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REVIEW ARTICLE

Unlocking the genome of perch – From genes to ecology and back again

Anti Vasemägi[1,2] | Mikhail Ozerov[1,3,4] | Kristina Noreikiene[2] | María-Eugenia López[1] | Anna Gårdmark[5]

[1]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

[2]Chair of Aquaculture, Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, Tartu, Estonia

[3]Department of Biology, University of Turku, Turku, Finland

[4]Biodiversity Unit, University of Turku, Turku, Finland

[5]Department of Aquatic Resources, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Anti Vasemägi, Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Stångholmsvägen 2, Drottningholm 17893, Sweden.
Email: anti.vasemagi@slu.se

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Abstract

Eurasian perch *Perca fluviatilis* has been a popular model species for decades in the fields of aquatic ecology, community dynamics, behaviour, physiology and ecotoxicology. Yet, despite extensive research, the progress of integrating genomic perspective into existing ecological knowledge in perch has been relatively modest. Meanwhile, the emergence of high-throughput sequencing technologies has completely changed the methods for genetic variation assessment and conducting biodiversity and evolutionary research. During the last 5 years, three genome assemblies of *P. fluviatilis* have been generated, allowing substantial advancement of our understanding of the interactions between ecological and evolutionary processes at the whole-genome level. We review the past progress, current status and potential future impact of the genomic resources and tools for ecological research in Eurasian perch focusing on the utility of recent whole-genome assemblies. Furthermore, we demonstrate the power of genome-wide approaches and newly developed tools and outline recent cases where genomics have contributed to new ecological and evolutionary knowledge. We explore how the availability of reference assembly enables the efficient application of various statistical tools, and how genomic approaches can provide novel insights into resource polymorphism, host–parasite interactions and to genetic and phenotypic changes associated with climate change and harvesting-induced evolution. In summary, we call for increased integration of genomic tools into ecological research for perch, as well as for other fish species, which is likely to yield novel insights into processes linking the adaptation and plasticity to ecosystem functioning and environmental change.

KEYWORDS
adaptation, evolution, genomic resources, RNA-seq, sequencing, SNP

1 | INTRODUCTION

Eurasian perch *Perca fluviatilis* (also known as European perch; henceforth: perch) has an exceptionally wide distribution range spanning the Arctic, boreal and temperate zone of Eurasia ranging from the British Isles to eastern Siberia, and from the Arctic Ocean to the Mediterranean, Black Sea and Caspian Sea basin (Collette & Bănărescu, 1977; Thorpe, 1977). Perch inhabits a broad range of habitats including freshwater lakes, ponds, rivers, streams, reservoirs and brackish water estuaries and archipelagos, and maintains a keystone predator role in many aquatic food webs (Diehl, 1992). Perch remains a popular species to study for freshwater food webs (e.g., Brönmark, 1994; Diehl, 1992), trophic interactions (e.g., Devlin et al., 2015; Persson & De Roos, 2012), ontogenetic shifts in diet (e.g., Byström et al., 2012; Jacobson et al., 2019), life-history tradeoffs (e.g., Heibo et al., 2005; Heibo & Vøllestad, 2006), sexual dimorphism (e.g., Estlander et al., 2017; Mandiki et al., 2004), behaviour (e.g., Sajdlová et al., 2018; Semeniuk et al., 2015), population dynamics (e.g., Rask et al., 2014; Svanbäck & Persson, 2009), intraspecific divergence along the littoral–pelagic environmental axis (e.g., Faulks et al., 2015; Svanbäck & Eklöv, 2002), spawning site fidelity (e.g., Hall et al., 2022; Nesbø et al., 1998; Tibblin et al., 2012), physiological adaptations (e.g., Ekström et al., 2021; Sandblom et al., 2016), as well as individual and population level responses to climate change (e.g., Huss et al., 2019; van Dorst et al., 2019). The aforementioned studies employed a wide variety of approaches including field surveys, controlled aquarium, mesocosm and even whole-lake experiments. Furthermore, the ecology of perch has fuelled modelling work revealing key mechanisms driving population dynamics, for example, cannibalism (Claessen et al., 2000), ontogenetic bottlenecks (De Roos & Persson, 2013) and warming driving changes in population cycles (Ohlberger et al., 2011).

Perch is also an important target for fisheries and recreational fishing (Watson, 2008), a regional indicator species in the EU Marine Strategy Framework Directive and regional seas commissions (HELCOM, 2018a), a promising new aquaculture species (Policar et al., 2015), a model in ecotoxicology (Reid et al., 2016) and invasive outside its natural distribution range (Froese & Pauly, 2019). As a result, we have through the study of perch as a model system gained fundamental knowledge of important ecological processes. These include the importance of ontogeny and intraspecific variation for population dynamics and food-web structure (De Roos & Persson, 2013), how feedback between food web structure and individual performance via population size structures determine community responses to harvesting or warming (Gårdmark & Huss, 2020; Ohlberger et al., 2011), identified mechanisms underlying alternative stable community states including those hampering recovery of predatory fish (Claessen et al., 2000) and how species interactions shape the phenotypic and behavioural variation (Svanbäck et al., 2017). However, we argue that the progress of integrating ecological and genomic perspectives to address many questions in perch biology has been relatively modest, in contrast to other popular model species amongst bony fishes (Teleostei), such as salmonids (Houston & Macqueen, 2019) and sticklebacks (Reid, Bell et al., 2021). For example, many questions remain, to a large extent, unexplored in perch. For example, how ecological processes shape the genome, how genetic polymorphisms translate into phenotypic, performance and fitness variation depending on the environment and how genetic changes feedback to the ecological processes. Yet we expect to see increased integration of genomic tools into ecological research in perch in the coming years, resulting in novel insights into processes linking adaptation and plasticity to ecosystem functioning and environmental change.

The emergence of high-throughput sequencing technologies (also known as NGS, Next-Generation Sequencing; see Box 1) approximately 20 years ago offers fast and cost-effective sequencing of millions of short DNA reads (Reuter et al., 2015). During the last decade, NGS has completely changed the way genetic variation is assessed and how biomedicine, biodiversity and evolutionary research is conducted (Beigh, 2016; Frese et al., 2013; Hunter et al., 2018; Segelbacher et al., 2022; Tan et al., 2019). Arguably, the most important consequence of the genomic revolution is the feasibility to determine the whole-genome sequences of the species, known as reference genomes. Typical animal cells contain both mitochondrial and nuclear genomes, which greatly differ in size and mode of inheritance. Mitochondrial genomes are circular, commonly ca. 16,000 base pairs long, haploid and maternally inherited. Barring a few exceptions, all animal mtDNA genomes contain 37 genes: 13 proteins, 2 ribosomal RNAs and 22 transfer RNAs (Figure 1a). Nuclear genomes, however, are much larger (up to billions of base pairs, or gigabases; 1 Gb = 1,000,000,000 bp), diploid and are inherited from both parents, and typically contain tens of thousands of genes.

A reference genome is the representation of the structure and organisation of the genome (nuclear and/or mitochondrial) of a species and can be considered a blueprint of a species. Similarly, to type specimens in taxonomic research, reference genomes serve as the basis and fundamental starting point for a wide range of all subsequent genomic analyses (Worley et al., 2017). The first reference genome of teleost species was published in 2007 for pufferfish (*Tetraodon nigroviridis*; Jaillon et al., 2004), followed by three-spined stickleback (*Gasterosteus aculeatus*; Jones et al., 2012), zebrafish (*Danio rerio*; Howe et al., 2013) and Atlantic salmon (*Salmo salar*; Lien et al., 2016). The availability of whole-genome information has considerably increased our understanding of vertebrate genome evolution, rediploidisation and function (Parey et al., 2020; Volff, 2005). Genomic analysis has also revealed that all extant teleost fish species have experienced whole-genome duplication events, dated at approximately 320 Mya (Jaillon et al., 2004). The advent of large international genome initiatives and declining sequencing prices are opening possibilities to acquire chromosome-scale reference genomes for many organisms across the tree of life (https://www.ncbi.nlm.nih.gov/datasets/). As a result, the number of bony fishes' genome assemblies tripled within the last 3 years (Figure 2a). Simultaneously, the quality of the assemblies has greatly improved due to the wide application of long-read sequencing approach, which enables the generation of high-quality chromosome-scale assemblies. The rapid increase

BOX 1 Glossary of genomic and genetic terms.

10X linked-read technology: a library preparation technology developed by 10X Genomics, which links unique molecular barcodes to individual high molecular weight DNA molecules for the following reconstruction of highly continuous scaffolds from short-reads using the barcode information to recognise reads from the same long DNA fragment (linked-reads).

BUSCO quality assessment: is a commonly applied approach to assess genome assembly and annotation completeness using sets of known genes, that is, Benchmarking Universal Single-Copy Orthologs, named BUSCO.

Contig: is a linear stretch of overlapping DNA segments that together represent a consensus region of DNA, which is built from a number of shorter, partially overlapped sequences (reads).

DNA microarray: also known as DNA chip, is a collection of microscopic spots of known DNA sequences on a solid surface, which is used, for example, to genotype multiple genomic regions or score expression levels of a large number of genes.

EST: Expressed Sequence Tags are short (usually <1000 bp) fragments of complementary DNA (cDNA) sequences prepared from messenger RNA (mRNA), that have been used to identify expressed genes in a given tissue.

GC content: is the proportion of nitrogenous bases, guanine and cytosine, in a DNA/RNA sequence.

Gene ontology (GO): is the classification applied to unify the representation of gene and gene product functions across all species.

Genetic architecture: the number of genetic variants that influence a phenotype, the size of their effects on the phenotype, the frequency of those variants, their interactions with each other and the environment.

Genome annotation: is a complex procedure of connecting biologically relevant information to genome sequence data, including prediction of protein-coding genes, repetitive elements and other functional genome components like structural, transfer and small RNAs; control regions; pseudogenes; transposons and other mobile elements.

Genome sequence assembly: is a process of computational reconstruction of longer original DNA sequences from a large number of shorter sequences aiming to generate representative sequences of the original chromosomes.

Metabarcoding: an approach allowing the identification of multiple species from a mixed sample (e.g., DNA, RNA, eDNA and eRNA) based on the amplification of certain DNA fragments followed by high throughput sequencing.

miRNA-seq: microRNA sequencing is a type of NGS RNA-seq allowing to characterise the quantity and expression of small non-coding RNA molecules, known as microRNA.

N50: is the sequence length of the shortest contig (or scaffold) at 50% of the total assembly length; it characterises assembly quality in terms of contiguity.

ncRNAseq: non-coding RNA sequencing is a type of RNA-seq allowing the detection and analysis of medium-sized non-coding RNAs.

Omics: refers to a field of study that ends with -omics, such as genomics, transcriptomics, proteomics or metabolomics focusing on the analysis of the genomes, proteomes, transcriptomes or metabolomes, respectively.

Read: is an inferred sequence of base pairs corresponding to a whole or a part of a single DNA/RNA fragment.

RNA-seq: an approach, which applies next-generation sequencing (NGS) to detect and analyse of mRNA in a biological sample.

