation structuring could be weakest in louse populations associated with hosts that breed and/or moult in rookeries on land (Baikal, grey and harbour seal) and strongest in populations on species that breed solitarily and moult on ice (ringed and harp seal). It is generally accepted that the existence and degree of spatial genetic structuring in parasites are influenced by their biological and behavioural traits, particularly dispersal ability (Martinů et al. 2018; Sweet and Johnson 2018; Doña et al. 2020). However, when considering single parasites occurring on multiple hosts, host population density, ecology and behaviour will further modulate the strength of spatial genetic structuring across populations (van Schaik et al. 2014; Harper et al. 2015) and among individuals within populations (Vilas et al. 2012; Vázquez-Prieto et al. 2015; Wohlfeil et al. 2020; Janecka et al. 2021).

4.4 | Host Population Size Determines Genetic Diversity in Seal Lice

Intraspecific genetic diversity is expected to be proportional to the long-term effective population size of species (Ellegren and Galtier 2016). In closely related species that share life-history traits, genetic diversity will therefore be largely determined by the current census population size (the total number of individuals), past demographic history and linked selection (Gillespie 2001; Banks et al. 2013; Ellegren and Galtier 2016).

Seals have been used extensively as a model group for elucidating factors that influence genetic diversity within natural populations and species. Seals are highly suitable for broad comparative analyses because their population sizes range from a few hundred in endangered (sub)species to millions in species inhabiting Arctic and Antarctic regions with little human presence (Stoffel et al. 2018; Peart et al. 2020; Liu et al. 2022; Löytynoja et al. 2023; Tange Olsen et al. 2025). These investigations have demonstrated that levels of current genetic diversity within species and populations have been shaped by sequential colonisation patterns (Liu et al. 2022) and past population fluctuations (Cammen et al. 2018; Peart et al. 2020), with the lowest diversities found in endangered (sub)species known to have been decimated by overhunting during the last few hundred years (Stoffel et al. 2018; Löytynoja et al. 2023; Hoelzel et al. 2024).

Comparative studies on many vertebrate taxa have revealed links between species-level genomic diversity and the current or past extent of suitable habitats (Brüniche-Olsen et al. 2021). For specialised parasites such as seal lice, the population size of the host(s) determines overall available habitat and resources, meaning that the level of genetic variation in parasites should be influenced by host abundance. However, many parasitic organisms are markedly subdivided into infrapopulations, which may further influence their levels of genetic diversity (Criscione and Blouin 2005; Huyse et al. 2005). In such cases, intraspecific genetic diversity may depend more on average infrapopulation size (i.e., infection rate) than on the number of infrapopulations (i.e., host population size). Surprisingly, these hypotheses—and the determinants of genetic diversity in parasites in general—have rarely been investigated (Criscione et al. 2005; Criscione and Blouin 2005; Barrett et al. 2008; Papkou et al. 2016). In accordance with the first hypothesis, we found that species- and population-level heterozygosity and theta in seal lice (Figure 3) were correlated with host population size (Figure 4). Support for a similar positive relationship was found by Leonardi et al. (2019) in a survey of southern-hemisphere seal lice. Although their study lacked enough comparisons for a statistical test, the relative ranking of species-level theta estimates was consistent with host abundance.

The relationship found in seal lice may, however, not be universal. Despite a similar range of theta values as in our study, Doña and Johnson (2023) found that species-level estimates in dove feather lice were correlated with host physical size rather than

with population size. Earlier studies based on more direct estimates of infestation intensities have likewise found a positive correlation between mitochondrial genetic diversity and average infrapopulation size in feather mites (Doña et al. 2015) and parasitic nematodes with direct life cycles (Criscione et al. 2005). The reasons for conflicting results from different host–parasite systems remain elusive, but we note that studies done to date have generally found low intensities of seal louse infestations, and that lice tend to be concentrated on areas of the body that are difficult to reach and groom (heads and flippers) (Herzog, Siebert, and Lehnert 2024). Observations that infestation intensities tend to be highest on pups and juveniles (Soto et al. 2022; Herzog, Siebert, and Lehnert 2024) likewise suggest that seal louse infrapopulation size is not determined by host body size per se.

5 | Conclusions and Future Directions

Our broad survey of the genomic properties of *E. horridus* seal lice on northern-hemisphere phocid seals supports the view that the genetic composition of wildlife parasite populations is determined by multiple hierarchically acting factors (Gorton et al. 2012; Thorn et al. 2023). In our focal seal lice, the main genetic divisions occur between allopatrically distributed host species and subspecies, with a further level of structuring arising among host individuals within populations. By contrast, lice associated with the distantly related but geographically and behaviourally overlapping western European grey and harbour seals are near-panmictic, and evidence of similar host shifts in the past is seen in that deep phylogenetic relationships among lice are not consistent with the seal phylogeny (see also Leonardi et al. 2019). Taken together, our results support a predominantly non-adaptive model of host–parasite diversification, where host distribution overlap, habitat sharing and social behaviour dictate opportunities for genetic differentiation and host shifts in parasites. In bird lice, host behaviours such as nest hole takeovers and sharing of dust bath sites have been suggested to facilitate gene flow and host-range expansions (Johnson, Weckstein, et al. 2021; Sweet, Boyd, et al. 2018). Overlaps in geographic ranges, diets and life histories also appear to be as important a factor as phylogeny in influencing the composition of gut microbiotas in seals (Pacheco-Sandoval et al. 2024) and sharing of rabies virus strains among closely related *Myotis* bat species (Jacquot et al. 2022). The relative importance of parasite adaptations to specific traits and defences of alternative hosts is, however, undoubtedly more important in many host–parasite systems (Nylin et al. 2018; Doña et al. 2019; Villa et al. 2019). In this respect, the extreme variation in ecological and life-history traits within the species-rich parasite communities of seals (Lunneryd 1991; Measures 2001; Nyman et al. 2021; Sromek et al. 2023) provides ample opportunities for studies focusing on factors that influence the likelihood of adaptive vs. non-adaptive genetic divergence and diversification in parasites.

Understanding the drivers, consequences and prevention of loss of species and intraspecific genetic diversity ranks among the most pressing global biodiversity challenges of today (Willi et al. 2022; Shaw et al. 2025). In our focal closely related louse populations, genome-level diversity is strongly connected to host population size, suggesting that genetic diversity in seal lice responds rapidly to host population bottlenecks. Direct comparisons of genetic diversity in seals and lice were in our case not possible because comparative studies of seals have thus far applied different measures of diversity and have included only different subsets of the hosts included in our study (Stoffel et al. 2018; Peart et al. 2020; Nebenführ et al. 2024). Nevertheless, we note that in those cases in which comparisons are possible (*cf.* Liu et al. 2022; Löytynoja et al. 2023; Sromek et al. 2024), the order of differences among louse populations is consistent with genetic diversity estimates in their hosts. In normally outbred populations, individual-level heterozygosity has been found to be associated with parasite prevalence (Hoffman et al. 2014; Ortego et al. 2021; Budischak et al. 2023) and parasite-induced mortality (Coltman et al. 1999; Acevedo-Whitehouse et al. 2006; Gutiérrez et al. 2024). However, in severely bottlenecked hosts, such relationships may be blurred by genetic purging (Hoffman et al. 2024), increased drift overriding adaptive responses in host physiological defences and parasite virulence traits (Gokhale et al. 2013; Papkou et al. 2021), loss of parasite species (Morand 2015; Sromek et al. 2023), and parallel erosion of genetic diversity in surviving parasite species (this study). Many seal species and populations across the world have experienced severe anthropogenic population collapses during the last few hundred years (Stoffel et al. 2018; Hoelzel et al. 2024; Hoffman et al. 2024). Studies on how loss of genetic variation across multiple trophic levels influences the prevalence and intensity of parasites in bottlenecked seals could provide important insights for the conservation of endangered host–parasite systems in general.

Author Contributions

T.N., L.S., K.P.J. and M.K. conceived the study. M.K., A.R.-A., B.-M.B., A.Ta., A.To., O.R., H.L.Z. and A.R.-G. collected samples. L.S. carried out bioinformatic and statistical analyses. L.S., T.N., M.K. and K.P.J. secured funding. L.S. and T.N. wrote the first version of the manuscript. All authors edited and approved the final version of the manuscript.

Acknowledgements

We are grateful to all the professional and amateur researchers and students who provided seal louse samples for our study: Marja Isomursu (Finnish Food Authority), Miina Auttila (Finnish Forest Management Authority), past and present members of the Saimaa Ringed Seal Research Group of the University of Eastern Finland, Eva Heitzmann (Ust-Barguzin), Eric Amirbai Lang (London), Jari Ylönen and Jouni Aspi (University of Oulu), Oliwia Mucha (University of Gdansk) and staff members and volunteers of the Seal Centre Friedrichskoog (Seehundstation Friedrichskoog gGmbH) and the Seal Centre Pieterburen. This study was funded by the National Science Centre (NCN) of Poland (project 2019/32/C/NZ8/00335 to LS) and the US National Science Foundation (grants DEB-1926919 and DEB-2328118 to KPJ). Sequencing costs were covered in part by grants from the Oskar Öflund Foundation, the Betty Väänänen Foundation, Societas Pro Fauna et Flora Fennica, the Raija and Ossi Tuuliainen Foundation, and the Nestori Foundation. New specimens were sequenced by Genomed S.A. Bioinformatic analyses were enabled by resources provided by the Finnish Centre for Scientific Computing (www.csc.fi).

