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Patterns, processes and conservation management consequences of intraspecific diversity, illustrated by fishes from recently glaciated lakes

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Abstract

1. Patterns in phenotypic and genotypic diversity within many species are becoming increasingly apparent, although there remain many species for which such patterns have yet to be described adequately.
2. Fishes from recently glaciated ecosystems are likely to be particularly rich in intraspecific diversity, yet current conservation management strategies are, in many parts of the world, particularly in Europe, conventionally and overwhelmingly focused on species, regardless of competing species concepts, and appropriate policies for managing diversity at a sub-specific level still have to be developed.
3. Occasional attempts to protect certain vulnerable ecotypes and proposed alternative units of conservation (e.g. 'Pragmatic Species' or 'Evolutionarily Significant Units') reinforce the conventional primacy of contemporary expressed patterns of variation.
4. Intraspecific phenotypic and genotypic patterns are ultimately the result of complex processes of divergence; conservation approaches that focus on the products of evolution largely ignore the processes that generate and maintain those patterns. Policies that acknowledge the continuation of evolution, the derivation of novel diversity over often very short time spans and the role of environment in initiating and perpetuating these processes are poorly integrated into management strategy.
5. To address possible deficits, where intraspecific diversity is not addressed in management practice, we believe it to be important first to characterize hidden genetic and phenotypic diversity, which may intimate eco-evolutionary processes, initially among species of high conservation status. A second step should be to use an approach to intraspecific diversity that illuminates the ultimate processes and mechanisms that bring about that diversity, which also concedes the central role of the environment and affords adequate protection to the ecosystems that

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drive these processes, such as the United Nations Convention on Biological Diversity (CBD) Ecosystems approach.

KEYWORDS

conservation units, cryptic diversity, intraspecific structuring, phenotypic plasticity, polymorphism, postglacial ecosystems, rapid divergence, species concepts

1 | INTRODUCTION

The concept that the diversity of the natural world can reasonably be sub-divided into units named 'species' is one that has persisted despite multiple challenges (De Queiroz, 2007; Linnæus, 1758). Two of these challenges (see below) are important in the context of describing and understanding the evolution and the origin and maintenance of biodiversity. They may, in addition, have implications for conservation management, which holds species to be the typical biological unit upon which, in many parts of the world, policy and practice are founded, such as the International Union for Conservation of Nature (IUCN) Red List. However, while the IUCN Red Listing process does permit entries at the sub-specific level, these are few when compared with the number of species listed. This is despite the stated position of the United Nations Convention on Biological Diversity (CBD) that cites the clear need to protect both 'within' and 'between' species diversity, as well as the ecosystems of which they are part. Regardless of this mandate, it is clear that the need to assess and protect within-species diversity has been significantly undervalued by policy makers worldwide (Hoban et al., 2021).

The first challenge is whether the species, as a level of organization, has a biological relevance for the natural world outside its utility as a method for categorizing organisms for the convenience of study and so on. This is important, as for any species-based conservation policy or action, a clear understanding is needed of the beneficiaries of that action. In most concepts of what constitutes a species, it is either explicit, or there is an implicit assumption, that a species is a biological unit of organization that has, at least, a highly restricted exchange of genes with other such units. A consequence of this is that any accumulated adaptation in a species is retained within the unit. Without such structure, any fitness-enhancing acquired trait risks being lost through outbreeding (Mayr, 1949; Mayr, 1996). Thus, by focusing on the species level, there is a reasonable expectation that the subject of management is an evolutionarily functional unit, with acquired adaptations that influence its fitness for the environment(s) in which it is found (Ryder, 1986).

The second challenge to the species concept is how a species might be defined. Science has collectively struggled with this question since the modern Latin binomial was clearly articulated by Linnæus (1758). Camp & Gillis (1943) recognized 12 different species definitions; Coyne & Orr (2004) found at least 25 in use. Despite more than two and a half centuries of wrestling with the issue, there remains no single definition that is universally accepted and appears to work in all circumstances. As a result, there are exemplars to which

the application of any single strict definition fails (Coyne & Orr, 2004; Hey, 2001). Competing concepts of what constitutes a species are generally described in the literature as the 'species problem' (De Queiroz, 2005; Hey, 2001; Mayr, 1996). The single conceptual definition that has been most widely adopted is the Biological Species Concept, which implies complete (Dobzhansky, 1937), or almost complete (Coyne & Orr, 2004; Mayr, 1942), reproductive isolation between putative species. In reality, however, most species are identified not by reproductive isolation from other species but, rather, operationally by different phenotypic characteristics, from which a lack of gene flow is inferred (Mayr, 1949), despite the potential to miss cryptic genetic variation (Paaby & Rockman, 2014) or to misattribute phenotypic variations arising through plasticity without great distinction in genotype (Pfennig et al., 2010; Schneider & Meyer, 2017; Thibert-Plante & Hendry, 2011; West-Eberhard, 2005).

The 'species' is the biological unit upon which conservation policy and practice is focused. This applies both within the domestic legislation of many countries and international initiatives, directives and conventions (Tucker, 2023). Of the 1171 current taxon designations in the eight most important lists that provide a conservation framework for flora and fauna in the United Kingdom (the Global Red List, UK Biodiversity Action Plan list, Habitats and Species Directive, Bern Convention, Wildlife and Countryside Act 1981, Bonn Convention, EC CITES & Birds Directive), 99.2% are designations for species (Joint Nature Conservation Committee (JNCC), 2023). The few remaining are at intra-species level, with most of these representing ill-defined or inconsistently defined sub-species (although a few hybrid plants have been designated).

One example that illustrates the link between species and conservation management is a major taxonomic review of the freshwater fishes of Europe undertaken by Kottelat & Freyhof (2007). This work approximately doubled the number of native fish species in Europe at that time (up to 546 from around 270). The expansion occurred through the re-evaluation of the species status of a wide range of previously described accounts of new species (usually with very limited range) mostly from Victorian naturalists (Adams & Maitland, 2007). But it also included descriptions of 47 species new to science. Two conservation-relevant consequences happened in the immediate aftermath of the publication of this work. First, the reported diversity of the freshwater fishes in Europe effectively doubled. Second, a large proportion (38%) of the listed species were evaluated as being 'Threatened', mostly as a result of a very restricted distribution. This taxonomic revision has had far-reaching effects on conservation for this group of taxa.

Although largely absent in Europe, some countries, notably in North America, have developed frameworks through which protection at a level below species may be offered. In the United States, 'Distinct Population Segments' of vertebrate species that are 'substantially reproductively isolated' and represent 'important component[s] in the evolutionary legacy of the species' may be recognized as deserving of conservation under the Endangered Species Act (Rogers & Foster, 1996). Similarly, in Canada, guidelines for the recognition of sub-specific 'Designatable Units' require that designated populations be both 'discrete' (i.e. reproductively isolated) and 'evolutionarily significant', as evidenced by genetic markers, heritable traits and so on (COSEWIC, 2020).