Scaffold: two or more contigs joined together using read-pair information. Scaffolds are composed of contigs and gaps. Gaps occur where reads from the two sequenced ends of at least one fragment overlap with other reads in two different contigs. Since the lengths of the fragments are roughly known, the number of bases between contigs can be estimated.

scRNA-seq: single-cell RNA sequencing is a type of RNA-seq using an optimised NGS technology to examine RNA transcripts within an individual cell.

Sequence alignment: is an arrangement of DNA, RNA or protein sequences to identify regions of similarity, which may reflect structural, functional or evolutionary relationships amongst the sequences.

Temporal scRNA-seq/live-seq: temporal single-cell RNA-sequencing (also known as live sequencing) is a technology that keeps the cell alive after transcriptome profiling using a cytoplasmic biopsy.

UTR: untranslated region is *the non-coding section of messenger RNAs (mRNAs)* located on each side of a coding sequence (5′UTR and 3′UTR).

in quantity and quality of teleost reference genomes allows for the increased integration of genomic and ecological research, with the potential to advance the understanding of feedback between ecological and evolutionary processes in the wild.

To explore this potential, we first describe the recent progress in generating reference genome assemblies of *P. fluviatilis* and the status of other genomic resources in perch. Next, we demonstrate the power of genome-wide approaches by comparing the resolution of (i)

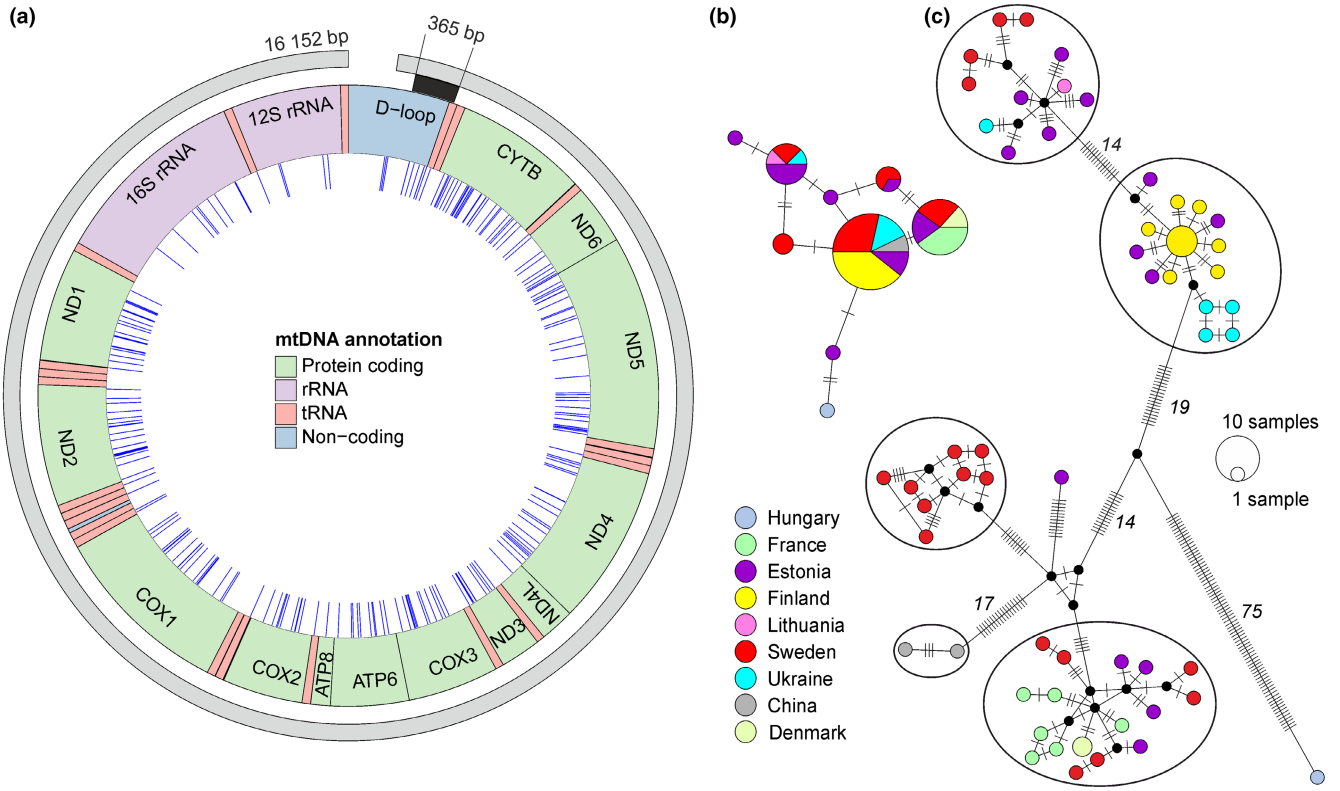

FIGURE 1 The increased resolution of whole-mitochondrial genome analysis to visualise evolutionary relationships between haplotypes. (a) Circular mtDNA molecule of perch encoding 13 proteins, 22 tRNAs and 2 rRNAs. Identified SNPs are shown as blue ticks, 365 bp D-loop and almost the whole mtDNA region (16,152 bp), which were used to generate haplotype network, are shown as black and grey lines around the circle, respectively. Median-joining haplotype network showing the relationships amongst haplotypes of 60 *Perca fluviatilis* sequences and datasets from GenBank based on (b) 365 bp D-loop region as in Nesbø et al. (1999) and (c) nearly complete mtDNA genome (16,152 bp). Haplotypes are represented by circles whose sizes are proportional to the number of individuals. Different colours represent the country of origin. Missing haplotypes are indicated by small black circles. Mutations are indicated by hatch marks; larger mutational steps are also provided as numbers in italics. Distinct haplotype clusters are indicated by ovals for a nearly complete mtDNA dataset, no distinct haplotype groups can be distinguished using a 365 bp mtDNA fragment.

whole-mitochondrial analysis with shorter mtDNA fragment used in earlier studies and (ii) 3722 nuclear single nucleotide polymorphisms (SNPs) with a smaller subset of markers using a newly developed genotyping array. Subsequently, we outline recent cases where genomics has already contributed to new ecological and evolutionary knowledge through whole-genome resequencing (Ozerov et al., 2022), transcriptome sequencing and metabarcoding approaches (Noreikiene et al., 2020), to shed light on adaptation and co-evolutionary responses in perch. Next, we explore how the availability of a reference genome enables the integration of analytical tools with ecological, physiological, developmental and evolutionary perspectives and finally, describe how genomic approaches can create a novel understanding of three important aspects of perch biology.

2 | MATERIALS AND METHODS

Below we describe the methods used for the comparative analyses of existing (mitochondrial DNA and whole-genome assemblies) and novel (SNP genotyping array) datasets for perch. To generate the mitochondrial haplotype network (Section 3.1), mitochondrial genome sequences were downloaded from GenBank (KM410088.1, CM020933.1, AP005995.1, MZ461595.1, AP018422.1 and LC495488.1) or extracted from published short read datasets (Table S1). The short reads were pre-processed by removing Illumina adapters, low-quality (average quality score < 25) and short (<60 bp) reads using trimmomatic ver. 0.36 (Bolger et al., 2014) for the 26 samples sequenced on HiSeq 2000, 2500 or 3000 instruments, or fastp ver. 0.20 (Chen et al., 2018) for the 14 samples sequenced on the NovaSeq 6000 instrument (see Table S1 for details). Filtered sequence reads of each sample were mapped to the Eurasian perch mitochondrial reference genome (NCBI: KM410088.1) with bowtie2 ver. 2.3.5.1 (Langmead et al., 2009) using the default parameters except for the modified score minimum threshold (–score-min L, −0.3, −0.3) and maximum fragment length for valid paired-end alignments (–X 700). Aligned consensus mtDNA sequences were extracted using bcftools ver. 1.8 (Li, 2011) whilst applying a minimum mapping quality of 20 (–q 20) and converted to fasta format using seqtk ver. 1.3 (Li, 2013). Some of the mtDNA sequences generated from RNA pools contained one or two ambiguous nucleotides. These were converted

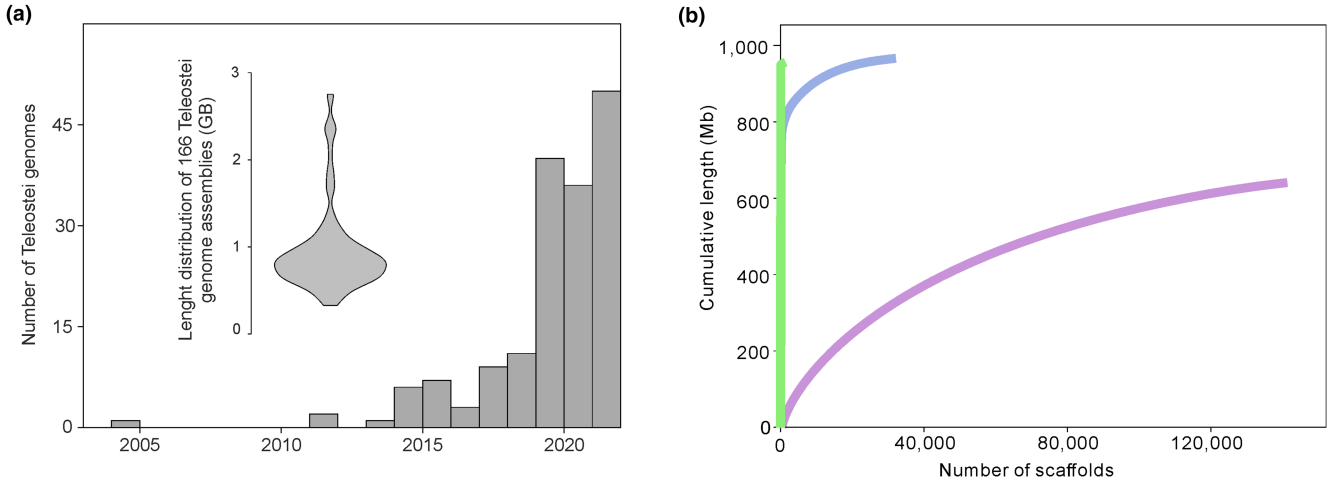

FIGURE 2 The progress, size and completeness of teleost genome assemblies. (a) The increase of teleost genome assemblies uploaded to the National Center for Biotechnology Information (NCBI) over time. The insert violin plot illustrates the size distribution of 166 assembled genomes. (b) Cumulative length of the three *Perca fluviatilis* genome assemblies available in NCBI GenBank. Perch genome assembly using Illumina short reads (GCA_900302645.1; Malmstrøm et al., 2017; solid light purple line), the assembly obtained using 10x linked-reads (GCA_003412525.1; Ozerov et al., 2018; solid light blue line) and the chromosome-level assembly using Illumina short and Oxford Nanopore long reads (GCA_010015445.1; Roques et al., 2020; solid light green line).

into two or four sequences, respectively, to represent all possible variants of an ambiguous nucleotide. The sequences were aligned using MUSCLE ver. 5.1 (Edgar, 2004). Due to the different lengths of the aligned sequences in the D-loop region, they were trimmed to a size of 16,152 bp using BioEdit ver. 7.2.5 (Hall, 1998). The same software was applied to extract a 365 bp long D-loop region used for phylogenetic analyses of perch earlier (Nesbø et al., 1999). Median-joining haplotype networks (Bandelt et al., 1999) for an almost complete mtDNA genome (16,152 bp) and for a 365 bp mtDNA D-loop region were generated in PopART ver. 1.7 (Leigh & Bryant, 2015).