Funding

This work was supported by Narodowe Centrum Nauki (2019/32/C/NZ8/00335); National Science Foundation (DEB-1926919, DEB-2328118); Oskar Öflund Foundation; Betty Väänänen Foundation;

Societas Pro Fauna et Flora Fennica; Raija and Ossi Tuuliainen Foundation; Nestori Foundation.

Disclosure

Benefit-sharing statement: Benefits from this research accrue from presenting information on the biology of many endangered host–parasite systems and the sharing of our data and results on public databases as described above. This study complies with laws governing the handling of endangered animals (see Section 2).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw sequence reads reported in this study are deposited in the NCBI Sequence Read Archive (SRA) under BioProject accession numbers: PRJNA490903–PRJNA490922, PRJNA490949, PRJNA490950 and PRJNA1103082. The SNP data file and other processed input files as well as scripts for all analyses are available on Zenodo (https://doi.org/10.5281/zenodo.15521502).

References

Abrahamson, W. G., and C. P. Blair. 2008. "Sequential Radiation Through Host-Race Formation: Herbivore Diversity Leads to Diversity in Natural Enemies." In *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*, edited by K. Tilmon, 188–202. University of California Press. https://doi.org/10.1525/california/9780520251328.003.0014.

Acevedo-Whitehouse, K., T. R. Spraker, E. Lyons, et al. 2006. "Contrasting Effects of Heterozygosity on Survival and Hookworm Resistance in California Sea Lion Pups." *Molecular Ecology* 15, no. 7: 1973–1982. https://doi.org/10.1111/j.1365-294X.2006.02903.x.

Alcala, N., T. Jenkins, P. Christe, and S. Vuilleumier. 2017. "Host Shift and Cospeciation Rate Estimation From Co-Phylogenies." *Ecology Letters* 20, no. 8: 1014–1024. https://doi.org/10.1111/ele.12799.

Althoff, D. M., K. A. Segraves, and M. T. J. Johnson. 2014. "Testing for Coevolutionary Diversification: Linking Pattern With Process." *Trends in Ecology & Evolution* 29, no. 2: 82–89. https://doi.org/10.1016/j.tree.2013.11.003.

Andersen, L., and M. T. Olsen. 2010. "Distribution and Population Structure of North Atlantic Harbour Seals (*Phoca vitulina*)." *NAMMCO Scientific Publications* 8: 15–35. https://doi.org/10.7557/3.2669.

Andrews, S. 2010. "FastQC: A Quality Control Tool for High Throughput Sequence Data." [Computer Software]. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/.

Árnason, Ú., K. Bodin, A. Gullberg, C. Ledje, and S. Mouchaty. 1995. "A Molecular View of Pinniped Relationships With Particular Emphasis on the True Seals." *Journal of Molecular Evolution* 40, no. 1: 78–85. https://doi.org/10.1007/BF00166598.

Artamonova, V. S., I. N. Bolotov, M. V. Vinarski, and A. A. Makhrov. 2021. "Fresh- and Brackish-Water Cold-Tolerant Species of Southern Europe: Migrants From the Paratethys That Colonized the Arctic." *Water* 13, no. 9: 1161. https://doi.org/10.3390/w13091161.

Ass, M. J. 1935. "Ektoparasiten der Baikalrobbe." *Trudy Baikal'skoi Limnologicheskoi Stantsii* 6: 23–29.

Baird, R. W. 2001. "Status of Harbour Seals, *Phoca vitulina*, in Canada." *Canadian Field-Naturalist* 115, no. 4: 663–675. https://doi.org/10.5962/p.363864.

Balbuena, J. A., R. Míguez-Lozano, and I. Blasco-Costa. 2013. "PACo: A Novel Procrustes Application to Cophylogenetic Analysis." *PLoS One* 8, no. 4: e61048. https://doi.org/10.1371/journal.pone.0061048.

Balbuena, J. A., T. Poisot, and M. Hutchinson. 2020. "Paco: Procrustes Application to Cophylogenetic Analysis." R Package Version 0.4.2. [Computer Software]. https://CRAN.R-project.org/package=paco.

Banks, S. C., G. J. Cary, A. L. Smith, et al. 2013. "How Does Ecological Disturbance Influence Genetic Diversity?" *Trends in Ecology & Evolution* 28, no. 11: 670–679. https://doi.org/10.1016/j.tree.2013.08.005.

Bar-On, Y. M., R. Phillips, and R. Milo. 2018. "The Biomass Distribution on Earth." *Proceedings of the National Academy of Sciences of the United States of America* 115, no. 25: 6506–6511. https://doi.org/10.1073/pnas.1711842115.

Barrett, L. G., P. H. Thrall, J. J. Burdon, and C. C. Linde. 2008. "Life History Determines Genetic Structure and Evolutionary Potential of Host–Parasite Interactions." *Trends in Ecology & Evolution* 23, no. 12: 678–685. https://doi.org/10.1016/j.tree.2008.06.017.

Bell, K. C., J. M. Allen, K. P. Johnson, J. R. Demboski, and J. A. Cook. 2021. "Disentangling Lousy Relationships: Comparative Phylogenomics of Two Sucking Louse Lineages Parasitizing Chipmunks." *Molecular Phylogenetics and Evolution* 155: 106998. https://doi.org/10.1016/j.ympev.2020.106998.

Bell, K. C., K. L. Calhoun, E. P. Hoberg, J. R. Demboski, and J. A. Cook. 2016. "Temporal and Spatial Mosaics: Deep Host Association and Shallow Geographic Drivers Shape Genetic Structure in a Widespread Pinworm, *Rauschtineria eutamii* (Nematoda: Oxyuridae)." *Biological Journal of the Linnean Society* 119, no. 2: 397–413. https://doi.org/10.1111/bij.12833.

Bell, K. C., J. R. Demboski, and J. A. Cook. 2018. "Sympatric Parasites Have Similar Host-Associated, but Asynchronous, Patterns of Diversification." *American Naturalist* 192, no. 3: E106–E119. https://doi.org/10.1086/698300.

Benesh, D. P., J. C. Chubb, and G. A. Parker. 2022. "Adaptive Division of Growth and Development Between Hosts in Helminths With Two-Host Life Cycles." *Evolution* 76, no. 9: 1971–1985. https://doi.org/10.1111/evo.14574.

Benovics, M., J. Vukić, R. Šanda, et al. 2023. "Monogeneans and Chubs: Ancient Host-Parasite System Under the Looking Glass." *Molecular Phylogenetics and Evolution* 179: 107667. https://doi.org/10.1016/j.ympev.2022.107667.

Berta, A., M. Churchill, and R. W. Boessenecker. 2022. "The Origin of Phocid Seals and Evolution of Key Behavioral Character Traits." In *Ethology and Behavioral Ecology of Phocids*, edited by D. P. Costa and E. A. McHuron, 3–30. Springer. https://doi.org/10.1007/978-3-030-88923-4_1.

Bista, D. 2019. "Reconstructing the Pleistocene Connectivity History of the Black Sea and the Caspian Sea Using Strontium Isotopes." PhD thesis, University of Bristol.

Booth, W., O. Balvín, E. L. Vargo, J. Vilímová, and C. Schal. 2015. "Host Association Drives Genetic Divergence in the Bed Bug, *Cimex lectularius*." *Molecular Ecology* 24, no. 5: 980–992. https://doi.org/10.1111/mec.13086.

Boyd, B. M., N.-P. Nguyen, J. M. Allen, et al. 2022. "Long-Distance Dispersal of Pigeons and Doves Generated New Ecological Opportunities for Host-Switching and Adaptive Radiation by Their Parasites." *Proceedings of the Royal Society B: Biological Sciences* 289, no. 1970: 20220042. https://doi.org/10.1098/rspb.2022.0042.

Brasseur, S. M. J. M. 2017. "Seals in Motion: How Movements Drive Population Development of Harbour Seals and Grey Seals in the North Sea." PhD thesis, Wageningen University. https://doi.org/10.18174/418009.

Brooks, D. R., V. León-Règagnon, D. A. McLennan, and D. Zelmer. 2006. "Ecological Fitting as a Determinant of the Community Structure of Platyhelminth Parasites of Anurans." *Ecology* 87, no. 7 Suppl: S76–S85. https://doi.org/10.1890/0012-9658(2006)87%255B76:efaado%255D2.0.co;2.

Brown, T. M., A. M. Dunn, R. J. Quinnell, E. Clarke, A. A. Cunningham, and S. J. Goodman. 2025. "An Interdisciplinary Approach to Improving Conservation Outcomes for Parasites." *Conservation Biology* 39, no. 1: e14431. https://doi.org/10.1111/cobi.14431.

Brüniche-Olsen, A., K. F. Kellner, J. L. Belant, and J. A. DeWoody. 2021. "Life-History Traits and Habitat Availability Shape Genomic Diversity in Birds: Implications for Conservation." *Proceedings of the Royal Society B: Biological Sciences* 288, no. 1961: 20211441. https://doi.org/10.1098/rspb.2021.1441.