Although the species is currently, and is likely to remain, at least in Europe, the focus of conservation actions directed towards organismal groups, there is a developing understanding that, for many groups, the species as a unit does not capture the full diversity of the natural world. In an age of 'omics, the development of now very sophisticated techniques to characterize the genome and phenotypes of groups of organisms, in conjunction with some very subtle analytical tools to model these data (Adams & Otárola-Castillo, 2013; Best et al., 2018; Crotti et al., 2020; Elmer, 2016; Jacobs & Elmer, 2021; Klingenberg, 2011; Schield et al., 2016; Strickland et al., 2023), is starting to provide insights into how phenotypes and the molecular mechanisms that beget them are structured in the natural world, to an extent previously not possible. As these techniques become increasingly affordable and accessible, they can be standardized across systems and geographical areas and make practical the monitoring of intraspecific diversity.

2 | DIVERSITY IN GENOTYPES AND PHENOTYPES

Within species, phenotypic and genotypic variation is generally thought of as continuous, most commonly (but not always) comprising a unimodal Gaussian frequency distribution across the species, which represents the breadth of diversity important for conservation consideration. However, measurable discontinuities, that is multimodal frequency peaks across a species, are becoming increasingly evident in many instances, which result in more or less clearly defined intraspecific groupings (Skúlason & Smith, 1995). Collectively, these within-species patterns of genotype and phenotype may be termed 'intraspecific structuring'.

Genetic structuring may either be adaptive, and thus influence fitness and result in the application of differential selection pressures (Hendry & Stearns, 2004); or neutral, the product (for example) of genetic drift or population bottlenecks (Frazer & Rusello, 2013). The patterns in such structuring provide insight into the connectivity, gene flow and rates of dispersal between populations within a species, as well as hint at historical colonization or events that have affected the genetic structuring (Holderegger et al., 2006).

Similarly, structuring of phenotype may reflect evolutionary responses to different local environments (Bolnick et al., 2011; Koene

et al., 2020; Recknagel et al., 2017), especially when structuring establishes between discrete habitats, both in allopatry and sympatry. The fragmented nature of freshwater systems is especially likely to promote allopatric structuring between catchments within obligate freshwater species with limited powers of dispersal, such as many freshwater fishes (Adams et al., 2016; Bush & Adams, 2007). However, within such allopatric systems, otherwise disparate populations may often converge upon similar phenotypes or groups of phenotypes; local selection pressures cut alternative paths to parallel phenotypic outcomes (Elmer & Meyer, 2011). Various underlying and interactive mechanisms may differ across populations (Gordeeva et al., 2015; Jacobs et al., 2020; Lundsgaard-Hansen et al., 2013) and thereby reveal intrinsic structuring across a species' range.

When such structuring manifests in sympatry, structuring most frequently takes the form of alternative phenotypes that are related to behavioural, morphological, physiological and/or life-history differences based upon differential niche use (well described in a range of species: Endler, 1980; Skúlason et al., 1999; Maan et al., 2008; Martínez et al., 2016; Hooker et al., 2017). Where such structuring is discrete, clearly expressed and related to resource use or diet, it has been termed resource or trophic polymorphism, whether in sympatry or allopatry, and the discrete groupings variously described as 'morphs', 'ecotypes' or 'ecomorphs' (Skúlason et al., 2019; Skúlason & Smith, 1995). Polymorphic species are relatively common among the major vertebrate groups and appear to be prominent among fishes found in recently glaciated lakes (Bernatchez & Wilson, 1998; Doenz et al., 2019; Skúlason & Smith, 1995).

3 | STRUCTURING PATTERNS PREDOMINATE IN POSTGLACIAL FISHES

Knowledge of the arrangements of phenotypic and genetic structuring have only begun to emerge over the last two decades, and there is much more to be understood before a full pattern might be clearly discerned. It has been known for some time that such arrangements appear in many animal species across many habitat types (Smith & Skúlason, 1996). However, it is becoming apparent that this kind of within-species structuring is more widespread in aquatic systems than terrestrial, and especially in recently glaciated lakes more than in other ecosystem types, notwithstanding important exceptions such as the African Great Lakes (Skúlason et al., 2019). Structuring among populations of many fish species from northern freshwater systems is particularly well documented; many species now have extensive genomic resources and the ecological tractability that follows from systems with well-understood geological and hydrological histories with known anthropological impacts (Skúlason et al., 2019). That postglacial fishes typically play key ecological roles, and are often of great economic and cultural importance, make them excellent models for studies of divergence and conservation.

The predominance of structuring in recently glaciated ecosystems over other habitat types has a good theoretical basis: Dieckmann & Doebeli (1999) showed, using statistical models, that the emanation and

perpetuation of structuring depends largely upon the existence of alternative ecological opportunities. As a result of the emergence from the Pleistocene glaciation, recently glaciated freshwater systems are relatively species-poor, supporting only those species that invaded in the last 12,000–15,000 years (Pabijan et al., 2015). Highly variable, streams may provide diverse selection pressures on fish phenotypes via discrete and contrasting habitat types (Jackson et al., 2001). Morphological analyses across 38 sites in Québec, Canada showed that polymorphisms were widespread among many species (Senay et al., 2014). Recently glaciated lakes, in particular, provide ecological contrast by offering alternative foraging resources that are distinct in size, in the habitats where they are located and in the behavioural skills and feeding apparatus that fish need to access these resources effectively. For example, alternative foraging specialisms exhibited in sympatry in several lacustrine fish species are commonly reported—populations diverge into specialist zooplankton feeders in the limnetic zone and macro-zoobenthos feeders in the littoral, each specialist sub-population with its own adaptations suited to its foraging mode (Fraser et al., 2008; Garduño-Paz & Adams, 2010; Hendry et al., 2009; Præbel et al., 2013). The extent to which polymorphic populations in recently glaciated areas exploit alternative resources follows a latitudinal or geographical gradient, with the most recently and fully glaciated northern latitudes showing the most prolific intraspecific diversity (Bernatchez & Wilson, 1998). For example, large radiations with up to seven sympatric ecomorphs of *Salvelinus* spp. have been described in the Kronotskoe basin, Russia (Markevich et al., 2018); Tasersuaq, Greenland (Doenz et al., 2019); and Þingvallavatn, Iceland (Jonsson et al., 1988).