Basic statistics for *P. fluviatilis* genome assemblies available in NCBI GenBank (Section 3.2) were generated using QUAST ver. 5.2.0 (Gurevich et al., 2013) with the default parameters. All genome assemblies' statistics were based on a scaffold of size ≥500 bp. The completeness of the genome assemblies was estimated with BUSCO ver. 5.1.2 (Manni et al., 2021; Simão et al., 2015) using a ray-finned fishes (Actinopterygii obd10) database consisting of 3640 orthologues from 26 fish species.

The newly developed DNA TRACEBACK® Fisheries SNP genotyping array FSHSTK1D (IdentiGEN Limited, Dublin, Ireland) was designed to perform genotyping in seven fish species (henceforth, MultiFishSNPChip_1.0; L. Andersson, unpublished). The performance of MultiFishSNPChip_1.0 in perch was evaluated by the genotyping of 4000 SNPs for a set of 42 individuals from 21 lakes (two individuals per lake) located in northern Europe and western Siberia (Table S2, Appendix S1). The SNP genotyping, allele calling, and quality control were performed at IdentiGEN Limited (Dublin, Ireland) genotyping facility. The average SNP call rate was >99.5% and 3722 highly polymorphic SNPs were retained for further analyses. The distribution of SNPs along the perch chromosomes was plotted using the R-package chromoMap 4.1.1 (Anand & Rodriguez Lopez, 2022) in R ver. 4.1.3 (R Core Team, 2022). The R package adegenet ver. 2.1.8 (Jombart, 2008; Jombart & Ahmed, 2011) was used to convert SNP data into a genind object. The relationships among individuals were illustrated using principal component analysis (PCA) with the dudi.pca function of the ade4 ver. 1.7–19 R-package (Dray & Dufour, 2007) on two sets of SNP loci: (i) all 3722 SNPs and (ii) randomly chosen 96 SNPs. Finally, the PCA plots were generated using factorextra ver. 1.0.7 R-package (Kassambara & Mundt, 2020).

3 | AVAILABLE GENOMIC RESOURCES

3.1 | Whole-mitochondrial genomes

The first available whole-mitochondrial genome assembly of perch was deposited to the NCBI GenBank in 2015 by Yang et al. (2016). At the time of writing this review, there were six whole-mitochondrial genome assemblies available at the NCBI GenBank. However, as described in Section 2 (Materials and Methods), we built consensus sequences for 54 nearly complete mitochondrial genomes from publicly available short-read datasets. To illustrate the increased resolution of whole-mitochondrial genome (Figure 1) analysis, we used median-joining haplotype networks to show the relationships based on nearly complete mtDNA genomes (16,152 bp; Figure 1c) and 365 bp long D-loop region (Figure 1b), as previously used in Nesbø et al. (1999) and Toomey et al. (2020). Four distinct haplotype clusters reflecting deep evolutionary split were distinguished for the nearly complete mtDNA dataset, whilst no obvious clustering was evident based on a short mtDNA fragment. In the latter case, 365 bp long haplotypes showed no obvious clustering and were separated from each other by only a few mutations, which may lead to incorrect inferences about the evolutionary history and colonisation routes. For example, a very distinct haplotype was observed for

the Hungarian sample from Lake Balaton showing deep divergence (>90 mutations) compared to all other nearly complete mtDNA haplotypes (Figure 1c). However, this deep evolutionary lineage was not apparent for the same samples when only 365 bp D-loop region was analysed (Figure 1b). Thus, any future studies aiming to resolve phylogenetic relationships and colonisation history in perch should focus on an analysis of much longer mitochondrial fragments to accurately infer the evolutionary relationships between haplotypes and populations. Furthermore, considering the functional importance of mitochondrial genes, there is an increasing interest in understanding both the neutral and selective processes that shape mtDNA variation (Consuegra et al., 2015; Vasemägi et al., 2017) and its link to adaptation to warmer environments (Pichaud et al., 2020) as well as potential coadaptation of mitochondrial and nuclear genes (Hill, 2019).

3.2 | Nuclear genome assemblies

The first nuclear whole-genome assembly of perch based on short-read sequences was deposited to NCBI in 2016 by Malmstrøm et al. (2017). This draft assembly, however, was very fragmented and incomplete (scaffold N50 = 5.9 Kb, BUSCO completeness of 44.3%; Table 1, Figure 2b) and severely limited its usefulness for genomic studies. The development of 10X Genomics linked-read sequencing allowed the generation of a ca. 1060 times more continuous, 4.5 times less fragmented and nearly two times more complete perch genome assembly (Ozerov et al., 2018; scaffold N50 = 6.3 Mb, BUSCO completeness of 87.6%). This has served as a backbone in several studies on perch adaptation and transcriptome activity (e.g., Jiang et al., 2022; Noreikiene et al., 2020; Ozerov et al., 2022). Finally, in 2020 a very high-quality chromosome-level assembly of perch (scaffold N50 = 39.6 Mb, BUSCO completeness of 97.6%), generated using long-reads technology (Roques et al., 2020), became publicly available. The recent genome assembly outperformed 10X linked-read version by ca. 6 times in continuity, by 100 times in fragmentation, yet only by 10% in completeness (Table 1; Figure 2b). Despite the lack of annotations in the first draft perch genome assembly due to a high level of fragmentation (Malmstrøm et al. (2017), the locations of genomic features were determined for more continuous assemblies by Ozerov et al. (2018) and Roques et al. (2020). Thus, the number of protein-coding genes found was 23,397 in the 10X linked-read assembly (Ozerov et al., 2018) and 24,326 in the chromosome-level assembly (Roques et al., 2020; Table 1). However, the number of functionally annotated proteins, mean protein lengths, and average numbers of and lengths of exons and introns were similar for both of the latest genome assemblies, with slightly higher numbers in the chromosome-level assembly (Table 1). Furthermore, the estimated proportion of repetitive DNA was similar between the two genome assemblies and comprised nearly 1/3 of the whole-perch genome (Table 1). This corroborates with observations in another freshwater Perciformes (Yuan et al., 2018). The number of protein-coding genes discovered in the Eurasian perch genome was close to those observed in yellow perch (*Perca flavescens*; 23,749; Feron et al., 2020) and pikeperch (*Sander lucioperca*; 24,727; Nguinkal et al., 2019), but higher than in more divergent species such as Arkansas darter (*Etheostoma cragini*; 21,827; Reid, Moran, et al., 2021) and orange throat darter (*Etheostoma spectabile*; 22,341; Moran et al., 2020).

3.3 | Transcriptomic resources

In addition to the progress in whole-genome assemblies, advances in high throughput sequencing also shed light on the intricate gene expression patterns, which can be considered as an intermediate molecular phenotype between DNA and organism-level phenotype. The early work aiming to uncover gene expression differences within and between individuals used expressed sequence tags (ESTs). ESTs could recover hundreds of expressed genes, but had several restrictions that limited sensitivity and were very labour-intensive requiring, amongst others, a cloning step (Adams et al., 1991). ESTs were also developed for perch by Rossi et al. (2007) to describe the most abundantly expressed genes in brain (n = 46) and liver (n = 104) tissues. Before long, high throughput sequencing of whole transcriptomes by employing the RNA-seq approach (Nagalakshmi et al., 2008) had become the preferred strategy for biomedical and ecological research (Alvarez et al., 2015; Byron et al., 2016; Todd et al., 2016). The power of RNA-seq for ecological systems is derived from the ability to obtain both qualitative and quantitative information simultaneously for tens of thousands of genes. This helps to establish potential links among gene expression variation, biological pathways and phenotypes, or even identify transcriptomic targets shaped by contemporary natural selection (Ahmad et al., 2021; Alvarez et al., 2015; Haas et al., 2013; Todd et al., 2016; Wang et al., 2009; Wolf, 2013).

Currently, most transcriptomic resources available for perch are generated using RNA-seq (Table 2). In consideration of other teleosts, perch transcriptomic information is comparatively limited and only a fraction of the information available for more intensively studied species, such as three-spined stickleback (Reid, Bell, & Veeramah, 2021) and Atlantic salmon (Houston & Macqueen, 2019). Furthermore, transcriptomic resources in perch to date are largely restricted to the use of female, pooled-sex and pooled-tissue or a limited number of tissues (Table 2). With the increase of RNA-seq accessibility and affordability, future studies will likely explore intraspecific variation in gene expression in greater detail, including characterisation of sex-specific, ontogenetic, seasonal or various experimental and in situ environmental factors (Oomen & Hutchings, 2017).

Additional benefits from using RNA-seq to explore gene regulation can be obtained by analysing the sequence reads that do not match the genome of the target species. Such unmapped reads usually correspond to <10% of all the total sequences and can belong to organisms other than the target species. This part of RNA-seq data can reveal important novel insights about symbionts, pathogens and parasites (Gouin et al., 2015; Gurgul et al., 2022; Laine et al., 2019;

TABLE 1 Eurasian perch (*Perca fluviatilis*) genome assembly and annotation statistics.

	GCA_900302645.1 Malmstrøm et al. (2017)	GCA_003412525.1 Ozerov et al. (2018)[a]	GCA_010015445.1 Roques et al. (2020)
Scaffold statistics			
Number of scaffolds	140,281	31,105	304
Total scaffold size (bp)	630,662,671	958,225,764	951,362,726
Scaffold N_{50} size (bp)	5973	6,260,519	39,550,354
Largest scaffold (bp)	73,288	29,260,448	48,724,115
GC/N (%)	40.6/0.20	40.9/11.12	40.9/0.03
Repetitive DNA (%)	N/A	32.72	36.11
BUSCO genome completeness			
Complete	1614 (44.3%)	3189 (87.6%)	3550 (97.6%)
Complete and single copy	1598 (43.9%)	3163 (86.9%)	3522 (96.8%)
Complete and duplicated	16 (0.4%)	26 (0.7%)	28 (0.8%)
Fragmented	570 (15.7%)	289 (4.5%)	30 (0.8%)
Missing	1456 (40.0%)	228 (7.9%)	60 (1.6%)
Annotation statistics			
Number of protein-coding genes	N/A	23,397	24,326
Number of functionally annotated proteins	N/A	23,171	23,551
Mean protein length (interquartile range, aa)	N/A	506 (224–614)	554 (237–678)
Longest protein (aa)	N/A	8907 (nesprin-1)	18,291 (titin-like)
Average number (length, interquartile range of length) of exon per gene	N/A	9 (228, 89–189 bp)	9 (298, 90–198 bp)
Average number (length; interquartile range of length) of intron per gene	N/A	8 (1224; 150–1340 bp)	8 (1753; 162–1483 bp)

[a]Minimum scaffold length is 1 kb.