Budischak, S. A., S. Halvorsen, and F. Finseth. 2023. "Genomic Heterozygosity Is Associated With Parasite Abundance, but the Effects Are Not Mediated by Host Condition." *Evolutionary Ecology* 37, no. 1: 75–96. https://doi.org/10.1007/s10682-022-10175-8.

Cammen, K. M., T. F. Schultz, W. Don Bowen, et al. 2018. "Genomic Signatures of Population Bottleneck and Recovery in Northwest Atlantic Pinnipeds." *Ecology and Evolution* 8, no. 13: 6599–6614. https://doi.org/10.1002/ece3.4143.

Capella-Gutiérrez, S., J. M. Silla-Martínez, and T. Gabaldón. 2009. "trimAl: A Tool for Automated Alignment Trimming in Large-Scale Phylogenetic Analyses." *Bioinformatics* 25, no. 15: 1972–1973. https://doi.org/10.1093/bioinformatics/btp348.

Carlson, C. J., T. A. Dallas, L. W. Alexander, A. L. Phelan, and A. J. Phillips. 2020. "What Would It Take to Describe the Global Diversity of Parasites?" *Proceedings of the Royal Society B: Biological Sciences* 287, no. 1939: 20201841. https://doi.org/10.1098/rspb.2020.1841.

Carroll, D., M. P. Ahola, A. M. Carlsson, M. Sköld, and K. C. Harding. 2024. "120-Years of Ecological Monitoring Data Shows That the Risk of Overhunting Is Increased by Environmental Degradation for an Isolated Marine Mammal Population: The Baltic Grey Seal." *Journal of Animal Ecology* 93: 525–539. https://doi.org/10.1111/1365-2656.14065.

Clay, T. 1949. "Some Problems in the Evolution of a Group of Ectoparasites." *Evolution* 3, no. 4: 279–299. https://doi.org/10.2307/2405715.

Clayton, D. H., S. E. Bush, B. M. Goates, and K. P. Johnson. 2003. "Host Defense Reinforces Host–Parasite Cospeciation." *Proceedings of the National Academy of Sciences of the United States of America* 100, no. 26: 15694–15699. https://doi.org/10.1073/pnas.2533751100.

Clayton, D. H., S. E. Bush, and K. P. Johnson. 2004. "Ecology of Congruence: Past Meets Present." *Systematic Biology* 53, no. 1: 165–173. https://doi.org/10.1080/10635150490265102.

Cole, R., and M. Viney. 2018. "The Population Genetics of Parasitic Nematodes of Wild Animals." *Parasites & Vectors* 11, no. 1: 590. https://doi.org/10.1186/s13071-018-3137-5.

Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton. 1999. "Parasite-Mediated Selection Against Inbred Soay Sheep in a Free-Living, Island Population." *Evolution* 53, no. 4: 1259–1267. https://doi.org/10.2307/2640828.

Criscione, C. D., and M. S. Blouin. 2005. "Effective Sizes of Macroparasite Populations: A Conceptual Model." *Trends in Parasitology* 21, no. 5: 212–217. https://doi.org/10.1016/j.pt.2005.03.002.

Criscione, C. D., R. Poulin, and M. S. Blouin. 2005. "Molecular Ecology of Parasites: Elucidating Ecological and Microevolutionary Processes." *Molecular Ecology* 14, no. 8: 2247–2257. https://doi.org/10.1111/j.1365-294X.2005.02587.x.

Danecek, P., A. Auton, G. Abecasis, et al. 2011. "The Variant Call Format and VCFtools." *Bioinformatics* 27, no. 15: 2156–2158. https://doi.org/10.1093/bioinformatics/btr330.

Danecek, P., J. K. Bonfield, J. Liddle, et al. 2021. "Twelve Years of SAMtools and BCFtools." *GigaScience* 10, no. 2: giab008. https://doi.org/10.1093/gigascience/giab008.

Davies, J. L. 1958. "Pleistocene Geography and the Distribution of Northern Pinnipeds." *Ecology* 39, no. 1: 97–113. https://doi.org/10.2307/1929971.

Desdevises, Y. 2007. "Cophylogeny: Insights From Fish-Parasite Systems." *Parassitologia* 49, no. 3: 125–128.

DiBlasi, E., K. P. Johnson, S. A. Stringham, et al. 2018. "Phoretic Dispersal Influences Parasite Population Genetic Structure." *Molecular Ecology* 27, no. 12: 2770–2779. https://doi.org/10.1111/mec.14719.

Dietrich, M., L. Beati, E. Elguero, T. Boulinier, and K. D. McCoy. 2013. "Body Size and Shape Evolution in Host Races of the Tick *Ixodes uriae*." *Biological Journal of the Linnean Society* 108, no. 2: 323–334. https://doi.org/10.1111/j.1095-8312.2012.02021.x.

Doña, J., and K. P. Johnson. 2023. "Host Body Size, Not Host Population Size, Predicts Genome-Wide Effective Population Size of Parasites." *Evolution Letters* 7, no. 4: 285–292. https://doi.org/10.1093/evlett/qrad026.

Doña, J., M. Moreno-García, C. D. Criscione, D. Serrano, and R. Jovani. 2015. "Species mtDNA Genetic Diversity Explained by Infrapopulation Size in a Host-Symbiont System." *Ecology and Evolution* 5, no. 24: 5801–5809. https://doi.org/10.1002/ece3.1842.

Doña, J., D. Serrano, S. Mironov, A. Montesinos-Navarro, and R. Jovani. 2019. "Unexpected Bird–Feather Mite Associations Revealed by DNA Metabarcoding Uncovers a Dynamic Ecoevolutionary Scenario." *Molecular Ecology* 28, no. 2: 379–390. https://doi.org/10.1111/mec.14968.

Doña, J., A. D. Sweet, and K. P. Johnson. 2020. "Comparing Rates of Introgression in Parasitic Feather Lice With Differing Dispersal Capabilities." *Communications Biology* 3: 610. https://doi.org/10.1038/s42003-020-01345-x.

Dong, Y., M. Zhao, and R. Shao. 2022. "Fragmented Mitochondrial Genomes of Seal Lice (Family Echinophthiriidae) and Gorilla Louse (Family Pthiridae): Frequent Minichromosomal Splits and a Host Switch of Lice Between Seals." *BMC Genomics* 23, no. 1: 283. https://doi.org/10.1186/s12864-022-08530-8.

Ekroth, A. K. E., C. Rafaluk-Mohr, and K. C. King. 2019. "Host Genetic Diversity Limits Parasite Success Beyond Agricultural Systems: A Meta-Analysis." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1911: 20191811. https://doi.org/10.1098/rspb.2019.1811.

Ellegren, H., and N. Galtier. 2016. "Determinants of Genetic Diversity." *Nature Reviews Genetics* 17, no. 7: 422–433. https://doi.org/10.1038/nrg.2016.58.

Ferguson, S. H., and J. W. Higdon. 2006. "How Seals Divide Up the World: Environment, Life History, and Conservation." *Oecologia* 150, no. 2: 318–329. https://doi.org/10.1007/s00442-006-0489-x.

Ferguson, S. H., J. W. Higdon, B. G. Young, et al. 2025. "A Comparative Analysis of Life-History Features and Adaptive Strategies of Arctic and Subarctic Seal Species—Who Will Win the Climate Change Challenge?" *Canadian Journal of Zoology* 103: 1–17. https://doi.org/10.1139/cjz-2024-0093.

Ferrer, T., P. Boveng, D. D. W. Hauser, et al. 2024. "Genetic and Evolutionary Divergence of Harbour Seals (*Phoca vitulina*) in Iliamna Lake, Alaska." *Biology Letters* 20, no. 10: 20240166. https://doi.org/10.1098/rsbl.2024.0166.

Fietz, K., A. Galatius, J. Teilmann, et al. 2016. "Shift of Grey Seal Subspecies Boundaries in Response to Climate, Culling and Conservation." *Molecular Ecology* 25, no. 17: 4097–4112. https://doi.org/10.1111/mec.13748.

Frichot, E., and O. François. 2015. "LEA: An R Package for Landscape and Ecological Association Studies." *Methods in Ecology and Evolution* 6: 925–929. https://doi.org/10.1111/2041-210X.12382.

Frichot, E., F. Mathieu, T. Trouillon, G. Bouchard, and O. François. 2014. "Fast and Efficient Estimation of Individual Ancestry Coefficients." *Genetics* 196: 973–983. https://doi.org/10.1534/genetics.113.160572.

Galatius, A., M. T. Olsen, M. Allentoft-Larsen, et al. 2024. "Evidence of Distribution Overlap Between Atlantic and Baltic Grey Seals." *Journal of the Marine Biological Association of the United Kingdom* 104: e30. https://doi.org/10.1017/S0025315424000213.

Ganz, H. H., and D. Ebert. 2010. "Benefits of Host Genetic Diversity for Resistance to Infection Depend on Parasite Diversity." *Ecology* 91, no. 5: 1263–1268. https://doi.org/10.1890/09-1243.1.

Gibson, A. K. 2022. "Genetic Diversity and Disease: The Past, Present, and Future of an Old Idea." *Evolution* 76, no. S1: 20–36. https://doi.org/10.1111/evo.14395.