4 | PROCESSES AND MECHANISMS THROUGH WHICH INTRASPECIFIC STRUCTURING ARISES

The phenotypic and genotypic patterns in formerly glaciated regions are often the result of complex processes of divergence. One possibility is that populations that had become fragmented in glacial refugia during the Quaternary climate oscillations, and diverged in allopatry thereafter, established secondary contact following invasions of new habitats emerging from the ice (van Riemsdijk et al., 2017). In such cases, ecological opportunity may maintain or accentuate divergence that began in allopatry (Garduño-Paz et al., 2012), but such structuring can also be the consequence of divergence in sympatry (Dieckmann & Doebeli, 1999; Garduño-Paz et al., 2012). Many populations of fishes, for example, are subjected variously to allopatric neutral divergence (through drift, founder effects, etc.) and natural selection imposed by local environments, resulting from habitat fragmentation, and often complicated by sympatric processes such as secondary contact, hybridization and introgression (Aurelle et al., 2002; Jacobs et al., 2020; Osinov et al., 2022). They are known to exhibit a high degree of genetic structuring that is the result of evolutionary and ecological processes (Adams et al., 2008; Ferguson & Taggart, 1991; Præbel et al., 2013; Verspoor & Cole, 1989; Wood et al., 2014).

Such structuring is often accompanied by large phenotypic differences correlated with trophic morphology or life history, such as two sympatric forms of walleye, *Sander vitreus*, in several lakes in the Canadian Shield of northern Québec, which are genetically distinct at population level: a rare 'blue' form with longer head and slower growth and a more common 'yellow' form (Paradis & Magnan, 2005). However, there are also cryptic examples, presumably in the very earliest stages of divergence, where there is genetic distinction without clear phenotypic differences (McCairns & Bernatchez, 2008; Paaby & Rockman, 2014). For example, populations of yellow perch, *Perca flavescens*, in the Lake Michigan basin show significant genetic differentiation, despite sharing drowned river mouth habitats for much of the year (Chorak et al., 2019; Shoen et al., 2016), although some morphological and resource-use differences have been noted (Parker et al., 2009). Brown trout, *Salmo trutta*, in two tiny, connected lakes in central Sweden show even clearer cryptic genetic structuring. After almost two decades of collecting ca. 4000 samples, clear genetic differences ($F_{ST} \geq 0.10$) were noted (Palmé et al., 2013), despite a lack of both obvious gene-flow barriers and the phenotypic hallmarks of trophic polymorphism (Andersson et al., 2017).

Phenotypic plasticity—the ability of a given genotype to express alternative phenotypes (West-Eberhard, 1989)—may allow discrete, specialized ecomorphs to develop quickly as a collection of functional traits induced by ecology (Bryce et al., 2016). Skúlason et al. (1999) propose a model that includes concepts of phenotypic plasticity as a force accelerating the divergence process; in the earliest stages, resource specialization may result in morphological differences generated solely through plasticity. Variation in DNA methylation may, for example, generate phenotypic divergence even in the absence of significant genetic variation (Angers et al., 2020; Crotti et al., 2021). If this then gives rise to assortative mating and selection against migrants and against hybridization (Garduño-Paz et al., 2020; Thibert-Plante & Hendry, 2011), genetic assimilation of traits and canalization may follow and contribute even further to divergence (Ehrenreich & Pfennig, 2016; Levis & Pfennig, 2019; Pigliucci et al., 2006). The process may even, though not necessarily, proceed to complete reproductive isolation (Parsons et al., 2011; Pfennig et al., 2010), as exemplified by the sympatric divergence of confirmed reproductively isolated Arctic charr, *Salvelinus alpinus*, morphs in Galtaból lake, Iceland (Brachmann et al., 2021; Gislason et al., 1999).

Arctic charr shows a great capacity for phenotypic plasticity (Klemetsen, 2013), and laboratory experiments have demonstrated that plasticity in functional foraging traits can lead to divergence (Adams & Huntingford, 2004). Phenotypic plasticity is hypothesized to have been the mechanism by which the earliest stages of sympatric divergence of Arctic charr occurred in several recently glaciated lakes, where there is evidence of divergence in situ (Garduño-Paz & Adams, 2010; Hooker et al., 2016). The fixation of traits that emerged plastically within a population can be surprisingly quick. For example, in response to a new environment, European whitefish, *Coregonus lavaretus*, from a translocated refuge population in Scotland have, within fewer than 10 generations, developed heritable morphological characteristics distinct from the threatened ancestral population,

reflected in the epigenome as differentially methylated loci, despite little genomic differentiation (Crotti et al., 2021; Koene et al., 2019). Rapidity of plasticity-first divergence (*sensu* Levis & Pfennig, 2016) may be accelerated by growing reproductive isolation of divergent ecotypes. Although threespine sticklebacks, *Gasterosteus aculeatus*, have long been known to exhibit polymorphisms derived from adaptive behavioural and morphological plasticity (Day et al., 1994; Day & McPhail, 1996), a recent study on these fish demonstrated that, in a diet-induced polymorphic captive population, expression of plastic morphology resulting from foraging specialization can also play a role in mate choice (Garduño-Paz et al., 2020).

Although initial divergence via phenotypic plasticity may result quickly in response to new niche exploitation, complete reproductive isolation does not necessarily follow; further divergence due to disruptive selection may be prevented by continued gene flow between the emerging groups resulting from only partial reproductive isolation (Hendry et al., 2009). European whitefish in various basins of Loch Lomond, Scotland, display, for example, different foraging ecologies (Etheridge et al., 2010) and small, but significant, genetic differences (Adams et al., 2016; Crotti et al., 2021). Disruptive selection pressure towards trophic polymorphism is balanced against the homogenizing effects of gene flow caused by regular straying between spawning sites (Adams et al., 2016).

During their freshwater period, the European eel, *Anguilla anguilla*, develops in two discrete ecotypes: narrow-head and broad-head morphs feed on soft invertebrates and hard-shelled molluscs and fish, respectively (Proman & Reynolds, 2002). The absence of intermediate forms suggests that strong disruptive selection plays a role in the observed pattern of variation (Cucherousset et al., 2011). However, random mating and larval dispersal ensure no apparent genetic structuring or reproductive isolation between these forms (Als et al., 2011; Pujolar et al., 2014). In this species (and probably many others), phenotypic structuring may be purely plastic through the mechanism of differential gene expression (De Meyer et al., 2016). However, the differentially expressed genes that result in discrete head shapes appear to be associated with genes linked to somatic growth rate and chemotaxis at an earlier, pre-feeding, developmental stage, which may influence habitat choice. This suggests that a combination of genetic differences and environmentally mediated plasticity is involved in ecotype delimitation (De Meyer et al., 2017). Regardless, instead of maintaining the polymorphism with balancing evolutionary processes in a steady state, every generation sees its collapse and re-establishment. More generally across fish taxa, it has recently become clear that similar phenotypes with the same trophic adaptations may result from different processes, both neutral and non-neutral genetic pathways; these pathways may even vary within a species (Elmer & Meyer, 2011).