Larsen et al., 2016; Noreikiene et al., 2020; Usman et al., 2017). For instance, a recent study in perch focused exclusively on unmapped reads and used a visceral organ and brain pool of perch for RNA-seq analysis (Hierweger et al., 2021). The authors identified novel filovirus, hantavirus and rhabdoviruses, which may contribute to pathologies in wild and aquaculture perch (Hierweger et al., 2021). With the ongoing accumulation of RNA-seq data, it is likely that future data-mining attempts that consider perch as a holobiont will reveal novel inter- and intraspecific variation (Borner & Burmester, 2017; Thind et al., 2021).

In parallel with technological advances, the repertoire of RNA-seq methodologies is constantly expanding. For example, single-cell RNA-seq that enables gene transcription analysis at single-cell resolution (scRNA-seq; Tang et al., 2009) has already been used to characterise the immune response at unprecedented resolution in several fish species (Athanasiadis et al., 2017; Attaya et al., 2022; Fuess & Bolnick, 2021; Wang et al., 2021). Most recently, scRNA-seq was further developed to "live-seq" to enable the temporal scanning of expression changes within the same cell (Chen, Guillaume-Gentil, et al., 2022). MicroRNA-seq (miRNA-seq) and non-coding RNA-seq (ncRNA-seq) are also fast-developing methodologies that focus on the diversity and function of different classes of RNA molecules that are important in gene regulation and other cellular functions. These approaches are already utilised for several fish models (Herkenhoff et al., 2018). The above-mentioned methods mostly rely on short-read sequencing (50–300 bp), which hinders the accurate detection of splicing-associated gene isoforms. This issue can be addressed with long-read RNA-seq (Wang et al., 2016) as done for three-spined sticklebacks (Naftaly et al., 2021). Therefore, despite technical biases and challenges with the RNA-seq approaches (Todd et al., 2016), we expect that transcriptome analyses will be increasingly incorporated into ecological and evolutionary research, addressing questions related to how fish respond to various environmental cues and adapt to present and future challenges.

3.4 | Types of genetic variation

Genetic variation can be defined as hereditary differences in the DNA sequence of individual genomes within or between populations and species. Genetic variation manifests in different forms, including changes at a single base pair (SNPs), in the variation of tandem repeat sizes (short tandem repeats – STRs or microsatellites and a variable number of tandem repeats – VNTRs or minisatellites), in short insertions and deletions (indels; <50 bp) and with structural variations (SVs) involving larger segments of DNA sequence. The latter includes inversions, duplications, translocations, insertions, deletions and copy number variations (Auton et al., 2015; Ho et al., 2020;

TABLE 2 Overview of transcriptomic datasets available for Eurasian perch (*Perca fluviatilis*).

Tissue or organ	Samples per tissue	Sex	Study design	Strategy	Platform	Bioproject access ID	Associated publication
Brain, gills, heart, muscle, liver, intestine, ovary and testis	1	Female, male	Interspecific comparison	miRNA-seq	Illumina HiSeq 2500	PRJNA256973	Desvignes et al. (2022)
Liver	12	Pooled male and female	Domestication process: F6 generation vs. wild population (Eltse River, Xinjiang, China)	RNA-seq	Illumina HiSeq 4000 (2×150 bp read length)	PRJNA733022	Jiang et al. (2022)
Pool of visceral organs and brain tissues	1	Juveniles	Viral metagenomics (pond in Germany)	RNA-seq	Illumina HiSeq 3000 (2×150 bp read length)	PRJNA661306	Hierweger et al. (2021)
Ovary	6 pools	Female	Exposure to radiation: ovaries of different development stages from individuals coming from 3 populations (irradiated lakes) and 1 mixed control population pool (lakes in Belarus and Ukraine)	RNA-seq	Illumina HiSeq. 2500 (2×125 bp read length)	PRJNA556365	Lerebours et al. (2020)
Whole eye	14	Female	Intraspecific habitat-dependent comparison (humic and clear-water lakes in Estonia)	RNA-seq	Illumina HiSeq 3000 (2×75 bp read length)	PRJNA589499 and PRJNA450919	Noreikiene et al. (2020)
Eggs (unfertilized)	32	Female	Domestication process: F7+ generations vs. F1 (originating from Geneva lake)	Microarray	SurePrint G3 Custom Gene Expression Microarray, 8x60K – Agilent Technologies	PRJNA490349	Almeida et al. (2019)
Retina	3	Not provided	Interspecific comparison (freshwater habitats in Czech Republic)	RNA-seq	Illumina HiSeq 2500 (2×80/125 bp read length)	PRJNA421052	Musilova et al. (2019)
Pooled brain, liver, heart, fin and gonad	1	Pooled female and male	Interspecific comparison (Irtysh River, Xinjiang, China)	RNA-seq	Illumina Hiseq 2500	PRJNA504352	Xie et al. (2019)
Liver	10	Female	Temporal difference in wild population (Baltic sea, coastal Sweden)	RNA-seq	Illumina HiSeq2500 (2×126 bp read length)	PRJNA529638	Förlin et al. (2019)
Pooled brain, heart, gill, liver, muscle, kidney and pancreas	4	Pooled female and male	Domestication process: F5 generation vs. wild population (Eltse River, Xinjiang, China)	RNA-seq	Ilumina Hiseq™4000, (2×150 bp read length)	PRJNA351886	Chen et al. (2017)
Brain, gills, heart, muscle, liver, kidney, bones, intestine, ovary, testis and embryo	1	Female, male	Interspecific comparison	RNA-seq	Illumina HiSeq2000 (2×100 bp read length)	PRJNA256973	Pasquier et al. (2016)

Ku et al., 2010). Despite large structural variations representing an important component of genetic and phenotypic variation, they remain poorly characterised in most teleosts (Bertolotti et al., 2020; Liu et al., 2021).

Until recent years, the genetic divergence and diversity in perch have been mainly studied by the analysis of STR (or microsatellites), whilst a few studies in the 1990s employed allozymes (Heldstab & Katoh, 1995), short mitochondrial DNA fragments (Nesbø et al., 1998) and random amplified polymorphic DNA markers (RAPD; Nesbø et al., 1999). Based on microsatellite analysis, the evidence of significant population genetic structuring in perch was observed at both small geographical scales within lakes (Bergek & Olsson, 2009; Gerlach et al., 2001, but see also Kalous et al., 2017 on lack of genetic differentiation) and at small spatial scales in the Baltic Sea (Bergek et al., 2010; Bergek & Björklund, 2009; Olsson et al., 2011). Other studies have documented the genetic divergence patterns at a broader geographical scale between waterbodies (Kánainé Sipos et al., 2021; Xu et al., 2022). In addition, microsatellites have been used to identify the genetic origin of perch for fish traceability (Pukk et al., 2016; Rolli et al., 2014) and to study the temporal changes and evolutionary consequences of overfishing (Pukk et al., 2013). However, whilst the analysis of a few tens of microsatellite loci may be sufficient for basic population genetic inferences, it cannot provide a genome-wide perspective of the genetic variability and divergence. One of the first attempts to generate genome-wide SNP data was performed by Pukk et al. (2015), who described genome complexity reduction methods using restriction enzymes and an Ion Torrent PGM sequencing platform. The authors discovered over 1200 SNPs, of which ca 5% were located in coding regions. Several highly divergent SNPs between commercially important freshwater and brackish water perch populations were also identified (Pukk et al., 2015). The same approach was also applied to discover new microsatellite loci in perch (Pukk et al., 2014). However, the recent breakthrough in high throughput sequencing technologies along with the decrease in sequencing costs has considerably increased the number of mitochondrial (Yang et al., 2016), nuclear (Table 1) and transcriptome data sets of perch (Table 2). In turn, access to the reference genome assembly has helped to discover hundreds of thousands of SNPs in perch (Ozerov et al., 2022) and fuelled the development of the Axiom SNP array platform (MultiFishSNPChip_1.0) which consists of nearly 4000 SNPs (Figure 3). The SNPs included in this array are distributed along 24 chromosomes (Figure 3a) and consist of both neutral, as well as putatively selected variants identified earlier (Ozerov et al., 2022; Figure 3b). To illustrate the power of the SNPs to resolve genetic relationships among populations, we genotyped 42 individual perch collected from 21 lakes in five countries (Figure 3d,e). We selected two individuals from each lake to evaluate how the number of SNPs influences the separation of within- and between population variation. Principal component analysis based on 3722 SNPs revealed that the samples were clustered according to geographical origin and individuals sampled from the same lakes showed high similarity with each other (Figure 3d). However, when only a small number of SNPs ($n = 96$) was used (Figure 3e), the genetic differences between individuals from the same lake were inflated and the overall differences between regions were resolved in considerably less detail. Thus, these findings illustrate the power of genome-wide approaches to accurately reflect within- and between population differences and similarities. We expect that this powerful and cost-efficient low-density genotyping tool will be widely used to address a range of evolutionary and ecological questions in perch.

4 | RECENT EXAMPLES OF HOW GENOMICS HAVE SHED LIGHT ON PERCH EVOLUTION AND ECOLOGY

4.1 | Case study 1: How adaptation to dark and acid environments shaped the genome of perch

Eurasian perch and its sister species yellow perch in North America are amongst the few fish species of northern latitudes that can live in very acidic humic lakes (e.g., Bertolo & Magnan, 2007; Hesthagen et al., 1992; Rask et al., 2014). Such dark-water lakes present almost "nocturnal" environments; they contain high levels of dissolved organic matter, which in addition to creating a challenging visual environment also affects a large number of other habitat parameters and biotic interactions (Marques et al., 2017; Noreikiene et al., 2020; Rask, 1984; Tranvik et al., 2018; Weyhenmeyer et al., 2019; Wood et al., 2011). However, the genetic targets of selection, and the evolutionary mechanisms and molecular processes that allow perch to thrive in these harsh conditions remain uncharacterized thus far. A recent study by Ozerov et al. (2022) represents the first attempt to employ whole-genome resequencing to fill this gap (Figure 4).