Gillespie, J. H. 2001. "Is the Population Size of a Species Relevant to Its Evolution?" *Evolution: International Journal of Organic Evolution* 55, no. 11: 2161–2169. https://doi.org/10.1111/j.0014-3820.2001.tb00732.x.

Gokhale, C. S., A. Papkou, A. Traulsen, and H. Schulenburg. 2013. "Lotka–Volterra Dynamics Kills the Red Queen: Population Size Fluctuations and Associated Stochasticity Dramatically Change Host-Parasite Coevolution." *BMC Evolutionary Biology* 13, no. 1: 254. https://doi.org/10.1186/1471-2148-13-254.

Gómez, J. M., M. Verdú, and F. Perfectti. 2010. "Ecological Interactions Are Evolutionarily Conserved Across the Entire Tree of Life." *Nature* 465, no. 7300: 918–921. https://doi.org/10.1038/nature09113.

Gorton, M. J., E. L. Kasl, J. T. Detwiler, and C. D. Criscione. 2012. "Testing Local-Scale Panmixia Provides Insights Into the Cryptic Ecology, Evolution, and Epidemiology of Metazoan Animal Parasites." *Parasitology* 139, no. 8: 981–997. https://doi.org/10.1017/S0031182012000455.

Goudet, J., and T. Jombart. 2022. "Hierfstat: Estimation and Tests of Hierarchical F-Statistics." R Package Version 0.5-11. [Computer Software]. https://CRAN.R-project.org/package=hierfstat.

Greenspoon, L., E. Krieger, R. Sender, et al. 2023. "The Global Biomass of Wild Mammals." *Proceedings of the National Academy of Sciences of the United States of America* 120, no. 10: e2204892120. https://doi.org/10.1073/pnas.2204892120.

Grossi, A. A., C. Tian, L. Lei, F. Zou, and D. R. Gustafsson. 2024. "Cospeciation Patterns of Two Groups of Chewing Lice (Insecta: Phthiraptera: Ischnocera and Amblycera) Infesting Asian Songbirds (Aves: Passeriformes)." *Journal of Parasitology* 110, no. 6: 649–665. https://doi.org/10.1645/24-87.

Gustafson, K. D., R. A. Newman, T. Rhen, and V. V. Tkach. 2018. "Spatial and Genetic Structure of Directly-Transmitted Parasites Reflects the Distribution of Their Specific Amphibian Hosts." *Population Ecology* 60, no. 3: 261–273. https://doi.org/10.1007/s10144-018-0605-x.

Gustafsson, D. R., O. Sychra, and A. A. Grossi. 2025. "An Estimate of the Diversity and Threat Levels of Avian Chewing Lice (Phthiraptera: Ischnocera, Amblycera), With a Call for "Pre-Emptive Red Listing"." *Biodiversity and Conservation* 34, no. 3: 1015–1037. https://doi.org/10.1007/s10531-024-03006-5.

Gutiérrez, J., M. Seguel, P. Saenz-Agudelo, G. Acosta-Jamett, and C. Verdugo. 2024. "Host Genetic Diversity and Body Condition Influence Parasite Resistance and Clearance in a Wild Marine Mammal Population." *Biology Letters* 20, no. 10: 20240302. https://doi.org/10.1098/rsbl.2024.0302.

Guzinski, J., C. M. Bull, S. C. Donnellan, and M. G. Gardner. 2009. "Molecular Genetic Data Provide Support for a Model of Transmission Dynamics in an Australian Reptile Tick, *Bothriocroton hydrosauri*." *Molecular Ecology* 18, no. 2: 227–234. https://doi.org/10.1111/j.1365-294X.2008.04023.x.

Hafner, M. S., P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes, and S. A. Nadler. 1994. "Disparate Rates of Molecular Evolution in Cospeciating Hosts and Parasites." *Science* 265, no. 5175: 1087–1090. https://doi.org/10.1126/science.8066445.

Harding, K. C., and T. J. Härkönen. 1999. "Development in the Baltic Grey Seal (*Halichoerus grypus*) and Ringed Seal (*Phoca hispida*) Populations During the 20th Century." *Ambio* 28, no. 7: 619–627.

Härkönen, T., R. Dietz, P. Reijnders, et al. 2006. "The 1988 and 2002 Phocine Distemper Virus Epidemics in European Harbour Seals." *Diseases of Aquatic Organisms* 68, no. 2: 115–130. https://doi.org/10.3354/dao068115.

Härkönen, T., K. C. Harding, S. Wilson, et al. 2012. "Collapse of a Marine Mammal Species Driven by Human Impacts." *PLoS One* 7, no. 9: e43130. https://doi.org/10.1371/journal.pone.0043130.

Harper, S. E., T. A. Spradling, J. W. Demastes, and C. S. Calhoun. 2015. "Host Behaviour Drives Parasite Genetics at Multiple Geographic Scales: Population Genetics of the Chewing Louse, Thomomydoecus Minor." *Molecular Ecology* 24, no. 16: 4129–4144. https://doi.org/10.1111/mec.13306.

Harrison, K., A. M. Tarone, T. DeWitt, and R. F. Medina. 2022. "Predicting the Occurrence of Host-Associated Differentiation in Parasitic Arthropods: A Quantitative Literature Review." *Entomologia Experimentalis et Applicata* 170, no. 1: 5–22. https://doi.org/10.1111/eea.13123.

Hassanin, A., G. Veron, A. Ropiquet, et al. 2021. "Evolutionary History of Carnivora (Mammalia, Laurasiatheria) Inferred From Mitochondrial Genomes." *PLoS One* 16, no. 2: e0240770. https://doi.org/10.1371/journal.pone.0240770.

Haubold, B., P. Pfaffelhuber, and M. Lynch. 2010. "mlRho—A Program for Estimating the Population Mutation and Recombination Rates From Shotgun-Sequenced Diploid Genomes." *Molecular Ecology* 19, no. Suppl 1: 277–284. https://doi.org/10.1111/j.1365-294X.2009.04482.x.

Hay, E. M., R. Poulin, and F. Jorge. 2020. "Macroevolutionary Dynamics of Parasite Diversification: A Reality Check." *Journal of Evolutionary Biology* 33, no. 12: 1758–1769. https://doi.org/10.1111/jeb.13714.

Hayer, S., B. P. Sturm, S. Büsse, T. H. Büscher, and S. N. Gorb. 2022. "Louse Flies Holding on Mammals' Hair: Comparative Functional Morphology of Specialized Attachment Devices of Ectoparasites (Diptera: Hippoboscoidea)." *Journal of Morphology* 283, no. 12: 1561–1576. https://doi.org/10.1002/jmor.21523.

Hebert, P. D. N., S. Ratnasingham, and J. R. de Waard. 2003. "Barcoding Animal Life: Cytochrome *c* Oxidase Subunit 1 Divergences Among Closely Related Species." *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270, no. Suppl_1: S96–S99. https://doi.org/10.1098/rsbl.2003.0025.

Hedrick, P. W. 2009. "Conservation Genetics and North American Bison (*Bison bison*)." *Journal of Heredity* 100, no. 4: 411–420. https://doi.org/10.1093/jhered/esp024.

Hernandez-Caballero, I., L. Garcia-Longoria, I. Gomez-Mestre, and A. Marzal. 2022. "The Adaptive Host Manipulation Hypothesis: Parasites Modify the Behaviour, Morphology, and Physiology of Amphibians." *Diversity* 14, no. 9: 739. https://doi.org/10.3390/d14090739.

Herzog, I., U. Siebert, and K. Lehnert. 2024. "High Prevalence and Low Intensity of *Echinophthirius horridus* Infection in Seals Revealed by High Effort Sampling." *Scientific Reports* 14, no. 1: 14258. https://doi.org/10.1038/s41598-024-64890-z.

Herzog, I., P. Wohlsein, A. Preuss, et al. 2024. "Heartworm and Seal Louse: Trends in Prevalence, Characterisation of Impact and Transmission Pathways in a Unique Parasite Assembly on Seals in the North and Baltic Sea." *International Journal for Parasitology: Parasites and Wildlife* 23: 100898. https://doi.org/10.1016/j.ijppaw.2023.100898.

Hesse, E., and A. Buckling. 2016. "Host Population Bottlenecks Drive Parasite Extinction During Antagonistic Coevolution." *Evolution* 70, no. 1: 235–240. https://doi.org/10.1111/evo.12837.

Hoekendijk, J. P. A., A. Grundlehner, S. Brasseur, B. Kellenberger, D. Tuia, and G. Aarts. 2023. "Stay Close, but Not Too Close: Aerial Image Analysis Reveals Patterns of Social Distancing in Seal Colonies." *Royal Society Open Science* 10, no. 8: 230269. https://doi.org/10.1098/rsos.230269.

Hoelzel, A. R., G. A. Gkafas, H. Kang, et al. 2024. "Genomics of Post-Bottleneck Recovery in the Northern Elephant Seal." *Nature Ecology & Evolution* 8, no. 4: 686–694. https://doi.org/10.1038/s41559-024-02337-4.

Hoffman, J. I., F. Simpson, P. David, et al. 2014. "High-Throughput Sequencing Reveals Inbreeding Depression in a Natural Population." *Proceedings of the National Academy of Sciences of the United States of America* 111, no. 10: 3775–3780. https://doi.org/10.1073/pnas.1318945111.