5 | NEW APPROACHES TO INTRASPECIFIC STRUCTURING

The underlying processes and mechanisms that facilitate sympatric intra-specific structuring are not fully understood at present.

Disruptive selection leading to differential fixation of alleles associated with particular phenotypic traits may be well documented (Schluter, 2009), as are transgenerational parental effects, such as gamete provisioning (Räsänen & Kruuk, 2007). Egg size, for example, has been shown to contribute significantly to diversification (Beck et al., 2022; Leblanc et al., 2023), while contrasting omega-3 fatty acid compositions in walleye ova have been linked to adult phenotypic characteristics in three populations in Canadian lakes (Wiegand et al., 2007). However, a number of promising areas of molecular research have only recently opened up with new approaches and techniques associated with genomics, transcriptomics and epigenetics. Beyond descriptive genetics, investigation of adaptive potential through genome-wide intraspecific variation has become more practical and, when approached in conjunction with ecological factors and fossil evidence, has the potential to yield insights into the genesis and extent of structuring (Mable, 2019). For example, divergent regions of the Arctic charr genome linked to specific phenotypic characteristics have been seen in ecomorph pairs that have diverged in parallel in a number of lakes (Elmer, 2016; Jacobs et al., 2020).

The field of epigenetics has similarly enjoyed a recent impetus with next-generation-sequencing techniques that can efficiently elucidate patterns of DNA methylation that directly regulate gene expression (Cerruti et al., 2019; Schield et al., 2016). Techniques developed for other organisms are now being applied increasingly to teleost fish and include post-transcriptional mechanisms (Best et al., 2018). Alternative splicing, in which the inclusion or exclusion of particular exons in the processing of mRNA during gene expression, presents opportunities for differential protein synthesis and may result in alternative phenotypes (Singh & Ahi, 2022; Verta & Jacobs, 2022; Wright et al., 2022). In a recent application to postglacial fish, a role has been suggested for alternative splicing in the divergent muscle development and functioning between Arctic charr morphs (Jacobs & Elmer, 2021). Although it has not yet been specifically tested, it is reasonable to hypothesize that this may be adaptive as differences in white muscle tissue are likely to result in swim-performance differences between morphs, each in correspondence with respective foraging behaviour.

The extent to which epigenetics are important mechanisms underlying phenotypic plasticity within a single individual lifespan, or may constitute transgenerational non-genetic inheritance, has recently become a topic of interest in evolutionary biology (Best et al., 2018; Burggren, 2014; Burggren & Crews, 2014; Heard & Martienssen, 2014). How this relates to intraspecific structuring in postglacial fishes is not at all clear, however. Indeed, even the quantification of the relative contributions of genetics and plasticity to ultimate sympatric salmonid ecomorphological phenotypes remains largely unexplored.

In summary, intraspecific structuring is the manifestation of the processes through which biodiversity emerges. Its importance rests with the insights it can provide into fundamental mechanisms of diversity genesis and with the fact that these mechanisms remain poorly understood. Despite this, it is clear that the environment to which diverging and recently diverged intraspecific groups are exposed is key to the very earliest stages of the emergence of novel

diversity and its subsequent maintenance (Skúlason et al., 1999). Integral to the biodiversity of the natural world (Bolnick et al., 2011), intraspecific structuring constitutes a significant component of the world's natural heritage, and the documentation and understanding of the mechanisms behind it are crucial for efficient policy and management of ecosystems and species (Des Roches et al., 2018; Des Roches et al., 2021).

6 | IMPLICATIONS FOR CONSERVATION POLICY AND MANAGEMENT

Although species remain the dominant conservation units within legislation and policies relating to biodiversity and wildlife management in most jurisdictions globally, the CBD, from which these tools to protect biodiversity are largely derived, states a clear need to protect within and between species diversity, as well as the ecosystems of which they are part. Moreover, the CBD promotes application of the ecosystems approach, in which the organism–environment relationships are considered in a dynamic and, to a considerable extent, process-based way, which can be tailored to incorporate intraspecific diversity and developmental (e.g. phenotypic plasticity) and evolutionary processes of diversification (CBD, 2010). Indeed, Principle 9 of the ecosystems approach holds that managers must recognize that change is inherent and inevitable ‘and should be cautious in making any decision that may foreclose options, but, at the same time, consider mitigating actions to cope with long-term changes such as climate change’ (CBD, 2007). Importantly, it recognizes that humans are integral constituents of many ecosystems and are the drivers of much change. Thus, the ecosystems approach can accommodate process-based concepts of biological diversity, especially through regular standardized monitoring and baseline ecological or evolutionary research and data based on adaptive management, with principles and strategies written into legislation and governmental rules, and with consideration of the local contexts of the respective ecosystems (Skúlason et al., 2023).

In recent years, attempts have been made to look beyond the conventional species-level approach. Identification of within-species diversity that is worthy of protection has, until now, primarily focused on identification of contemporary expressed patterns of intraspecific variation, rather than the processes and mechanisms that have resulted in these patterns. This has resulted in specific protection for some vulnerable ecotypes. Uniquely within Europe, statutory conservation agencies within Great Britain have developed guidelines for the identification of designated conservation sites that particularly recognize intra-species diversity within freshwater fishes and formally acknowledge the need to protect and maintain the habitats which support it (Bean et al., 2018). These new guidelines replace the previous guidelines for identifying important conservation sites that, although recognizing intra-specific diversity in the form of ‘local races’, failed fully to safeguard this diversity; nor did the guidelines adequately recognize the link between the natural environment, intra-specific diversity and the evolutionary processes that create and maintain it (Nature Conservancy Council, 1989). This approach has

resulted in Great Britain recognizing a need for protection of anadromous forms of brown trout (sea trout), the large piscivorous *ferox* brown trout lineage and the genetically distinct, spring migrant component of Atlantic salmon, *Salmo salar*, as well as species that exhibit unusually high degrees of phenotypic and genetic diversity.

An important element of conservation policy is to acknowledge, describe and subsequently protect, the diversity that exists within all species. It is also important to recognize that for species that manifest significant within-species phenotypic variation, even when that variation may be discontinuous at a local level, it may not be appropriate to apply a simple trait-based or Pragmatic Species Concept (Seifert, 2014). This is likely to result in a species splitting that does not adequately reflect the evolutionary processes that result in species cohesion and retention of acquired adaptive traits. This is particularly true of fishes occupying recently glaciated lakes but is likely to be equally true of other taxa in other habitat types where the expression of high levels of variation is supported by the environment and where phenotypic plasticity forms a major component of the mechanisms resulting in the expression of such variation.