Based on the analysis of 32 whole nuclear genomes and more than 800,000 SNPs, Ozerov et al. (2022) found that the footprints of selection associated with humic environments comprise hundreds of regions scattered across the genome of perch (Figure 4a). In total, over 3000 genes with diverse functions were shown to be potentially influenced by humic selection. Most frequently, the identified candidate genes were involved in the processes of regulating organism development, nervous system development and calcium/potassium/sodium exchange. This suggests a possible role during early development and in the maintenance of ion balance (Figure 4d). As an example, a strong signal of divergent selection involving >30 SNPs was observed around the *MYLIP* (Myosin Regulatory Light Chain Interacting Protein) gene on chromosome 13 (Figure 4b). *MYLIP* plays an important role in embryonic development, which also involves calcium-dependent mechanisms during gastrulation in zebrafish (Knowlton et al., 2003). This suggests that the observed signal of adaptive variation around the *MYLIP* gene in perch may be linked to Ca^{2+} deficiency compensation during embryonic development in humic lakes. Alternatively, *MYLIP* has an important role in lipid metabolism and low-density-lipoprotein cholesterol regulation (Hong et al., 2010; Lindholm et al., 2009; van Loon et al., 2019; Zelcer et al., 2009) and therefore, the identified footprint of selection may instead be associated with alterations in lipid metabolism

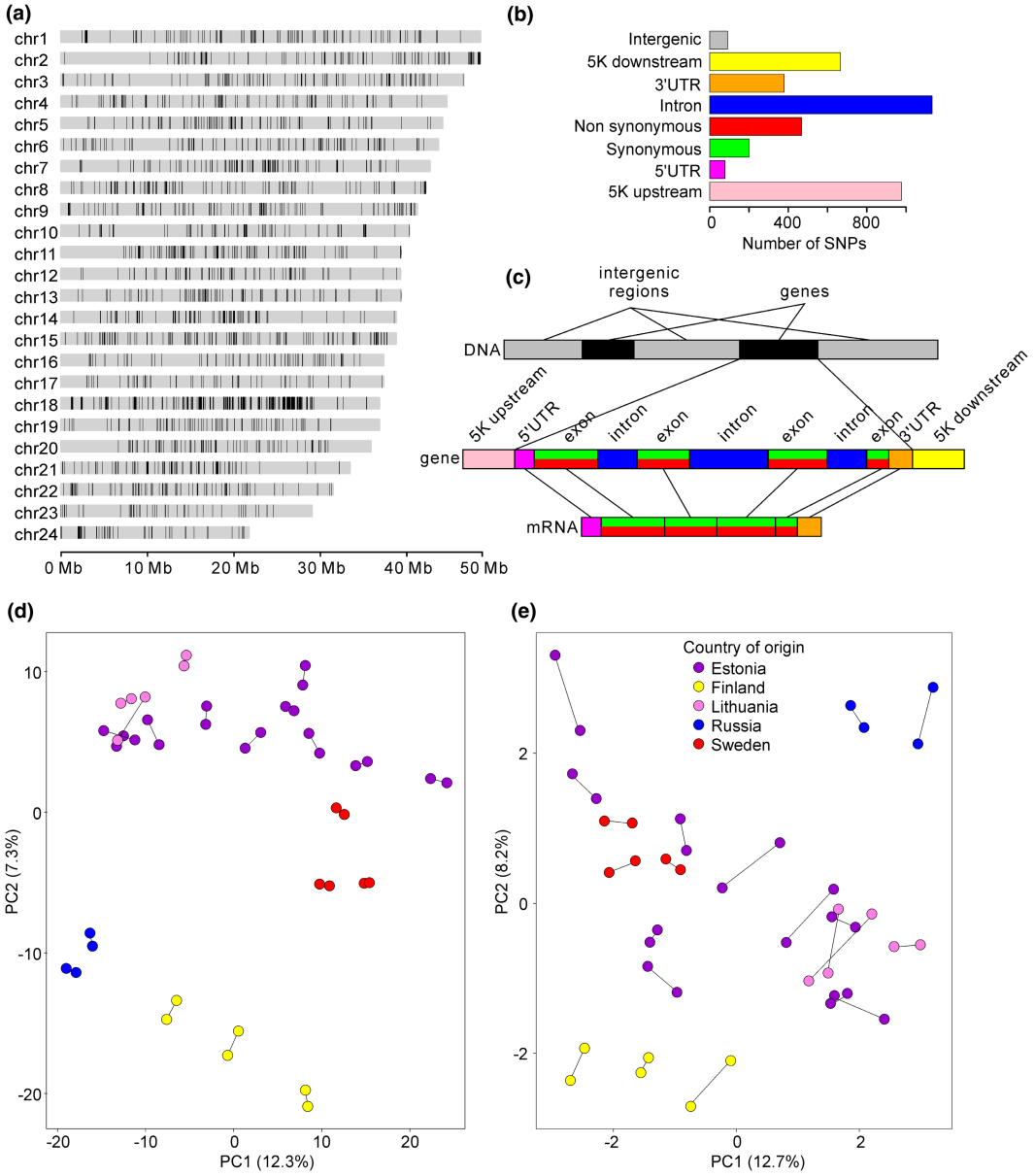

FIGURE 3 Development and application of Axiom SNP genotyping array (MultiFishSNPChip_1.0) in perch (*Perca fluviatilis*). (a) Distribution of 4000 SNPs along 24 chromosomes. (b) Functional classification of SNPs included in the array. (c) Different functional parts of the gene; principal component analysis (PCA) of 42 individual perch from 21 lakes based on (d) 3722 SNPs and (e) 96 random SNPs. Individuals originating from the same lake are linked with lines.

and availability of nutrients in humic lakes. Interestingly, Ozerov et al. (2022) also identified two non-synonymous SNPs in *MYLIP* showing large allele frequency differences between humic and clear-water lakes. Such differences can potentially serve as the targets of selection, but additional protein modelling and functional analysis are needed to further characterise the effects of amino acid variation of *MYLIP* on the individual performance and fitness of perch.

As expected, the majority of candidate SNPs were detected in intergenic and intronic regions (Figure 4c), which represent the largest part of the perch genome (Ozerov et al., 2018). However, Ozerov et al. (2022) also found a significant excess of candidate SNPs in regulatory regions (5′UTR, 3′UTR and 5K downstream gene regions). This indicates that the modification of gene expression levels likely plays an important role in humic adaptation. This finding corroborates with an increasing number of studies implying that natural selection is predominantly acting in regulatory regions (e.g., Fagny & Austerlitz, 2021; Glaser-Schmitt & Parsch, 2018; Verta & Jones, 2019). For example, Fraser (2013) showed that local adaptation in humans involved transcript abundance variation more than ten times more frequently than changes in the amino acid composition of protein sequences. The overrepresentation of candidate SNPs in 5′ and 3′UTRs observed in perch concurred as UTRs play an essential role in post-transcriptional regulation of gene expression (Barrett et al., 2012). 5′UTRs, found

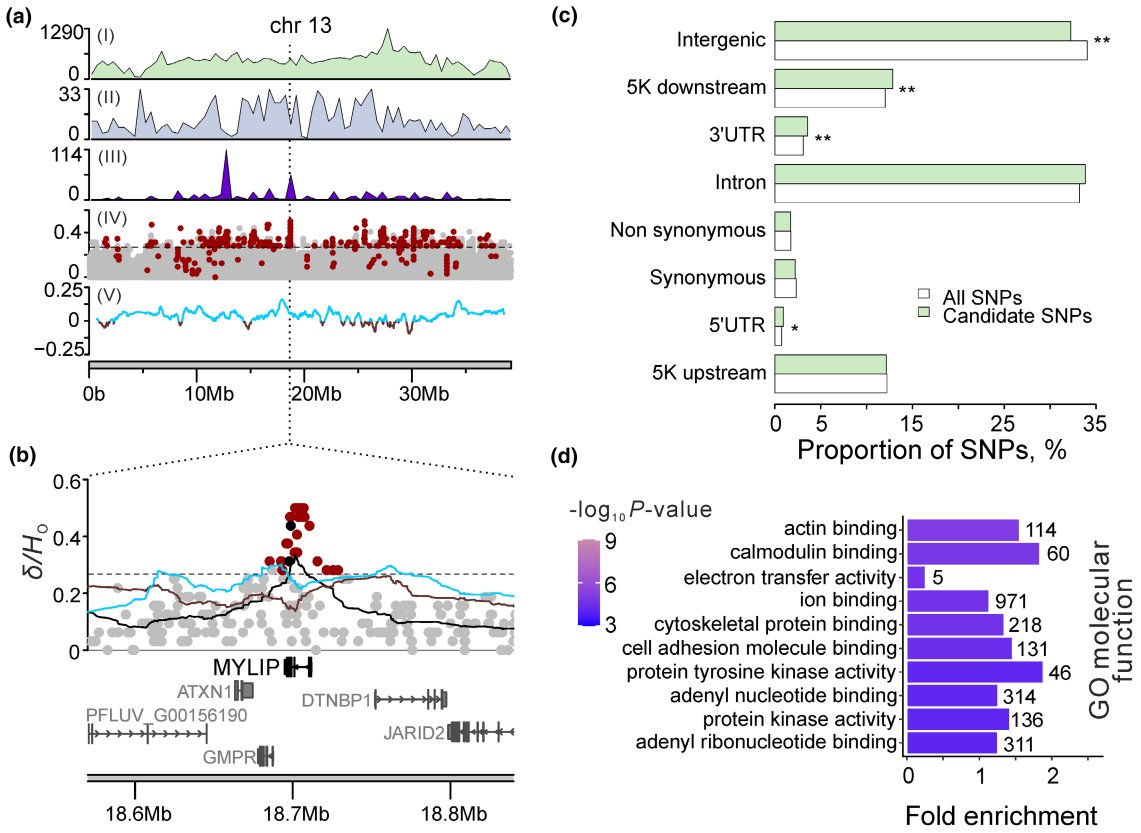

FIGURE 4 Adaptive divergence and complementary evidence of natural selection associated with adaptation to the humic environment in *Perca fluviatilis* (Ozerov et al., 2022). (a) The density distribution of SNPs (I, light green), genes (II, light blue), candidate SNP density (III, purple), genetic divergence (IV) and differences of genetic diversity between clear-water and humic perch (V) along chromosome 13. Candidate and neutral SNPs on IV are shown as red and grey dots, respectively. (b) Example of a candidate region in chromosome 13 involved in humic adaptation showing high genetic divergence (δ) between humic and clear-water perch. Candidate SNPs, nonsynonymous candidate SNPs and other SNPs are shown by red, black and grey dots, respectively. Gene symbols are presented as human orthologues. The dashed line indicates δ threshold = 0.268, which corresponds to 2.5 SD of mean δ. (c) Distribution and enrichment of candidate SNPs in relation to genomic location. The largest proportion of SNPs were found in intergenic and intronic regions. Significant enrichment of candidate SNPs under selection is found in 5K downstream of a gene and in 3′ and 5′UTR regions. (d) Top 10 significantly enriched gene ontology (GO) terms (FDR ≤ 0.05) among the 3245 candidate genes linked to molecular function. The bar length and numbers on the right represent the fold enrichment and number of enriched genes for each GO term, respectively.

upstream of the protein-coding sequence, are important for controlling translation initiation, and diversity in 5′UTRs enables variation in expression from a single gene and tissue-specific expression patterns (Barrett et al., 2012). Whereas 3′UTR regions are downstream of the protein-coding region and typically affect post-transcriptional and translational processes. 3′UTR regions also influence the fate of mRNAs including mRNA localization (Andreassi & Riccio, 2009) and both the stability (Goldstrohm & Wickens, 2008) and levels of expression (Matoulkova et al., 2012). In general, polymorphism and length variability are greater in 3′UTRs compared to those in 5′UTRs, thus corresponding to a greater evolutionary potential of the former (Barrett et al., 2012; Steri et al., 2018). Such potential is illustrated by the number of SNPs found in 3′UTR regions of the perch genome which exceeded those in 5′UTRs by nearly four times (Figure 4c). The important role of 3′UTRs in teleost evolution has been recently highlighted in cichlids, indicating that these regions may function as key regulators of post-transcriptional processes during rapid adaptation and speciation (Xiong et al., 2018). Therefore, the whole-genome analysis suggests that the changes in regulatory regions, rather than mutations in protein sequences, likely play a major role in the humic adaptation of perch. However, despite recent progress in prokaryotes (van Hijum Sacha et al., 2009), functional characterisation of regulatory variation for non-model organisms is far from trivial (Clark et al., 2020).