Hoffman, J. I., D. L. J. Vendrami, K. Hench, et al. 2024. "Genomic and Fitness Consequences of a Near-Extinction Event in the Northern Elephant Seal." *Nature Ecology & Evolution* 8, no. 12: 2309–2324. https://doi.org/10.1038/s41559-024-02533-2.

Hood, G. R., A. A. Forbes, T. H. Q. Powell, et al. 2015. "Sequential Divergence and the Multiplicative Origin of Community Diversity." *Proceedings of the National Academy of Sciences of the United States of America* 112, no. 44: E5980–E5989. https://doi.org/10.1073/pnas.1424717112.

Hutchinson, M. C., E. F. Cagua, J. A. Balbuena, D. B. Stouffer, and T. Poisot. 2017. "paco: Implementing Procrustean Approach to Cophylogeny in R." *Methods in Ecology and Evolution* 8, no. 8: 932–940. https://doi.org/10.1111/2041-210X.12736.

Huyse, T., R. Poulin, and A. Théron. 2005. "Speciation in Parasites: A Population Genetics Approach." *Trends in Parasitology* 21, no. 10: 469–475. https://doi.org/10.1016/j.pt.2005.08.009.

IUCN-Marine Mammal Protected Areas Task Force. 2021. "Caspian Seal Transitory Migration and Feeding Area IMMA." https://www.marinemammalhabitat.org/wp-content/uploads/imma-factsheets/BlackSeaTurkishStraitsCaspianSea/Caspian-Seal-Transitory-Migration-Feeding-BlackSeaTurkishStraitsCaspianSea.pdf.

Ives, A. R., and D. Li. 2018. "rr2: An R Package to Calculate R^2s for Regression Models." *Journal of Open Source Software* 3, no. 30: 1028. https://doi.org/10.21105/joss.01028.

Jacquot, M., M. A. Wallace, D. G. Streicker, and R. Biek. 2022. "Geographic Range Overlap Rather Than Phylogenetic Distance Explains Rabies Virus Transmission Among Closely Related Bat Species." *Viruses* 14, no. 11: 2399. https://doi.org/10.3390/v14112399.

Janecka, M. J., F. Rovenolt, and J. F. Stephenson. 2021. "How Does Host Social Behavior Drive Parasite Non-Selective Evolution From the Within-Host to the Landscape-Scale?" *Behavioral Ecology and Sociobiology* 75, no. 11: 150. https://doi.org/10.1007/s00265-021-03089-y.

Janiszewska, A., T. Rewicz, P. Minias, et al. 2025. "Host-Related Genetic Differentiation of a Polyxenic Avian Ectoparasite, *Ornithomya avicularia* (Hippoboscidae)." *International Journal for Parasitology: Parasites and Wildlife* 27: 101081. https://doi.org/10.1016/j.ijppaw.2025.101081.

Jefferson, T. A., M. A. Webber, and R. L. Pitman. 2015. "6—Pinnipeds." In *Marine Mammals of the World*, edited by T. A. Jefferson, M. A. Webber, and R. L. Pitman, 2nd ed., 358–522. Academic Press. https://doi.org/10.1016/B978-0-12-409542-7.50005-6.

Jeon, J. Y., A. N. Black, E. J. Heenkenda, et al. 2024. "Genomic Diversity as a Key Conservation Criterion: Proof-of-Concept From Mammalian Whole-Genome Resequencing Data." *Evolutionary Applications* 17, no. 9: e70000. https://doi.org/10.1111/eva.70000.

Jephcott, T. G., T. Sime-Ngando, F. H. Gleason, and D. J. Macarthur. 2016. "Host–Parasite Interactions in Food Webs: Diversity, Stability, and Coevolution." *Food Webs* 6: 1–8. https://doi.org/10.1016/j.fooweb.2015.12.001.

Johnson, K. P., R. J. Adams, R. D. M. Page, and D. H. Clayton. 2003. "When Do Parasites Fail to Speciate in Response to Host Speciation?" *Systematic Biology* 52, no. 1: 37–47. https://doi.org/10.1080/10635150390132704.

Johnson, K. P., J. D. Weckstein, S. Virrueta Herrera, and J. Doña. 2021. "The Interplay Between Host Biogeography and Phylogeny in Structuring Diversification of the Feather Louse Genus *Penenirmus*." *Molecular Phylogenetics and Evolution* 165: 107297. https://doi.org/10.1016/j.ympev.2021.107297.

Johnson, K. P., B. L. Williams, D. M. Drown, R. J. Adams, and D. H. Clayton. 2002. "The Population Genetics of Host Specificity: Genetic Differentiation in Dove Lice (Insecta: Phthiraptera)." *Molecular Ecology* 11, no. 1: 25–38. https://doi.org/10.1046/j.0962-1083.2001.01412.x.

Johnson, P., D. M. Calhoun, W. E. Moss, et al. 2021. "The Cost of Travel: How Dispersal Ability Limits Local Adaptation in Host–Parasite Interactions." *Journal of Evolutionary Biology* 34, no. 3: 512–524. https://doi.org/10.1111/jeb.13754.

Jombart, T., and I. Ahmed. 2011. "Adegenet 1.3-1: New Tools for the Analysis of Genome-Wide SNP Data." *Bioinformatics* 27, no. 21: 3070–3071. https://doi.org/10.1093/bioinformatics/btr521.

Katoh, K., and D. M. Standley. 2013. "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability." *Molecular Biology and Evolution* 30, no. 4: 772–780. https://doi.org/10.1093/molbev/mst010.

Kelly, B. P., J. L. Bengtson, P. L. Boveng, et al. 2010. "Status Review of the Ringed Seal (*Phoca hispida*)." U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-212.

Kolencik, S., E. L. Stanley, A. Punnath, et al. 2024. "Parasite Escape Mechanisms Drive Morphological Diversification in Avian Lice." *Proceedings of the Royal Society B: Biological Sciences* 291, no. 2019: 20232665. https://doi.org/10.1098/rspb.2023.2665.

Koop, J. A. H., K. E. DeMatteo, P. G. Parker, and N. K. Whiteman. 2014. "Birds Are Islands for Parasites." *Biology Letters* 10, no. 8: 20140255. https://doi.org/10.1098/rsbl.2014.0255.

Kovacs, K. M., A. Aguilar, D. Aurioles, et al. 2012. "Global Threats to Pinnipeds." *Marine Mammal Science* 28, no. 2: 414–436. https://doi.org/10.1111/j.1748-7692.2011.00479.x.

Krafft, B. A., K. M. Kovacs, and C. Lydersen. 2007. "Distribution of Sex and Age Groups of Ringed Seals *Pusa hispida* in the Fast-Ice Breeding Habitat of Kongsfjorden, Svalbard." *Marine Ecology Progress Series* 335: 199–206. https://doi.org/10.3354/meps335199.

Kunnasranta, M., M. Niemi, M. Auttila, M. Valtonen, J. Kammonen, and T. Nyman. 2021. "Sealed in a Lake — Biology and Conservation of the Endangered Saimaa Ringed Seal: A Review." *Biological Conservation* 253: 108908. https://doi.org/10.1016/j.biocon.2020.108908.

Kurochkin, Y. V., and B. I. Badamshin. 1968. "Finding of the Seal Lice *Echinophthirius horridus* Olfers, 1816 on the Caspian Seal and the Problem of Origin of Its Parasite Fauna." *Trudy Astrakhanskogo Zapovednika* 11: 199–208.

Kwak, M. L., P. A. Burns, M. W. Hastriter, J. Jenkins Shaw, and R. Nakao. 2024. "The Threatened Pookila (*Pseudomys novaehollandiae*) Hosts a Diverse Macrobiome of Arthropods at Varying Risks of Co-Extinction." *Journal of Insect Conservation* 28, no. 3: 449–458. https://doi.org/10.1007/s10841-024-00559-2.

Lafferty, K. D., S. Allesina, M. Arim, et al. 2008. "Parasites in Food Webs: The Ultimate Missing Links." *Ecology Letters* 11, no. 6: 533–546. https://doi.org/10.1111/j.1461-0248.2008.01174.x.

Laidre, K. L., H. Stern, K. M. Kovacs, et al. 2015. "Arctic Marine Mammal Population Status, Sea Ice Habitat Loss, and Conservation Recommendations for the 21st Century." *Conservation Biology* 29, no. 3: 724–737. https://doi.org/10.1111/cobi.12474.

Langmead, B., and S. L. Salzberg. 2012. "Fast Gapped-Read Alignment With Bowtie 2." *Nature Methods* 9, no. 4: 357–359. https://doi.org/10.1038/nmeth.1923.

Laws, R. M. 1981. "Biology of Antarctic Seals." *Science Progress* 67, no. 267: 377–397.

Lazarev, S., K. F. Kuiper, O. Oms, et al. 2021. "Five-Fold Expansion of the Caspian Sea in the Late Pliocene: New and Revised Magnetostratigraphic and 40Ar/39Ar Age Constraints on the Akchagylian Stage." *Global and Planetary Change* 206: 103624. https://doi.org/10.1016/j.gloplacha.2021.103624.