The concept of ‘evolutionary significant units’ (ESUs) is an attempt to recognize biological units in nature that, although they may not constitute formal species, still capture some of the important components of a species, especially accumulated adaptations accruing from evolutionary processes in a group of organisms (Ryder, 1986). However, precisely defining an ESU is, in practice, fraught with many of the same difficulties as defining a species, with at least 10 definitions of the term (Casacci et al., 2014). In the United States, ESUs are recognized under the Endangered Species Act (Fox, 1991), and the criteria for designation as Distinct Population Segments are based upon the ESU concept (Waples, 2006). Despite definition, taxonomic and legal challenges, Distinct Population Segment designations have been used as key tools in management below the species level (Haig et al., 2006; Johnson, 2018; Rosen, 2007). For anadromous *Oncorhynchus* spp. salmonids in the Pacific Northwest, ESUs and Distinct Population Segments have been a basis of conservation efforts since 1991, which include freshwater habitat restoration (Barnas et al., 2015; Fox, 1991). Fraser & Bernatchez (2001) preface their discussion of historical attempts to define the ESU concept with Mayr's (1960) apposite warning: ‘The exact definition of an ‘evolutionary novelty’ faces the same insuperable difficulty as the definition of the species’. Any conservation approach that focuses on ESUs, like any focused on species, primarily emphasizes the products of processes that result in divergence. Although protecting what currently exists is undoubtedly important, such product-focused strategies fail to provide the direct protection of emergent and future diversity.

Pattern-centred conservation approaches largely ignore the processes that lead to diversity. In contrast, process-oriented approaches that concentrate on adaptive potential and its drivers, the evo-devo concept of ‘evolvability’ (Hendrikse et al., 2007; Pigliucci, 2008) and the eco-evo-devo concept of developmental dynamism responding to environmental and genetic impetus (Campbell et al., 2017; Skúlason et al., 2019) directly address evolutionary potential and the fluidity of diversity. A requirement of this approach is the recognition that it is the environment that promotes the

evolutionary processes that precipitate the emergence of new diversity and the maintenance of diversity once it does emerge. This role of the wider environment is poorly represented both conceptually, and practically, in current conservation management planning, despite several calls for the incorporation of conceptual frameworks within conservation policy that include both genetic mechanisms that delineate phenotypes and how the environment contributes to phenotypic variation (Campbell et al., 2017).

Beyond delineation and organization of genetic and phenotypic variation, it is the evolutionary theatre in which diversity proliferates and, specifically, the habitats that influence underlying evolutionary processes, which should ultimately determine how such diversity is managed in the future (Mable, 2019). Within this broader approach, there must be an acceptance that pressures—often anthropogenic—on key habitats may well result in changes in ecosystem functioning that can cause the extirpation of populations or the emergence of environmental conditions that can result in evolutionary changes (see Raffard et al., 2019; Skúlason et al., 2019; Vonlanthen et al., 2012). We argue that, while trying to minimize human pressures, there is an imperative to consider such changes in conservation policy; conservation effort should not be directed towards the restoration of nature at the point a pattern was described.

In summary, appropriate methods that enable conservation bodies adequately to describe both biodiversity and the continuing evolutionary processes that underpin divergence have not been integrated into conservation policy. Current policy emphasizes the conservation of contemporary patterns of diversity, but even this is not executed particularly well in practice, with the protected patterns overwhelmingly focused upon species. This disregards many of the patterns of diversity that are found below the species level, manifest as the intraspecific genetic and phenotypic structuring now well described in some freshwater taxa. Although many concepts of ESUs have been proposed as an alternative to the species approach, one major conceptual difficulty that may be impeding consideration of sub-specific structuring is that of defining the units themselves. Regardless, focus on contemporary diversity patterns as the products of evolution largely ignores the processes that generate and continually change these patterns. Conceptually poorly incorporated into much conservation management are policies that acknowledge the continuation of evolutionary processes, incessantly deriving new diversity over very short time spans (evidenced by the emergence of novel diversifications in freshwater fishes since the latest glaciation) and that it is the ecosystem that drives and perpetuates these processes. There is an urgency for the conservation of freshwater fishes, especially those in Arctic and sub-Arctic areas disposed to rapid changes, to add to conservation policy a consideration of the environment precipitating the processes that result in new diversity. We advocate an approach that explicitly moves away from consideration of species, or any other pattern of contemporary diversity, towards conservation that prioritizes protection of those ecosystems, such as recently glaciated lakes, that facilitate the dynamic processes of evolution and allows operation of the mechanisms that lead to greater diversity. The ecosystems approach of the CBD can fulfil these criteria without recourse to

identifying species at risk. Although contemporary patterns may assist in identifying such ecosystems, we recommend protection of the environment, not to preserve past or current patterns of biodiversity but rather to secure the processes that generate biodiversity.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

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REFERENCES

- Adams, C.E., Bean, C.W., Dodd, J.A., Down, A., Etheridge, E.C., Gowans, A.R.D. et al. (2016). Inter and intra-population phenotypic and genotypic structuring in the European whitefish *Coregonus lavaretus*, a rare freshwater fish in Scotland. *Journal of Fish Biology*, 88(2), 580–594. <https://doi.org/10.1111/jfb.12855>
- Adams, C.E. & Huntingford, F.A. (2004). Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnean Society*, 81(4), 611–618. <https://doi.org/10.1111/j.1095-8312.2004.00314.x>
- Adams, C.E. & Maitland, P.S. (2007). Arctic charr in Britain and Ireland—15 species or one? *Ecology of Freshwater Fish*, 16(1), 20–28. <https://doi.org/10.1111/j.1600-2006.00179.x>
- Adams, C.E., Wilson, A.J. & Ferguson, M.M. (2008). Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes. *Biological Journal of the Linnean Society*, 95(4), 748–757. <https://doi.org/10.1111/j.1095-8312.2008.01066.x>
- Adams, D.C. & Otárola-Castillo, E. (2013). Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4(4), 393–399. <https://doi.org/10.1111/2041-210X.12035>
- Als, T.D., Hansen, M.M., Maes, G.E., Castonguay, M., Riemann, L., Aarestrup, K. et al. (2011). All roads lead to home: panmixia of European eel in the Sargasso Sea. *Molecular Ecology*, 20(7), 1333–1346. <https://doi.org/10.1111/j.1365-294X.2011.05011.x>