For further consideration, the study of Ozerov et al. (2022) demonstrates the multifaceted nature of humic-driven selection and the power of whole-genome analysis to pinpoint genomic regions and the specific genes involved in adaptation to specific environments. However, it also serves as a good reminder that it is not trivial to identify the causative polymorphisms under selection or to predict the targets of selection based on available ecological and environmental knowledge. Therefore, to understand the functional role of genetic variation, considering its physiological, phenotypic and ecological

effects, we ultimately need to bridge the gaps between cell, tissue, whole animal, population and community level knowledge.

4.2 | Case study 2: How RNA-seq revealed novel host–parasite–environment interactions in perch

Combining the use of mapped and unmapped RNA-seq reads can serve as a rich ground for formulating new hypotheses about ecology and the interactions between species. For example, Noreikiene et al. (2020) aimed to identify the differentially expressed genes associated with clear-water and humic lakes using RNA-seq on whole-eye transcriptomes in perch (Figure 5). These could serve as candidate genes for adaptation to a dark-water visual environment characterised by a red-shifted light spectrum (Huovinen et al., 2003; Noreikiene et al., 2020). However, rather unexpectedly, the top gene ontology (GO) process terms among 69 enriched terms were related to the immune system. Differentially expressed genes primarily included interferon-induced proteins, interleukins, immunoglobulins, MHCII beta subunit and T-cell receptors. These were mostly upregulated in perch sampled from clear-water lakes. To obtain greater insight, the authors explored the remaining 6% of reads that failed to map to the perch genome. Thereby, they identified the presence of parasitic flatworms' sequences from the Diplostomoidea superfamily in most of the clear-water samples. Simultaneously, parasitic flatworm sequences were absent in the studied transcriptomes of perch from the humic lakes. Further effort was made to characterise infection patterns and inter- and intraspecific diversity of eye flukes using targeted diplostomid-specific metabarcoding based on an extended number of samples (Figure 5c,d). This analysis confirmed the absence of eye parasites in the perch living in humic lakes and a high prevalence of eye fluke *Tylodephys clavata* (Trematoda, Diplostomidae) in clear-water perch. Furthermore, Noreikiene et al. (2020) proposed a possible ecological mechanism behind the observed parasite prevalence patterns suggesting that perch in humic lakes are able to escape from vision-debilitating eye fluke infection (Vivas Muñoz et al., 2017, 2019, 2021) because the humic environment negatively affects the abundance of gastropods which serve as the intermediate hosts for fish eye flukes. Thus, analysis of transcriptome responses in perch eyes enabled the discovery of a novel host–parasite-environment interaction. More generally, this study demonstrates how next-generation sequencing facilitates the characterisation of new parasitic, mutual or symbiotic relationships between species (McKenna et al., 2021).

5 | METHODOLOGICAL APPROACHES THAT UTILISE THE AVAILABLE REFERENCE GENOME OF PERCH

5.1 | Genotype–phenotype links

Perch possesses a high phenotypic variability in a number of morphological, behavioural, physiological and life-history characteristics, both within and among populations (Thorpe, 1977). For example, the vertical stripe pattern of perch shows variation in the number of stripes, stripe width, stripe distance, the presence or absence of y-shaped stripes and intensity of pigmentation in dorsal vs. ventral parts (Pimakhin, 2012). Perch living in transparent environments also exhibit sexual dichromatism, with males having a more colourful belly than females, in contrast to the lack of differences in coloration between sexes in dark-water lakes (Kekäläinen et al., 2010). Furthermore, coloration has been also shown to correlate with other traits, such as susceptibility to macroparasites (Roch et al., 2015).

Earlier studies have also demonstrated that perch have large morphological differences between different lakes and habitats (Hjelm et al., 2000, 2001; Magnhagen & Heibo, 2004; Olsson et al., 2007; Svanbäck & Eklöv, 2002, 2003). For example, the number of gill rakers in perch has been shown to negatively correlate with the biomass of planktivorous fish, indicating the occurrence of character displacement as a consequence of competition in the zooplanktivorous niche (Hjelm et al., 2000). Additionally, in lakes where the availability of benthic resources is low, perch have higher body height and larger mouth that is a suggested consequence of natural selection for increased efficiency in the benthic niche (Hjelm et al., 2000). In addition to intraspecific competition, predation has also shown to shape phenotypic variation in perch, selecting for smaller eye size in a non-vegetated habitat (Svanbäck & Johansson, 2019).

In addition to morphology, earlier studies have also found considerable inter-individual variation among perch in their physiological tolerance to temperature, salinity and dissolved oxygen concentration (Thorpe, 1977). For example, it was found that perch originating from different habitats show different levels of tolerance to maximum salinity (Christensen et al., 2019) and to low pH (Rask & Virtanen, 1986), which, conceivably, reflects local adaptation. Further studies in perch have shown variability as well as plasticity related to homing, selection of habitat, movements, social interaction, competition within and among cohorts and between species, behaviour as a prey or as a predator or as a cannibal (reviewed in Semeniuk et al., 2015).

Once potentially adaptive phenotypic variation has been detected, it becomes important to understand the relative importance of genetic variation and phenotypic plasticity in observed intra- and inter-population differences. Common garden experiments in perch have revealed that phenotypic plasticity plays a major role in some traits (e.g., Hall et al., 2021; Hellström & Magnhagen, 2011; Olsson et al., 2007; Svanbäck & Eklov, 2006), yet small proportion of variation can be explained by the genetic component (Svanbäck & Eklov, 2006). Despite a large number of studies on a diverse set of phenotypic characters in perch, the underlying genetic basis of traits (i.e., genetic architecture) remains mostly unresolved. However, given the advances in high-throughput sequencing and genotyping, we expect to witness an increasing number of genomic studies aiming to link phenotypic traits to specific genes and genetic variants in perch.

Several strategies can be used to link phenotypic (trait measurements) and genotypic information. Quantitative trait locus (QTL) analysis aims to detect the regions of the genome that correlate with the variation of a particular phenotypic trait (Falconer &

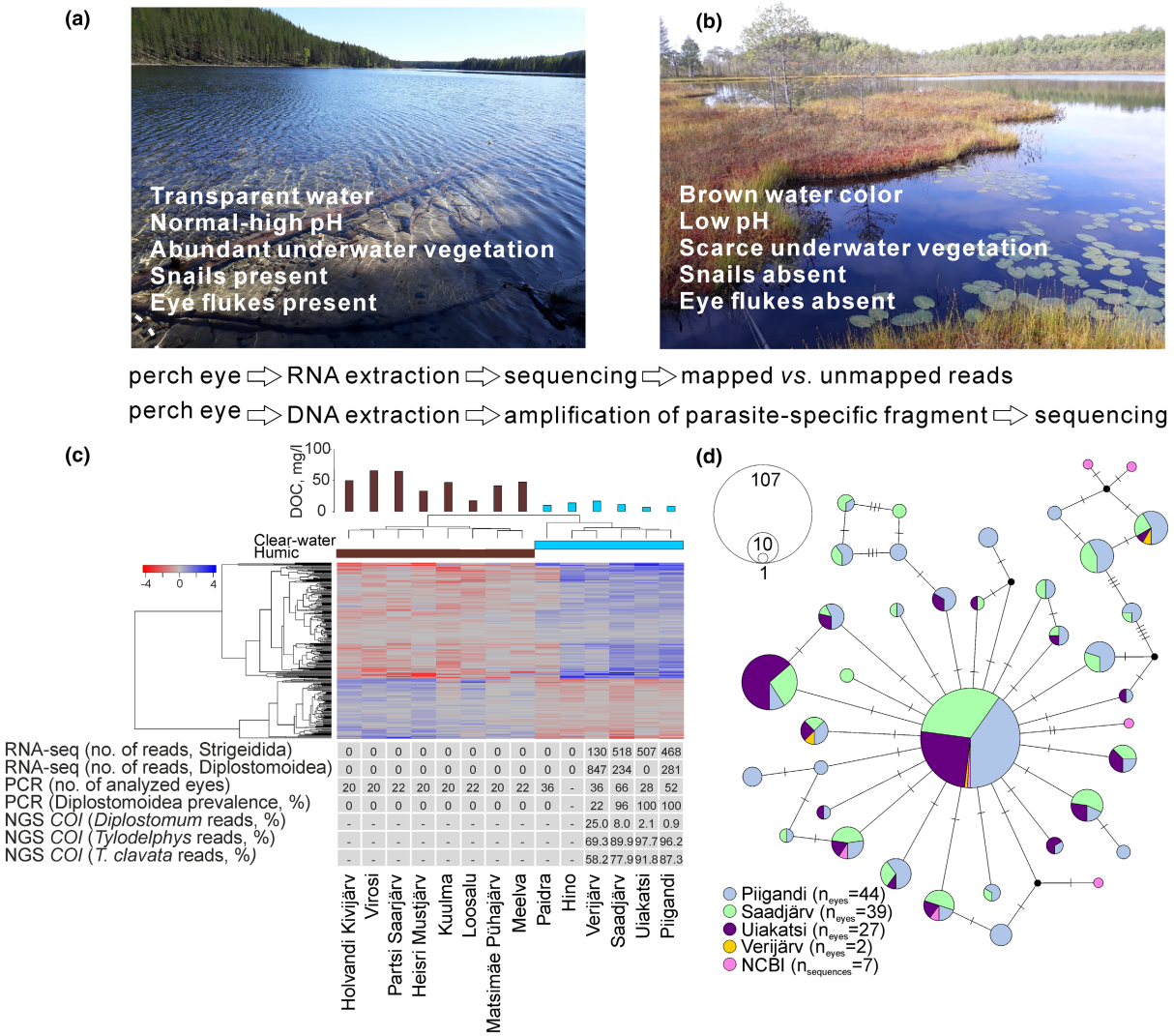

FIGURE 5 Effects of environment and parasite infection on *Perca fluviatilis* gene expression variation, and molecular characterisation of eye flukes. Photographs illustrate key environmental differences between (a) clear water and (b) humic lake habitat. (c) Heatmap showing differentially expressed genes ($n = 265$, $p_{adj} \leq .05$) between humic and clear-water habitat. Upregulated and downregulated transcript abundances in perch from the clear-water lakes are shown as blue and red colour, respectively. Dissolved organic carbon (DOC) concentration (mg/L) in each studied lake is shown in the bar-plot figure above. The table indicates the number of reads that were assigned to the order Strigeidida and the superfamily Diplostomoidea; the results of PCR amplification of diplostomid-specific *cox1* gene in humic and clear-water lakes; and the proportion of diplostomid-specific cox1 reads assigned to the genus *Diplostomum* and *Tylodelphys* and to the species *Tylodelphys clavata* in four clear-water lakes. (d) Haplotype network of *cox1* sequences in *T. clavata*. The frequency of each haplotype is depicted by circle size. Perch populations from different lakes are represented by different colours; n_{eyes} – refers to the number of screened eye samples and $n_{sequences}$ – refers to the number of sequences from the NCBI database.