Lee, L., D. J. X. Tan, J. Oboňa, D. R. Gustafsson, Y. Ang, and R. Meier. 2022. "Hitchhiking Into the Future on a Fly: Toward a Better Understanding of Phoresy and Avian Louse Evolution (Phthiraptera) by Screening Bird Carcasses for Phoretic Lice on Hippoboscid Flies (Diptera)." *Systematic Entomology* 47, no. 3: 420–429. https://doi.org/10.1111/syen.12539.

Lei, H.-P., I. Jakovlić, S. Zhou, et al. 2024. "Geography, Phylogeny and Host Switch Drive the Coevolution of Parasitic *Gyrodactylus* Flatworms and Their Hosts." *Parasites & Vectors* 17, no. 1: 42. https://doi.org/10.1186/s13071-023-06111-6.

Leidenberger, S., K. Harding, and T. Härkönen. 2007. "Phocid Seals, Seal Lice and Heartworms: A Terrestrial Host-Parasite System Conveyed to the Marine Environment." *Diseases of Aquatic Organisms* 77: 235–253. https://doi.org/10.3354/dao01823.

Leonardi, M. S., E. A. Crespo, J. A. Raga, and F. J. Aznar. 2013. "Lousy Mums: Patterns of Vertical Transmission of an Amphibious Louse." *Parasitology Research* 112, no. 9: 3315–3323. https://doi.org/10.1007/s00436-013-3511-3.

Leonardi, M. S., J. E. Crespo, F. Soto, and C. R. Lazzari. 2021. "How Did Seal Lice Turn Into the Only Truly Marine Insects?" *Insects* 13, no. 1: 46. https://doi.org/10.3390/insects13010046.

Leonardi, M. S., S. Virrueta Herrera, A. Sweet, J. Negrete, and K. P. Johnson. 2019. "Phylogenomic Analysis of Seal Lice Reveals Codivergence With Their Hosts." *Systematic Entomology* 44, no. 4: 699–708. https://doi.org/10.1111/syen.12350.

Li, S.-H., Y. Liu, C.-F. Yeh, et al. 2022. "Not out of the Woods Yet: Signatures of the Prolonged Negative Genetic Consequences of a Population Bottleneck in a Rapidly Re-Expanding Wader, the Black-Faced Spoonbill *Platalea minor*." *Molecular Ecology* 31, no. 2: 529–545. https://doi.org/10.1111/mec.16260.

Li, Y., R. Zhang, S. Liu, et al. 2017. "The Molecular Evolutionary Dynamics of Oxidative Phosphorylation (OXPHOS) Genes in Hymenoptera." *BMC Evolutionary Biology* 17: 269. https://doi.org/10.1186/s12862-017-1111-z.

Liu, X., S. Rønhøj Schjøtt, S. M. Granquist, et al. 2022. "Origin and Expansion of the World's Most Widespread Pinniped: Range-Wide Population Genomics of the Harbour Seal (*Phoca vitulina*)." *Molecular Ecology* 31, no. 6: 1682–1699. https://doi.org/10.1111/mec.16365.

Löytynoja, A., J. Pohjoismäki, M. Valtonen, et al. 2025. "Deep Origins, Distinct Adaptations, and Species-Level Status Indicated for a Glacial Relict Seal." *Proceedings of the National Academy of Sciences of the United States of America* 122, no. 25: e2503368122. https://doi.org/10.1073/pnas.2503368122.

Löytynoja, A., P. Rastas, M. Valtonen, et al. 2023. "Fragmented Habitat Compensates for the Adverse Effects of Genetic Bottleneck." *Current Biology* 33, no. 6: 1009–1018.e7. https://doi.org/10.1016/j.cub.2023.01.040.

Lunneryd, S. G. 1991. "Anisakid Nematodes in the Harbour Seal *Phoca vitulina* From the Kattegat-Skagerrak and the Baltic." *Ophelia* 34, no. 2: 105–115. https://doi.org/10.1080/00785326.1991.10429699.

Lymbery, A. J., and N. J. Smit. 2023. "Conservation of Parasites: A Primer." *International Journal for Parasitology: Parasites and Wildlife* 21: 255–263. https://doi.org/10.1016/j.ijppaw.2023.07.001.

Martinů, J., V. Hypša, and J. Štefka. 2018. "Host Specificity Driving Genetic Structure and Diversity in Ectoparasite Populations: Coevolutionary Patterns in *Apodemus* Mice and Their Lice." *Ecology and Evolution* 8, no. 20: 10008–10022. https://doi.org/10.1002/ece3.4424.

Mazé-Guilmo, E., S. Blanchet, K. D. McCoy, and G. Loot. 2016. "Host Dispersal as the Driver of Parasite Genetic Structure: A Paradigm Lost?" *Ecology Letters* 19, no. 3: 336–347. https://doi.org/10.1111/ele.12564.

Measures, L. N. 2001. "Lungworms of Marine Mammals." In *Parasitic Diseases of Wild Mammals*, edited by W. M. Samuel, M. J. Pybus, and A. A. Kocan, 2nd ed., 279–300. Iowa State University Press. https://doi.org/10.1002/9780470377000.ch10.

Meirmans, P. G. 2012. "The Trouble With Isolation by Distance." *Marine Ecology* 21, no. 12: 2839–2846. https://doi.org/10.1111/j.1365-294X.2012.05578.x.

Minh, B. Q., H. A. Schmidt, O. Chernomor, et al. 2020. "IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era." *Molecular Biology and Evolution* 37, no. 5: 1530–1534. https://doi.org/10.1093/molbev/msaa015.

Morand, S. 2015. "(Macro-) Evolutionary Ecology of Parasite Diversity: From Determinants of Parasite Species Richness to Host Diversification." *International Journal for Parasitology: Parasites and Wildlife* 4, no. 1: 80–87. https://doi.org/10.1016/j.ijppaw.2015.01.001.

Nazarizadeh, M., M. Nováková, G. Loot, et al. 2023. "Historical Dispersal and Host-Switching Formed the Evolutionary History of a Globally Distributed Multi-Host Parasite—The *Ligula intestinalis* Species Complex." *Molecular Phylogenetics and Evolution* 180: 107677. https://doi.org/10.1016/j.ympev.2022.107677.

Nebenführ, M., U. Arnason, and A. Janke. 2024. "Whole-Genome Re-Sequencing of the Baikal Seal and Other Phocid Seals for a Glimpse Into Their Genetic Diversity, Demographic History, and Phylogeny." *GigaByte* 2024: gigabyte142. https://doi.org/10.46471/gigabyte.142.

Nessner, C. E., J. J. Andersen, M. A. Renshaw, M. M. Giresi, and J. E. Light. 2014. "Characterization of 17 Novel Polymorphic Microsatellite Loci in the Mammal Chewing Louse *Geomydoecus ewingi* (Insecta: Phthiraptera) for Population Genetic Analyses." *Journal of Parasitology* 100, no. 6: 873–877. https://doi.org/10.1645/13-415.1.

Nylin, S., S. Agosta, S. Bensch, et al. 2018. "Embracing Colonizations: A New Paradigm for Species Association Dynamics." *Trends in Ecology & Evolution* 33, no. 1: 4–14. https://doi.org/10.1016/j.tree.2017.10.005.

Nyman, T., E. Papadopoulou, E. Ylinen, et al. 2021. "DNA Barcoding Reveals Different Cestode Helminth Species in Northern European Marine and Freshwater Ringed Seals." *International Journal for Parasitology: Parasites and Wildlife* 15: 255–261. https://doi.org/10.1016/j.ijppaw.2021.06.004.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2022. "vegan: Community Ecology Package." R Package Version 2.6–4 [Computer Software]. https://github.com/vegandevs/vegan.

Ortego, J., V. Céspedes, A. Millán, and A. J. Green. 2021. "Genomic Data Support Multiple Introductions and Explosive Demographic Expansions in a Highly Invasive Aquatic Insect." *Molecular Ecology* 30, no. 17: 4189–4203. https://doi.org/10.1111/mec.16050.

Ortiz, E. M. 2019. "vcf2phylip v2.0: Convert a VCF Matrix Into Several Matrix Formats for Phylogenetic Analysis." [Computer software]. https://doi.org/10.5281/zenodo.2540861.

Pacheco-Sandoval, A., Y. Schramm, G. Heckel, I. Giffard-Mena, and A. Lago-Lestón. 2024. "Unraveling the Gut Microbiota of Mexican Pinnipeds: The Dominance of Life Histories Over Phylogeny." *Applied and Environmental Microbiology* 90, no. 6: e02030-23. https://doi.org/10.1128/aem.02030-23.

Palo, J. U., and R. Väinölä. 2006. "The Enigma of the Landlocked Baikal and Caspian Seals Addressed Through Phylogeny of Phocine

Mitochondrial Sequences." *Biological Journal of the Linnean Society* 88, no. 1: 61–72. https://doi.org/10.1111/j.1095-8312.2006.00607.x.

Papkou, A., C. S. Gokhale, A. Traulsen, and H. Schulenburg. 2016. "Host–Parasite Coevolution: Why Changing Population Size Matters." *Zoology* 119, no. 4: 330–338. https://doi.org/10.1016/j.zool.2016.02.001.