- Andersson, A., Johansson, F., Sundbom, M., Ryman, N. & Laikre, L. (2017). Lack of trophic polymorphism despite genetic differentiation in sympatric brown trout (*Salmo trutta*) population. *Ecology of Freshwater Fish*, 26(4), 643–652. <https://doi.org/10.1111/eff.12308>
- Angers, B., Perez, M., Menicucci, T. & Leung, C. (2020). Sources of epigenetic variation and their applications in natural populations. *Evolutionary Applications*, 13(6), 1262–1278. <https://doi.org/10.1111/eva.12946>
- Aurelle, D., Cattaneo-Berrebi, G. & Berrebi, P. (2002). Natural and artificial secondary contact in brown trout (*Salmo trutta*, L.) in the French western Pyrenees assessed by allozymes and microsatellites. *Heredity*, 89(3), 171–183. <https://doi.org/10.1038/sj.hdy.6800120>
- Barnas, K.A., Katz, S.L., Hamm, D.E., Diaz, M.C. & Jordan, C.E. (2015). Is habitat restoration targeting relevant ecological needs for endangered species? Using Pacific salmon as a case study. *Ecosphere*, 6(7), 110. <https://doi.org/10.1890/ES14-00466.1>
- Bean, C.W., Mainstone, C.P., Hall, R.A., Hatton-Ellis, T.W., Lee, A.S.L. & Boon, P.J. (2018). *Guidelines for the selection of biological SSSIs. Part 2: detailed guidelines for habitats and species groups. Chapter 19 freshwater fish*. Peterborough: Joint Nature Conservation Committee.
- Beck, S.V., Räsänen, K., Kristjánsson, B.K., Skúlason, S., Jónsson, Z.O., Tsinganis, M. et al. (2022). Variation in egg size and offspring phenotype among and within seven Arctic charr morphs. *Ecology and Evolution*, 12(10), e9427. <https://doi.org/10.1002/ece3.9427>
- Bernatchez, L. & Wilson, C.C. (1998). Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology*, 7(4), 431–452. <https://doi.org/10.1046/j.1365-294X.1998.00319.x>
- Best, C., Ikert, H., Kostyniuk, D.J., Craig, P.M., Navarro-Martin, L., Marandel, L. et al. (2018). Epigenetics in teleost fish: from molecular mechanisms to physiological phenotypes. *Comparative Biochemistry and Physiology, Part B*, 224, 210–244. <https://doi.org/10.1016/j.cbpb.2018.01.006>
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Brachmann, M.K., Parsons, K., Skúlason, S. & Ferguson, M.M. (2021). The interaction of resource use and gene flow on the phenotypic divergence of benthic and pelagic morphs of Icelandic Arctic charr (*Salvelinus alpinus*). *Ecology and Evolution*, 11(12), 7315–7334. <https://doi.org/10.1002/ece3.7563>
- Bryce, C., Fraser, A., Knudsen, R., Greer, R. & Adams, C. (2016). Divergent functional traits in three sympatric Arctic charr *Salvelinus alpinus* morphs are not coupled with age of the lineage divergence. *Hydrobiologia*, 783(1), 177–189. <https://doi.org/10.1007/s10750-016-2964-7>
- Burggren, W.W. (2014). Epigenetics as a source of variation in comparative animal physiology—or – Lamarck is lookin' pretty good these days. *The Journal of Experimental Biology*, 217(5), 682–689. <https://doi.org/10.1242/jeb.086132>
- Burggren, W.W. & Crews, D. (2014). Epigenetics in comparative biology: why we should pay attention. *Integrative and Comparative Biology*, 54(1), 7–20. <https://doi.org/10.1093/icb/ucu013>
- Bush, V. & Adams, C. (2007). Using phenotypic variation to determine conservation value: application of a novel approach to Arctic charr. *Ecology of Freshwater Fish*, 16(1), 29–33. <https://doi.org/10.1111/j.1600-0633.2006.00169.x>
- Camp, W.H. & Gillis, C.L. (1943). The structure and origin of species. *Brittonia*, 4(3), 323–385. <https://doi.org/10.2307/2804896>
- Campbell, C.S., Adams, C.E., Bean, C.W. & Parsons, K.J. (2017). Conservation evo-devo: preserving biodiversity by understanding its origins. *Trends in Ecology & Evolution*, 32(10), 746–759. <https://doi.org/10.1016/j.tree.2017.07.002>
- Casacci, L.P., Barbero, F. & Balletto, E. (2014). The 'Evolutionary Significant Unit' concept and its applicability in biological conservation. *The Italian Journal of Zoology*, 81(2), 182–193. <https://doi.org/10.1080/11250003.2013.870240>
- CBD (Secretariat of the Convention on Biological Diversity). (2007). *Ecosystems Approach//Principles*. <https://www.cbd.int/ecosystem/principles.shtml>
- CBD (Secretariat of the Convention on Biological Diversity). (2010). *Ecosystems Approach//Description*. <https://www.cbd.int/ecosystem/description.shtml>
- Cerruti, E., Comino, C., Acquadro, A., Marconi, G., Repetto, A.M., Pisanu, A.B. et al. (2019). Analysis of DNA methylation patterns associated with in vitro propagated globe artichoke plants using an EpiRADseq-based approach. *Genes*, 10(4), 263–282. <https://doi.org/10.3390/genes10040263>
- Chorak, G.M., Ruetz, C.R.R., Thum, R.A., Partridge, C.G., Janetski, D.J., Höök, T.O. et al. (2019). Yellow perch genetic structure and habitat use among connected habitats in eastern Lake Michigan. *Ecology and Evolution*, 9(16), 8922–8932. <https://doi.org/10.1002/ece3.5219>
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). (2020). *COSEWIC guidelines for recognizing designatable units*. <https://cosewic.ca/index.php/en-ca/reports/preparing-status-reports/guidelines-recognizing-designatable-units>
- Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sunderland, MA: Sinauer Associates.
- Crotti, M., Adams, C.E. & Elmer, K.R. (2020). Population genomic SNPs from epigenetic RADs: gaining genetic and epigenetic data from a single established next-generation sequencing approach. *Methods in Ecology and Evolution*, 11(7), 839–849. <https://doi.org/10.1111/2041-210X.13395>
- Crotti, M., Yohannes, E., Winfield, I.J., Lyle, A.A., Adams, C.E. & Elmer, K.R. (2021). Rapid adaptation through genomic and epigenomic responses following translocations in an endangered salmonid. *Evolutionary Applications*, 14(10), 2470–2489. <https://doi.org/10.1111/eva.13267>
- Cucherousset, J., Acou, A., Blanchet, S., Britton, J.R., Beaumont, W.R.C. & Gozlan, R.E. (2011). Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. *Oecologia*, 167(1), 75–84. <https://doi.org/10.1007/s00442-011-1974-4>
- Day, T. & McPhail, J.D. (1996). The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia*, 108(2), 380–388. <https://doi.org/10.1007/BF00334665>
- Day, T., Pritchard, J. & Schluter, D. (1994). A comparison of two sticklebacks. *Evolution*, 48(5), 1735–1741. <https://doi.org/10.1111/j.1558-5646.1994.tb02209.x>
- De Meyer, J., Christiaens, J. & Adriaens, D. (2016). Diet-induced phenotypic plasticity in European eel (*Anguilla anguilla*). *Journal of Experimental Biology*, 219(3), 354–363. <https://doi.org/10.1242/jeb.131714>
- De Meyer, J., Maes, G.E., Dirks, R.P. & Adriaens, D. (2017). Differential gene expression in narrow- and broad-headed European glass eels (*Anguilla anguilla*) points to a transcriptomic link of head shape dimorphism with growth rate and chemotaxis. *Molecular Ecology*, 26(15), 3943–3953. <https://doi.org/10.1111/mec.14155>
- De Queiroz, K. (2005). Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences*, 102(suppl_1), 6600–6607. <https://doi.org/10.1073/pnas.0502030102>
- De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, 56(6), 879–886. <https://doi.org/10.1080/10635150701701083>
- Des Roches, S., Pendleton, L.H., Shapiro, B. & Palkovacs, E.P. (2021). Conserving intraspecific variation for nature's contributions to people. *Nature Ecology, & Evolution*, 5, 574–582. <https://doi.org/10.1038/s41559-021-01403-5>
- Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T. et al. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2, 57–64. <https://doi.org/10.1038/s41559-017-0402-5>