Mackay, 1996; Kearsey, 1998; Lynch & Walsh, 1998). For QTL mapping, individuals are typically crossed to generate a progeny (mapping population) with known relatedness. QTL mapping requires two or more populations exhibiting genetic differences at the trait of interest and genetic markers, which can discriminate parental lines. After the crosses of parental lines are produced (F1), they are subsequently crossed again using a different design (Darvasi, 1998) and the genotypes and phenotypes of the next cohort (F2) are evaluated (Miles & Wayne, 2008). Alternatively, QTL mapping can be performed using within-population crosses in F1 generation to identify segregating loci that affect phenotypic variation (e.g., Vasemägi et al., 2016). QTL mapping has been successfully used to identify a myriad of QTLs in teleost fish (reviewed in Ashton et al., 2017). Such QTL provides evolutionary insights on the level of parallelism for body shape variation in lake whitefish (*Coregonus clupeaformis*) species pairs (Laporte et al., 2015), pigmentation variation in cichlid fish (*Metriaclima zebra*; O'Quin et al., 2013), and salinity tolerance in salmonids (Norman et al., 2012). Although QTL analysis is a powerful method to identify regions of the genome that co-segregate with a given trait, it has several limitations. For example, QTL mapping can only detect the differences existing between parental populations/individuals, whilst QTL regions are typically wide, extending

over hundreds or even thousands of genes. Moreover, QTL experiments in organisms with long generation times are inevitably time consuming.

An alternative strategy to link phenotypic variation with genome-wide genetic variants is Genome-Wide Association Study (GWAS; Tam et al., 2019, Uffelmann et al., 2021, Visscher et al., 2017). GWAS does not rely on experimental crosses and takes advantage of linkage disequilibrium (LD) between genetic variants and causative loci affecting the phenotype. GWAS requires high-density genotype data, usually consisting of tens to hundreds of thousands of SNPs, allowing for more accurate localization of QTL (Mackay et al., 2009; Schaid et al., 2018). Limitations of GWAS include the potential confounding effect of population structure and the detection of false-positive associations (Korte & Farlow, 2013; Platt et al., 2010). Given the complementary nature of QTL mapping and GWAS, both methods can augment each other since QTL mapping can efficiently link larger genomic regions in controlled crosses, whilst GWAS can provide population-level information on the genetic architecture of the trait (Khan et al., 2021; Korte & Farlow, 2013; Sallam et al., 2022). Progression in the development of relatively inexpensive SNP arrays eases GWAS in teleost fish. For example, GWAS was applied to study the pigmentation variation in brown trout (*Salmo trutta*; Valette et al., 2022) and the sexual maturity in Atlantic salmon (Sinclair-Waters et al., 2022). However, to date, there are no published GWAS on perch. Recent whole-genome resequencing in perch that revealed nearly a million SNPs (Ozerov et al., 2022) and the availability of high-throughput SNP genotyping technologies will certainly facilitate characterisation of genotype–phenotype links in the future. We, therefore, expect an increasing integration of ecological and evolutionary genomics perspectives in the coming years, enabling effectively linking perch genes and phenotypes with whole-organism performance and ecological processes.

5.2 | Detection of selective sweeps

As most species occupy heterogeneous environments throughout their geographical distribution, divergent selection can cause local populations to evolve traits that provide an advantage under their local environmental conditions. For successful adaption, the populations should not be constrained by a lack of genetic variation or hindered by gene flow and genetic drift (Blanquart et al., 2013; Kawecki & Ebert, 2004; Savolainen et al., 2013). Thus, the local adaptation process can be seen as a balance between locus-specific (e.g., selection) and genome-wide (e.g., gene flow and genetic drift) population genetic processes (Lim et al., 2021; Lindholm et al., 2009). This balance determines the extent of local adaptation evolution (Blanquart et al., 2013). If there is sufficient standing genetic variation for selection to work on, and gene flow is reduced, specialised genotypes can be maintained in an isolated population thus reinforcing local adaptation. However, when gene flow overrides the effect of selection, the genotype that on average is the best, increases in frequency within the population and leads to a loss of local adaptation (Lenormand, 2002). Yet, gene flow between populations also has the potential to mitigate maladaptation due to climate change (Aitken & Whitlock, 2013). Furthermore, genetic drift can reduce the likelihood of local adaptation by decreasing genetic variance, reducing the efficacy of selection and potentially causing the random fixation of alleles (Blanquart et al., 2012; Yeaman & Otto, 2011). Since natural selection acts on a phenotypic trait, changes in allele frequencies in loci influencing this trait towards a new optimum trait will lead to adaptive divergence of trait and allele frequencies (Hoban et al., 2016).

During the last decade, population genomics has been increasingly used for identifying loci under disruptive selection in diverging populations or in recently derived species by screening variable sites (usually SNPs) across the genome for the signatures of natural selection (e.g., Fumagalli et al., 2015). This approach, also known as the outlier test, selective sweep mapping or genome scan, makes no assumption about the trait. It can, therefore, be implemented without prior knowledge of the nature of adaptive traits (Luikart et al., 2003; Stinchcombe & Hoekstra, 2008) and without the need to define candidate genes (Ross-Ibarra et al., 2007). The identification of genomic regions shaped by selection and having putative fitness effect is relevant not only because it sheds light on adaptive evolution, but also because such loci represent biologically meaningful variation and functional importance (Nielsen et al., 2005; Vitti et al., 2013). Through this approach, the genetic makeup of many adaptive traits has been elucidated, such as lactase persistence in humans (Tishkoff et al., 2007), or armoured plates in sticklebacks (Jones et al., 2012). Yet, most traits are complex in nature and influenced by the environment and a large number of genes, each with a small effect (Boyle et al., 2017). In perch, the genome-wide quests for selective sweeps are just beginning to emerge, assisted by the availability of annotated whole-genome assembly (Ozerov et al., 2022, Case study 1).

There are several complementary approaches available to identify regions of the genome that are potentially shaped by natural selection (Ellegren & Sheldon, 2008). Such methods typically aim to detect unusual patterns along the chromosomes, including elevated genetic divergence between populations or species (often measured as F_{ST}) or reduced genetic variation (Luikart et al., 2003) that cannot be explained by sampling variation and genome-wide effects of genetic drift and gene flow. Likewise, natural selection favouring certain alleles or haplotypes can cause increased linkage disequilibrium (LD) along the chromosome and can be used to identify putative footprints of selection (Schlötterer, 2003). Another increasingly popular analytical method for understanding how organisms adapt to their environment is gene–environmental association (GEA) analysis (Luo et al., 2021), which examines the extent to which spatial environmental variation coincides with genotypic variants (Frichot et al., 2013; Rellstab et al., 2015). By discerning loci that are correlated with the environmental factors, GEA may identify genomic regions or genes driving local adaptation (Joost et al., 2007; Lv et al., 2014) or even predict which populations are at the highest risk of extinction if the environmental conditions change in the future (Lotterhos & Whitlock, 2015). A common strategy to address

outlier method weaknesses is to prioritise loci that are outliers identified by multiple methods (Lotterhos & Whitlock, 2015; Vasemägi & Primmer, 2005). Irrespective of the outlier approach, all of them benefit tremendously from the availability of a high-quality reference genome. We expect that the availability of reference genomes will drive the next wave of selective sweep mapping and GEA efforts revealing new insights into the interplay between environment, genes and adaptive processes, and their role in perch ecology.

6 | AREAS WHERE OMICS ARE EXPECTED TO IMPROVE UNDERSTANDING OF PERCH ECOLOGY

6.1 | Resource polymorphism

Perch displays a large degree of individual variation in morphological characters and diet, as individuals living in littoral habitats have a deep/robust body whereas pelagic fish are more streamlined (Svanbäck & Eklöv, 2002, 2003). Littoral perch feed predominantly on benthic macroinvertebrates whilst pelagic fish reside in open water and feed mainly on zooplankton (Svanbäck & Eklöv, 2002). Thus, there is a coupling between the morphological characteristics and feeding efficiency in littoral/pelagic habitats, a phenomenon known as resource polymorphism (Robinson & Wilson, 1994; Smith & Skúlason, 1996). The process of phenotypic and genetic diversification that occurs in response to variation in available resources is described for several fish species in postglacial lakes (e.g., Skulason & Smith, 1995). It is suggested that resource polymorphism can play an important role in population divergence and some circumstances in speciation (Robinson, 2000; Skúlason et al., 2019).

The ecological aspects of the littoral–pelagic habitat use and morphological divergence in perch have been characterised in detail (e.g., Svanbäck et al., 2008; Svanbäck & Eklöv, 2002; Svanbäck & Eklöv, 2003; Svanbäck & Persson, 2009). The habitat-associated morphologies in perch have been shown largely to be driven by plastic responses (Hjelm et al., 2001; Olsson & Eklov, 2005), but also by a small genetic component (Svanbäck & Eklov, 2006). However, very little is known about the relationships between phenotypic and genetic divergence, and the roles of natural selection and phenotypic plasticity in perch resource polymorphism (Svanbäck & Persson, 2009). Based on an analysis of 96 amplified fragment length polymorphisms of littoral and pelagic perch, Faulks et al. (2015) found evidence for the assortative mating within and genetic divergence between the littoral and pelagic perch. This indicates that females are more likely to mate with a genetically similar male, which can lead to genome-wide divergence between the littoral and pelagic perch. Furthermore, the extent of both genetic and morphological divergence between the littoral and pelagic perch differed between lakes and reflects the varying levels of separation along the littoral–pelagic axis. However, the authors found no significant coupling between genetic and morphological divergence. These results suggest that both phenotypic plasticity and genetic divergence mechanisms may act simultaneously in the littoral and pelagic perch. Therefore, the incorporation of genomic perspective is not only necessary to accurately quantify the divergence across the genome, but also important for potentially pinpointing specific genes and genetic variants involved in littoral and pelagic divergence, and to understand fine-scale spatial population structuring in perch. More generally, by combining a genome-wide perspective with quantitative analysis of morphological and environmental variation, we are likely to learn a great deal about how multiple evolutionary processes interact simultaneously to shape population divergence (Bolnick et al., 2018).