Papkou, A., R. Schalkowski, M.-C. Barg, S. Koepper, and H. Schulenburg. 2021. "Population Size Impacts Host–Pathogen Coevolution." *Proceedings of the Royal Society B: Biological Sciences* 288, no. 1965: 20212269. https://doi.org/10.1098/rspb.2021.2269.

Paplauskas, S., A. B. Duthie, and M. C. Tinsley. 2025. "An 'Epidemic Diversity' Conceptual Model Explains How Host Genetic Diversity Affects Variation in Parasite Success." Version 2. *bioRxiv*. https://doi.org/10.1101/2024.05.28.596150.

Paradis, E., and K. Schliep. 2019. "Ape 5.0: An Environment for Modern Phylogenetics and Evolutionary Analyses in R." *Bioinformatics* 35, no. 3: 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Park, T., G. Burin, D. Lazo-Cancino, et al. 2024. "Charting the Course of Pinniped Evolution: Insights From Molecular Phylogeny and Fossil Record Integration." *Evolution* 78, no. 7: 1212–1226. https://doi.org/10.1093/evolut/qpae061.

Paterson, A. M., and J. Banks. 2001. "Analytical Approaches to Measuring Cospeciation of Host and Parasites: Through a Glass, Darkly." *International Journal for Parasitology* 31, no. 9: 1012–1022. https://doi.org/10.1016/S0020-7519(01)00199-0.

Peart, C. R., S. Tusso, S. D. Pophaly, et al. 2020. "Determinants of Genetic Variation Across Eco-Evolutionary Scales in Pinnipeds." *Nature Ecology & Evolution* 4, no. 8: 1095–1104. https://doi.org/10.1038/s41559-020-1215-5.

Peschko, V., S. Müller, P. Schwemmer, et al. 2020. "Wide Dispersal of Recently Weaned Grey Seal Pups in the Southern North Sea." *ICES Journal of Marine Science* 77, no. 5: 1762–1771. https://doi.org/10.1093/icesjms/fsaa045.

Pilosof, S., M. A. Fortuna, J.-F. Cosson, et al. 2014. "Host–Parasite Network Structure Is Associated With Community-Level Immunogenetic Diversity." *Nature Communications* 5, no. 1: 1. https://doi.org/10.1038/ncomms6172.

Pinheiro, J., D. Bates, and R Core Team. 2023. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-162. [Computer software]. https://CRAN.R-project.org/package=nlme.

Poulin, R. 2014. "Parasite Biodiversity Revisited: Frontiers and Constraints." *International Journal for Parasitology* 44, no. 9: 581–589. https://doi.org/10.1016/j.ijpara.2014.02.003.

Preuss, A., T. H. Büscher, I. Herzog, P. Wohlsein, K. Lehnert, and S. N. Gorb. 2024. "Attachment Performance of the Ectoparasitic Seal Louse *Echinophthirius horridus*." *Communications Biology* 7: 36. https://doi.org/10.1038/s42003-023-05722-0.

Price, P. W. 1980. *Evolutionary Biology of Parasites*. Princeton University Press. https://www.jstor.org/stable/j.ctvx8b6r1.

Puechmaille, S. J. 2016. "The Program STRUCTURE Does Not Reliably Recover the Correct Population Structure When Sampling Is Uneven: Subsampling and New Estimators Alleviate the Problem." *Molecular Ecology Resources* 16, no. 3: 608–627. https://doi.org/10.1111/1755-0998.12512.

Quinn, C. B., S. Preckler-Quisquater, M. R. Buchalski, and B. N. Sacks. 2024. "Whole Genomes Inform Genetic Rescue Strategy for Montane Red Foxes in North America." *Molecular Biology and Evolution* 41, no. 9: msae193. https://doi.org/10.1093/molbev/msae193.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing* [Computer Software]. R Foundation for Statistical Computing. https://www.R-project.org/.

Reed, D. L., and M. S. Hafner. 1997. "Host Specificity of Chewing Lice on Pocket Gophers: A Potential Mechanism for Cospeciation." *Journal of Mammalogy* 78, no. 2: 655–660. https://doi.org/10.2307/1382916.

Rosing-Asvid, A., A. Löytynoja, P. Momigliano, et al. 2023. "An Evolutionarily Distinct Ringed Seal in the Ilulissat Icefjord." *Molecular Ecology* 32: 5932–5943. https://doi.org/10.1111/mec.17163.

Sanderson, M. J. 2002. "Estimating Absolute Rates of Molecular Evolution and Divergence Times: A Penalized Likelihood Approach." *Molecular Biology and Evolution* 19: 101–109. https://doi.org/10.1093/oxfordjournals.molbev.a003974.

Sasal, P., Y. Desdevises, and S. Morand. 1998. "Host-Specialization and Species Diversity in Fish Parasites: Phylogenetic Conservatism?" *Ecography* 21, no. 6: 639–643.

Shaw, R. E., K. A. Farquharson, M. W. Bruford, et al. 2025. "Global Meta-Analysis Shows Action Is Needed to Halt Genetic Diversity Loss." *Nature* 638, no. 8051: 704–710. https://doi.org/10.1038/s41586-024-08458-x.

Smith, T. G., M. O. Hammill, and G. Taugbøl. 1991. "A Review of the Developmental, Behavioural and Physiological Adaptations of the Ringed Seal, *Phoca hispida*, to Life in the Arctic Winter." *Arctic* 44, no. 2: 124–131. https://doi.org/10.14430/arctic1528.

Solari, K. A., S. Morgan, A. D. Poyarkov, et al. 2025. "Exceedingly Low Genetic Diversity in Snow Leopards due to Persistently Small Population Size." *Proceedings of the National Academy of Sciences of the United States of America* 122, no. 41: e2502584122. https://doi.org/10.1073/pnas.2502584122.

Soto, F. A., J. Crespo, J. Negrete, and M. S. Leonardi. 2023. "Tell Me Who You Go With and I Will Tell You What You Do: Antarctic Seal Lice Behave Differently." *Marine Biology* 171: 68. https://doi.org/10.1007/s00227-023-04386-y.

Soto, F. A., J. Negrete, M. J. Klaich, and M. S. Leonardi. 2022. "Effect of Host Age, Sex and Life Stage on the Prevalence and Abundance of Sucking Lice on Weddell Seal in the Antarctic Peninsula." *Anais da Academia Brasileira de Ciências* 94, no. Suppl 1: e20210566. https://doi.org/10.1590/0001-3765202220210566.

Southwell, C., J. Bengtson, M. N. Bester, et al. 2012. "A Review of Data on Abundance, Trends in Abundance, Habitat Utilisation and Diet for Southern Ocean Ice-Breeding Seals." *CCAMLR Science* 19: 1–49.

Sromek, L., K. P. Johnson, M. Kunnasranta, et al. 2024. "Population Genomics of Seal Lice Provides Insights Into the Postglacial History of Northern European Seals." *Molecular Ecology* 33, no. 20: e17523. https://doi.org/10.1111/mec.17523.

Sromek, L., K. P. Johnson, M. Kunnasranta, et al. 2025. "Host Co-Occurrence and Population Size Explain Genetic Differentiation and Diversity in Seal Lice." [Dataset]. *Zenodo*. 10.5281/zenodo.15521502.

Sromek, L., E. Ylinen, M. Kunnasranta, et al. 2023. "Loss of Species and Genetic Diversity During Colonization: Insights From Acanthocephalan Parasites in Northern European Seals." *Ecology and Evolution* 13, no. 10: e10608. https://doi.org/10.1002/ece3.10608.

Stefan, L. M., E. Gómez-Díaz, S. V. Mironov, J. González-Solís, and K. D. McCoy. 2018. "More Than Meets the Eye: Cryptic Diversity and Contrasting Patterns of Host-Specificity in Feather Mites Inhabiting Seabirds." *Frontiers in Ecology and Evolution* 6: 97. https://doi.org/10.3389/fevo.2018.00097.

Štefka, J., P. E. Hoeck, L. F. Keller, and V. S. Smith. 2011. "A Hitchhikers Guide to the Galápagos: Co-Phylogeography of Galápagos Mockingbirds and Their Parasites." *BMC Evolutionary Biology* 11, no. 1: 284. https://doi.org/10.1186/1471-2148-11-284.

Stireman, J. O. I., J. D. Nason, and S. B. Heard. 2005. "Host-Associated Genetic Differentiation in Phytophagous Insects: General Phenomenon or Isolated Exceptions? Evidence From a Goldenrod-Insect Community."

Evolution 59, no. 12: 2573–2587. https://doi.org/10.1111/j.0014-3820.2005.tb00970.x.

Stoffel, M. A., E. Humble, A. J. Paijmans, et al. 2018. "Demographic Histories and Genetic Diversity Across Pinnipeds Are Shaped by Human Exploitation, Ecology and Life-History." *Nature Communications* 9, no. 1: 4836. https://doi.org/10.1038/s41467-018-06695-z.

Stoldt, M., M. N. Macit, E. Collin, and S. Foitzik. 2022. "Molecular (Co) evolution of Hymenopteran Social Parasites and Their Hosts." *Current Opinion in Insect Science* 50: 100889. https://doi.org/10.1016/j.cois.2022.100889.

Strobel, H. M., S. J. Hays, K. N. Moody, M. J. Blum, and D. C. Heins. 2019. "Estimating Effective Population Size for a Cestode Parasite Infecting Three-Spined Sticklebacks." *Parasitology* 146, no. 7: 883–896. https://doi.org/10.1017/S0031182018002226.