- Dieckmann, U. & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400, 354–357. <https://doi.org/10.1038/22521>
- Dobzhansky, T. (1937). *Genetics and the origin of species*. New York: Columbia University Press.
- Doenz, C.J., Krähnenbühl, A.K., Walker, J., Seehausen, O. & Brodersen, J. (2019). Ecological opportunity shapes a large Arctic charr species radiation. *Proceedings of the Royal Society B*, 286, 20191992. <https://doi.org/10.1098/rspb.2019.1992>
- Ehrenreich, I.M. & Pfennig, D.W. (2016). Genetic assimilation: a review of its potential proximate causes and evolutionary consequences. *Annals of Botany*, 117(5), 769–779. <https://doi.org/10.1093/aob/mcv130>
- Elmer, K.R. (2016). Genomic tools for new insights to variation, adaptation, and evolution in the salmonid fishes: a perspective for charr. *Hydrobiologia*, 783(1), 191–208. <https://doi.org/10.1007/s10750-015-2614-5>
- Elmer, K.R. & Meyer, A. (2011). Adaptation in the age of ecological genomics: insights from parallelism and convergence. *Trends in Ecology & Evolution*, 26(6), 298–306. <https://doi.org/10.1016/j.tree.2011.02.008>
- Endler, J.A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34(1), 76–91. <https://doi.org/10.1111/j.1558-5646-1980.tb04790.x>
- Etheridge, E.C., Harrod, C., Bean, C.W. & Adams, C.E. (2010). Has habitat heterogeneity promoted phenotypic and ecological sub-structuring among a *Coregonus lavaretus* population in a large Scottish lake? *Journal of Fish Biology*, 77(10), 2391–2404. <https://doi.org/10.1111/j.1095-8649.2010.02827.x>
- Ferguson, A. & Taggart, J.B. (1991). Genetic differentiation among the sympatric brown trout (*Salmo trutta*) populations of lough Melvin, Ireland. *Biological Journal of the Linnean Society*, 43(3), 221–237. <https://doi.org/10.1111/j.1095-8312.1991.tb00595.x>
- Fox, W.W. (1991). Policy on applying the definition of species under the endangered species act to Pacific salmon. *Federal Register*, 56(224), 58612–58618. <https://media.fisheries.noaa.gov/2022-11/service-il-fedreg-fr056-fr056224-fr056224.pdf>
- Fraser, D., Huntingford, F.A. & Adams, C.E. (2008). Foraging specialisms, prey size and life-history patterns: a test of predictions using sympatric polymorphic Arctic charr (*Salvelinus alpinus*). *Ecology of Freshwater Fish*, 17(1), 1–9. <https://doi.org/10.1111/j.1600-0633.2007.00245.x>
- Fraser, D.J. & Bernatchez, L. (2001). Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology*, 10(12), 2741–2752. <https://doi.org/10.1046/j.0962-1083.2001.01411.x>
- Frazer, K.K. & Rusello, M.A. (2013). Lack of parallel genetic patterns underlying the repeated ecological divergence of beach and stream spawning kokanee salmon. *Journal of Evolutionary Biology*, 26(12), 2606–2621. <https://doi.org/10.1111/jeb.12250>
- Garduño-Paz, M.V. & Adams, C.E. (2010). Discrete prey availability promotes foraging segregation and early divergence in Arctic charr, *Salvelinus alpinus*. *Hydrobiologia*, 650(1), 15–26. <https://doi.org/10.1007/s10750-009-0055-8>
- Garduño-Paz, M.V., Adams, C.E., Verspoor, E., Knox, D. & Harrod, C. (2012). Convergent evolutionary processes driven by foraging opportunity in two sympatric morph pairs of Arctic charr with contrasting post-glacial origins. *Biological Journal of the Linnean Society*, 106(4), 794–806. <https://doi.org/10.1111/j.1095-8312.2012.01906>
- Garduño-Paz, M.V., Huntingford, F.A., Garrett, S. & Adams, C.E. (2020). A phenotypically plastic magic trait promoting reproductive isolation in sticklebacks? *Evolutionary Ecology*, 34(1), 123–131. <https://doi.org/10.1007/s10682-019-10015-2>
- Gíslason, D., Ferguson, M.M., Skúlason, S. & Snorrason, S.S. (1999). Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56(12), 2229–2234. <https://doi.org/10.1139/f99-245>
- Gordeeva, N.V., Alekseyev, S.A., Matveev, A.N. & Samusenok, V.P. (2015). Parallel evolutionary divergence in Arctic char *Salvelinus alpinus* complex from Transbaikalia: variation in differentiation degree and segregation of genetic diversity among sympatric forms. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(1), 96–115. <https://doi.org/10.1139/cjfas-2014-0014>
- Haig, S.M., Beever, E.A., Chambers, S.M., Draheim, H.M., Dugger, B.D., Dunham, S. et al. (2006). Taxonomic considerations in listing subspecies under the U.S. endangered species act. *Conservation Biology*, 20(6), 1584–1594. <https://doi.org/10.1111/j.1523-1739.2006.00530.x>
- Heard, E. & Martienssen, R.A. (2014). Transgenerational epigenetic inheritance: myths and mechanisms. *Cell*, 157(1), 95–109. <https://doi.org/10.1016/j.cell.2014.02.045>
- Hendrikse, J.L., Parsons, T.E. & Hallgrímsson, B. (2007). Evolvability as the proper focus of evolutionary developmental biology. *Evolution & Development*, 9(4), 393–401. <https://doi.org/10.1111/j.1525-142X.2007.00176.x>
- Hendry, A. & Stearns, S. (2004). *Evolution illuminated: salmon and their relatives*. Oxford: Oxford University Press.
- Hendry, A.P., Bolnick, D.I., Berner, D. & Peichel, C.L. (2009). Along the species continuum in sticklebacks. *Journal of Fish Biology*, 75(8), 2000–2036. <https://doi.org/10.1111/j.1095-8649.2009.02419.x>
- Hey, J. (2001). The mind of the species problem. *Trends in Ecology & Evolution*, 16(7), 326–329. [https://doi.org/10.1016/S0169-5347\(01\)02145-0](https://doi.org/10.1016/S0169-5347(01)02145-0)
- Hoban, S., Campbell, C.D., da Silva, J.M., Ekblom, R., Funk, W.C., Garner, B.A. et al. (2021). Genetic diversity is considered important but interpreted narrowly in country reports to the convention on biological diversity: current actions and indicators are insufficient. *Biological Conservation*, 261, 109233. <https://doi.org/10.1016/j.biocon.2021.109233>
- Holderegger, R., Kamm, U. & Gugerli, F. (2006). Adaptive vs. neutral divergence: implications for landscape genetics. *Landscape Ecology*, 21(6), 797–807. <https://doi.org/10.1007/s10980-005-5245-9>
- Hooker, O.E., Barry, J., Van Leeuwen, T.E., Lyle, A., Newton, J., Cunningham, P. et al. (2016). Morphological, ecological and behavioural differentiation of sympatric profundal and pelagic Arctic char (*Salvelinus alpinus*) in Loch Dughall Scotland. *Hydrobiologia*, 783(1), 209–221. <https://doi.org/10.1007/s10750-015-2599-0>
- Hooker, O.E., Van Leeuwen, T.E. & Adams, C.E. (2017). The physiological costs of prey switching reinforce foraging specialization. *Journal of Animal Ecology*, 83(3), 605–614. <https://doi.org/10.1111/1365-2656.12632>
- Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1), 157–170. <https://doi.org/10.1139/f00-239>
- Jacobs, A., Caruthers, M., Yurchenko, A., Gordeeva, N.V., Alekseyev, S.S., Hooker, O. et al. (2020). Parallelism in eco-morphology and gene expression despite variable evolutionary and genomic backgrounds in a Holarctic fish. *PLoS Genetics*, 16(4), e1008658. <https://doi.org/10.1371/journal.pgen.1008658>
- Jacobs, A. & Elmer, K.R. (2021). Alternative splicing and gene expression play contrasting roles in parallel phenotypic divergence of a salmonid fish. *Molecular Ecology*, 30(20), 4955–4969. <https://doi.org/10.1111/mec.15817>
- JNCC (Joint Nature Conservation Committee). (2023). *Conservation Designations for UK Taxa 2023*. [https://hub.jncc.gov.uk/assests/478f7160-967b-4366-acdf-8941fd33850b#:~:text=This%20collection%20of%20files%20details,Great%20Britain%20or%20the%20UK.\[Accessed 30th November 2023\].](https://hub.jncc.gov.uk/assests/478f7160-967b-4366-acdf-8941fd33850b#:~:text=This%20collection%20of%20files%20details,Great%20Britain%20or%20the%20UK.[Accessed 30th November 2023].)
- Johnson, C.M. (2018). Ecotypes and killer whales: a scientific concept to guide the endangered species Act's “distinct population segment”. *University of Colorado Law Review*, 89(3), 967–999. <https://scholar.law.colorado.edu/cgi/viewcontent.cgi?article=1286&context=lawreview>