6.2 | Host–parasite interactions

As a consequence of their wide geographical distribution, high tolerance to diverse habitats and generalist feeding, perch are exposed to a range of parasites and pathogens. It is estimated that perch can be infected by close to 150 parasites belonging to myxozoan, protozoan and metazoan groups (Craig, 2000; Craig et al., 2015). However, the actual number of pathogens in perch is most likely greater due to the widespread underreporting of viruses, bacteria and fungi (Becker et al., 2016; Caruso et al., 2019; Garver et al., 2018; Hierweger et al., 2021; Kashinskaya et al., 2020; Langdon et al., 1986; Marsh et al., 2002; Pallandre et al., 2022; Ruane et al., 2014; Wahli et al., 2015). As perch is regularly a target species in biomonitoring projects (e.g., HELCOM, 2018b) and an abundant fish throughout most of its range, cross-sectional parasitological studies have a long history and data are available for many habitats and geographical localities (Andersen, 1978; Andrews, 1979; Balling & Pfeiffer, 1997; Juhásová et al., 2019; Morley et al., 2008; Morozinska-Gogol, 2013; Nikolic & Simonovic, 1996; Rolbiecki et al., 2002; Shukerova et al., 2010; Sobecka & Słomińska, 2007; Tuuha et al., 1992; Wierzbicka et al., 2005; Wierzbicki, 1970). This has revealed location-specific and seasonally fluctuating parasite assemblages (Andersen, 1978; Karvonen et al., 2005; Skorping, 1981; Valtonen et al., 1993), a tendency for higher diversity and abundance with increasing age and ontogenetic shift from pelagic to littoral zones (Behrmann-Godel, 2013; Kuchta et al., 2009; Lee, 1981). Most of the parasitological studies conducted so far relied on classical techniques which are (i) laborious, (ii) not suitable for cryptic or uncultivable species detection and (iii) require a high degree of expertise for the specific parasite group. With the use of modern genomic tools such as metabarcoding, whole-genome sequencing or RNA-seq (see Box 1), it is possible to overcome some of these restrictions and provide qualitatively new information on parasite communities, their relative abundance and intraspecific genetic variation (e.g., Noreikiene et al., 2020).

More widespread use of genomics in perch parasitological studies would undoubtedly increase the number of known pathogens that are using perch as a host (Hierweger et al., 2021). Genomic methods can also illuminate parasite intraspecific diversity (see also Case study 2), population structuring, infection or introduction pathways. Perch is a potential vector species for some fish pathogens

(Matras et al., 2019) and zoonotic infections (e.g., *Clinostonum complanatum*; Menconi et al., 2020, or *Eustrongylides* spp.; Branciari et al., 2016, Dezfuli et al., 2015, Franceschini et al., 2022, Rusconi et al., 2022). Yet, currently, it is unclear if certain perch populations are more susceptible to specific viral strains or other pathogens (Pascoli et al., 2015) hence precluding accurate forecasting of the epidemiological outcome. Combining host and parasite genomic data will be useful for biosafety aspects to better understand and predict disease outbreaks in areas inhabited by perch within its native and invasive ranges and also in aquaculture settings (Behrmann-Godel et al., 2014; Branciari et al., 2016; Juhásová et al., 2019; Langdon, 1989; Matras et al., 2019; Menconi et al., 2020; Morley et al., 2008; Rupp et al., 2019; Schwabl et al., 2017). Moreover, the use of high-throughput sequencing would expand the spatial and temporal range of host–parasite investigations enabling to better predict parasite spread as well as host vulnerability under future climatic conditions (Björklund et al., 2015; Lõhmus & Björklund, 2015; Schwabl et al., 2017).

Modern genomic tools can provide unprecedented levels of molecular information about perch as a host and its interaction with parasite communities or specific parasite species. One of the fascinating examples of perch-parasite interactions involves diplostomids (Diplostomidae, Trematoda). This fluke family is a widespread and species-rich trematode group infecting aquatic gastropods and fishes before reaching birds or fish-eating mammals as definitive hosts (Chappell, 1995; Faltýnková et al., 2007). Ocular infection generally causes visual disturbances or even blindness in affected fish, reducing its ability to forage and avoid predation, which benefits parasite transmission (Faltýnková et al., 2007; Gopko et al., 2017; Vivas Muñoz et al., 2019). Perch is infected by several diplostomid species and often has high infection prevalence as well as parasite load making it a popular subject for host–parasite investigations (Höglund & Thulin, 1990; Karvonen et al., 2009; Rellstab et al., 2011; Sobecka & Słomińska, 2007). *Tylodephys clavata* (von Nordmann) is one of the most common fluke species in perch eyes. Depending on habitat and population, close to 100% of mature perch carry *T. clavata* in the vitreous humour of the eye (Kozicka & Niewiadomska, 1960; Noreikiene et al., 2020; Shukerova et al., 2010; Slivko et al., 2021). Infection from this parasite reduces an individual's ability to detect prey, compete with lesser infected perch and changes its dietary preferences (Vivas Muñoz et al., 2017, 2019, 2021). Infection with *T. clavata* triggers an immune response linked gene expression change in perch eyes (Noreikiene et al., 2020; see Case study 2). However, for this and other parasites, we are yet to fully understand if there is a differential response at a molecular level in reaction to parasite species or community, haplotype composition, site of entry and site of infections. Host–parasite–microbiome interaction and probiotic search are other areas, which highly benefit from advancements in genomic technologies, and will likely be more frequently addressed in the near future (Minich et al., 2022). Perch skin and gut microbiome shows high inter-individual variability and sex-dependent patterns and is influenced by intrinsic and extrinsic environmental factors (Berggren et al., 2022; Chen, Hou, et al., 2022; Kashinskaya et al., 2020; Zha et al., 2018). Thus, dissection of the intricate molecular details of how the relationships between host–parasite and host–commensal may change under near-future environmental conditions becomes achievable by the use of high-throughput sequencing technologies.

6.3 | Linking genetic and phenotypic changes associated with global warming and fisheries exploitation

Recent advances in genetic methods can support a new understanding of how anthropogenic environmental change affects the adaptability, diversity and functioning of fish and aquatic food webs. Global warming of aquatic environments (IPCC, 2019) can strongly affect fish phenotypes (Sheridan & Bickford, 2011). A whole-ecosystem heating experiment over four decades showed that the body growth of small perch increased with warming (Huss et al., 2019), but whether warming also leads to adaptive evolutionary changes in fish traits is still unknown (Merilä & Hendry, 2014). Several traits impacted by warming, however, have a high heritability in fish (Carlson & Seamons, 2008), and could therefore potentially evolve in response to increasing temperatures. Fish also show strong plastic changes in gene regulation when acclimated to different temperatures, in parallel to their altered performance (e.g., weight loss; Windisch et al., 2014). For example, perch in the heating experiment have higher mitochondrial respiration and higher expression of the *nd4* mitochondrial gene than perch in natural temperatures (Pichaud et al., 2020). However, sequencing of mtDNA showed no divergence between the two perch populations (although the analysis covered only partial sequences of three mitochondrial genes from very few individuals; Pichaud et al., 2020). Thus, whether such warming-induced changes in gene expressions also correspond to heritable alterations in gene frequencies is an open question. To address this, combining multi-generational warming experiments (e.g., Loisel et al., 2019) with nuclear and mitochondrial genome sequencing and analyses of gene expression and epigenetic changes, in parallel to measurements of fish traits and fish performance hold great promise.

Combining selection experiments with whole-genome sequencing has revealed, for example, the importance of ecological conditions for the genomic responses to fisheries-induced selection (Crespel et al., 2021). Whereas the phenotype among zebrafish escapees from simulated trawl fishing differed consistently from that of caught individuals, the genotypic variation depended on the population density they had been reared in. Analyses of SNPs mapped to the whole-genome showed that the genes differing between escapees and caught fish were linked to neurological functions, but the particular genes involved depended on population density. Thus, combining selection experiments using multiple ecological factors with whole-genome sequencing, SNP identification and GWAS revealed differences in genotypic and phenotypic variation dependent on ecological conditions. Selection experiments across multiple

generations with such combined approaches could test for long-term genetic changes and resulting impacts on phenotypes and fish performance. This is particularly important in light of the concurrent changes in multiple variables in aquatic environments caused by human activities.

The advances in high throughput sequencing, the discovery of hundreds of thousands of SNPs and the generation of multiple transcriptome profiles, further enable integrating genomic analyses with quantification of phenotypic trait changes over long time series to study adaption to environmental change in the wild. Until recently, human-induced trait adaptation in wild fish has mostly been addressed by analysing directional changes in reaction norms over time (Hutchings, 2011) or quantification of selection differentials and their effect on trait changes observed over long times series (Swain et al., 2007). Without genetic evidence, these methods can potentially indicate but not demonstrate evolution. They were originally used to study fisheries-induced evolution (Dieckmann & Heino, 2007; Swain et al., 2007), but have recently been applied also to trait responses to warming (Crozier et al., 2011; Niu et al., 2023). For example, perch in a multi-generational heating experiment in the wild mature at a smaller size than perch in the control site with natural temperatures (Niu et al., 2023). High-throughput sequencing allows us to combine these findings on trait changes with analyses of genetic variation among individuals from both the heated and the control population at multiple time points throughout the 40-year heating experiment (Niu et al., 2023). Thereby, we can study whether warming also leads to heritable genetic differences and through GWAS any warming-induced genetic changes in key fish traits. Similarly, genome-wide information (obtained from WGS) on changes of allele frequencies over time in spatially replicated populations across gradients of environmental variation caused by humans can help understand both the role of random genetic drift and selection and its effect on phenotypic change in wild fish populations.

7 | CONCLUSIONS

Our review suggests that the recent advances in whole-genome assembly and annotation can contribute to major progress in understanding the role of genes in ecology and the role of ecological processes shaping phenotypic and genomic variation. However, it is unlikely that a comprehensive understanding of the genetic basis of complex ecologically relevant traits will be achieved very quickly. Still, we argue that it will be particularly important – and now also possible thanks to the reference perch genome – to combine meticulous ecological experiments with omics technologies to shed light on how genetic variants and plasticity translate to phenotypic trait variation and how abiotic and biotic factors are sorting out the biological diversity through selection. Thus, despite nearly 300 years have passed since the first scientific description of Eurasian perch by a founder of modern ichthyology, Swedish naturalist Peter Artedi (Wheeler, 1985), we still are at the beginning of the journey, which concerns acquiring the knowledge of how genetic variability between individuals leads to differences in an individual's phenotype, trait and performance in perch. Equipped with a growing arsenal of genomic tools, we should be quite ready for this new adventure.

AUTHOR CONTRIBUTIONS

With input from all authors, A.V. and M. O. conceived the study and were in charge of overall direction and planning. All authors contributed to the literature review. M. O. and M-E. L. assembled and analysed both the existing and new genomic data. M. O. and A. V. designed the figures. All authors contributed to the revision of the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

DNA- and RNA-seq data used in this study are openly available in NCBI GenBank database at https://www.ncbi.nlm.nih.gov/, reference numbers are available in the Section 2 (Material and methods), Tables 1 and 2; Table S1. The data on the 4K SNP genotyping array (*MultiFishSNPChip_1.0*) are available from the corresponding author upon reasonable request.

ORCID

Anti Vasemägi https://orcid.org/0000-0002-2184-5534

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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