Sweet, A. D., B. M. Boyd, J. M. Allen, et al. 2018. "Integrating Phylogenomic and Population Genomic Patterns in Avian Lice Provides a More Complete Picture of Parasite Evolution." *Evolution* 72, no. 1: 95–112. https://doi.org/10.1111/evo.13386.

Sweet, A. D., S. E. Bush, D. R. Gustafsson, et al. 2018. "Host and Parasite Morphology Influence Congruence Between Host and Parasite Phylogenies." *International Journal for Parasitology* 48, no. 8: 641–648. https://doi.org/10.1016/j.ijpara.2018.01.007.

Sweet, A. D., and K. P. Johnson. 2018. "The Role of Parasite Dispersal in Shaping a Host–Parasite System at Multiple Evolutionary Scales." *Molecular Ecology* 27, no. 24: 5104–5119. https://doi.org/10.1111/mec.14937.

Tange Olsen, M., A. Löytynoja, M. Valtonen, et al. 2025. "Complex Origins and History of the Relict Fennoscandian Ringed Seals." *Ecology and Evolution* 15, no. 3: e71067. https://doi.org/10.1002/ece3.71067.

Thorn, C. S., R. W. Maness, J. M. Hulke, K. E. Delmore, and C. D. Criscione. 2023. "Population Genomics of Helminth Parasites." *Journal of Helminthology* 97: e29. https://doi.org/10.1017/S0022149X23000123.

Tietjen, M., M. D. Esteve-Gasent, I. Castro-Arellano, and R. F. Medina. 2022. "Genomic Evidence for Host-Associated Differentiation in an Animal Parasite, *Dermacentor variabilis*, the American Dog Tick." *Entomologia Experimentalis et Applicata* 170, no. 1: 95–107. https://doi.org/10.1111/eea.13120.

Trifonov, V. G., A. S. Tesakov, A. N. Simakova, et al. 2024. "Geological and Biotic Context of the Plio-Pleistocene Evolution of the Caucasus-Caspian Region (Akchagylian Transgression)." *Quaternary International* 686: 120–141. https://doi.org/10.1016/j.quaint.2023.03.011.

Ukkonen, P. 2002. "The Early History of Seals in the Northern Baltic." *Annales Zoologici Fennici* 39, no. 3: 187–207.

Van der Auwera, G. A., and B. D. O'Connor. 2020. *Genomics in the Cloud: Using Docker, GATK, and WDL in Terra*. O'Reilly Media.

van Schaik, J., G. Kerth, N. Bruyndonckx, and P. Christe. 2014. "The Effect of Host Social System on Parasite Population Genetic Structure: Comparative Population Genetics of Two Ectoparasitic Mites and Their Bat Hosts." *BMC Evolutionary Biology* 14, no. 1: 18. https://doi.org/10.1186/1471-2148-14-18.

Vázquez-Prieto, S., R. Vilas, E. Paniagua, and F. M. Ubeira. 2015. "Influence of Life History Traits on the Population Genetic Structure of Parasitic Helminths: A Minireview." *Folia Parasitologica* 62: 060. https://doi.org/10.14411/fp.2015.060.

Vihtakari, M. 2024. "ggOceanMaps: Plot Data on Oceanographic Paps Using "ggplot2"." R Package Version 2.2.0 [Computer software]. https://mikkovihtakari.github.io/ggOceanMaps/.

Vilas, R., S. Vázquez-Prieto, and E. Paniagua. 2012. "Contrasting Patterns of Population Genetic Structure of *Fasciola hepatica* From Cattle and Sheep: Implications for the Evolution of Anthelmintic Resistance." *Infection, Genetics and Evolution* 12, no. 1: 45–52. https://doi.org/10.1016/j.meegid.2011.10.010.

Villa, S. M., J. C. Altuna, J. S. Ruff, et al. 2019. "Rapid Experimental Evolution of Reproductive Isolation From a Single Natural Population." *Proceedings of the National Academy of Sciences of the United States of America* 116, no. 27: 13440–13445. https://doi.org/10.1073/pnas.1901247116.

Virrueta Herrera, S., K. P. Johnson, A. D. Sweet, E. Ylinen, M. Kunnasranta, and T. Nyman. 2022. "High Levels of Inbreeding With Spatial and Host-Associated Structure in Lice of an Endangered Freshwater Seal." *Molecular Ecology* 31, no. 18: 4593–4606. https://doi.org/10.1111/mec.16569.

Walden, H. S., A. L. Bryan, A. McIntosh, et al. 2020. "Helminth Fauna of Ice Seals in the Alaskan Bering and Chukchi Seas, 2006–15." *Journal of Wildlife Diseases* 56, no. 4: 863–872. https://doi.org/10.7589/2019-09-228.

Weir, B. S., and C. C. Cockerham. 1984. "Estimating F-Statistics for the Analysis of Population Structure." *Evolution* 38, no. 6: 1358–1370. https://doi.org/10.2307/2408641.

Weir, B. S., and J. Goudet. 2017. "A Unified Characterization of Population Structure and Relatedness." *Genetics* 206, no. 4: 2085–2103. https://doi.org/10.1534/genetics.116.198424.

Wells, K., D. I. Gibson, and N. J. Clark. 2019. "Global Patterns in Helminth Host Specificity: Phylogenetic and Functional Diversity of Regional Host Species Pools Matter." *Ecography* 42, no. 3: 416–427. https://doi.org/10.1111/ecog.03886.

Whiteman, N. K., R. T. Kimball, and P. G. Parker. 2007. "Co-Phylogeography and Comparative Population Genetics of the Threatened Galápagos Hawk and Three Ectoparasite Species: Ecology Shapes Population Histories Within Parasite Communities." *Molecular Ecology* 16, no. 22: 4759–4773. https://doi.org/10.1111/j.1365-294X.2007.03512.x.

Willi, Y., T. N. Kristensen, C. M. Sgrò, A. R. Weeks, M. Ørsted, and A. A. Hoffmann. 2022. "Conservation Genetics as a Management Tool: The Five Best-Supported Paradigms to Assist the Management of Threatened Species." *Proceedings of the National Academy of Sciences of the United States of America* 119, no. 1: e2105076119. https://doi.org/10.1073/pnas.2105076119.

Wilson, J.-J., K.-W. Sing, R. M. Floyd, and P. D. N. Hebert. 2017. "DNA Barcodes and Insect Biodiversity." In *Insect Biodiversity*, edited by R. G. Foottit and P. H. Adler, 575–592. John Wiley & Sons. https://doi.org/10.1002/9781118945568.ch17.

Wohlfeil, C. K., S. S. Godfrey, S. T. Leu, J. Clayton, and M. G. Gardner. 2020. "Spatial Proximity and Asynchronous Refuge Sharing Networks Both Explain Patterns of Tick Genetic Relatedness Among Lizards, but in Different Years." *Austral Ecology* 45, no. 4: 493–501. https://doi.org/10.1111/aec.12899.

Zheng, X., D. Levine, J. Shen, S. M. Gogarten, C. Laurie, and B. S. Weir. 2012. "A High-Performance Computing Toolset for Relatedness and Principal Component Analysis of SNP Data." *Bioinformatics* 28, no. 24: 3326–3328. https://doi.org/10.1093/bioinformatics/bts606.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Collection data for the 82 seal louse individuals included in our study. **Table S2:** Between- and within-group uncorrected percent COI sequence divergence among the main clades of the *E. horridus* mtDNA phylogeny (Figure S4b). Numbers represent means across all pairwise comparisons of sequences, with minimum and maximum values given in parentheses. **Table S3:** Estimates of genetic diversity in the focal seal louse populations. **Figure S1:** Cross-entropy in relation to different numbers of ancestral populations (K). **Figure S2:** LEA plots for $K = 2$–9 ancestral populations. The optimal

$K = 7$ is indicated by a square frame. **Figure S3:** PCA plot for seal louse individuals. Each dot represents an individual louse and is coloured according to the seal host sub(species). **Figure S4:** Maximum-likelihood phylogenies of seal lice based on (a) nuclear genomic data from 50 randomly selected 50-kb genomic windows and (b) mitochondrial coding sequences, and (c) corresponding phylogeny of seal hosts based on mitochondrial coding sequences assembled from sequencing reads extracted from seal lice. Individual lice (a, b) and seals (c) are coloured according to the seal host sub(species). The inset in (b) shows the full tree including also outgroup taxa. **Figure S5:** (a) PACo ordination plot and ultrametricized phylogenetic trees of seal lice and their hosts after pruning both trees to one tip per seal host (sub)species (inset). (b) F_{ST} between louse populations in relation to mitochondrial divergence between seal host (sub)species. **Figure S6:** (a) Distribution of mean standardised genetic distance between pairs of seal lice from the same infrapopulation when louse identities are permuted among seal individuals within seal host populations. The red arrow shows mean standardised distance between lice from the same infrapopulation in the real data. (b) Pairwise genetic distances between lice collected from the same or a different seal host individual (i.e., within or between infrapopulations (see legend)) within seal hosts with more than one louse from more than one seal individual. Large dots show mean distances within each group and lines denote ranges of twice the standard deviations.