- Jonsson, B., Skúlason, S., Snorrason, S.S., Sandlund, O.T., Malmquist, H.J., Jónsson, P.M. et al. (1988). Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(9), 1537–1547. <https://doi.org/10.1139/f88-182>
- Klemetsen, A. (2013). The most variable vertebrate on earth. *Journal of Ichthyology*, 53(10), 781–791. <https://doi.org/10.1134/S0032945213100044>
- Klingenberg, C.P. (2011). MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, 11(2), 353–357. <https://doi.org/10.1111/j-1755-0998.2010.02924.x>
- Koene, J.P., Crotti, M., Elmer, K.R. & Adams, C.E. (2019). Differential selection pressures result in a rapid divergence of donor and refuge populations of a high conservation value freshwater fish *Coregonus lavaretus* (L.). *Evolutionary Ecology*, 33(4), 533–548. <https://doi.org/10.1007/s10682-019-09995-y>
- Koene, J.P., Elmer, K.R. & Adams, C.E. (2020). Intraspecific variation and structuring of phenotype in a lake-dwelling species are driven by lake size and elevation. *Biological Journal of the Linnean Society*, 131(3), 585–599. <https://doi.org/10.1093/biolinnean/blaa137>
- Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Berlin: Publications Kottelat, Cornol and Freyhof.
- Leblanc, C.A., Schreck, C., Kristjánsson, B.K., Skúlason, S. & Noakes, D.L. (2023). Egg size-related traits during the first year of growth and smolting in hatchery and wild juveniles of steelhead trout *Oncorhynchus mykiss*. *Environmental Biology of Fishes*, 106(5), 1061–1078. <https://doi.org/10.1007/s10641-022-01377-8>
- Levis, N.A. & Pfennig, D.W. (2016). Evaluating ‘plasticity-first’ evolution in nature: key criteria and empirical approaches. *Trends in Ecology & Evolution*, 31(7), 563–574. <https://doi.org/10.1016/j.tree.2016.03.012>
- Levis, N.A. & Pfennig, D.W. (2019). Phenotypic plasticity, canalization, and the origins of novelty: evidence and mechanisms from amphibians. *Seminars in Cell & Developmental Biology*, 88, 80–90. <https://doi.org/10.1016/j.semcdb.2018.01.012>
- Linnæus, C. (1758). *Systema naturæ*. 10th edition, Stockholm: Salvius.
- Lundsgaard-Hansen, B., Matthews, B., Vonlanthen, P., Taverna, A. & Seehausen, O. (2013). Adaptive plasticity and genetic divergence in feeding efficiency during parallel adaptive radiation of whitefish (*Coregonus* spp.). *Journal of Evolutionary Biology*, 26(3), 483–498. <https://doi.org/10.1111/jeb.12063>
- Maan, M.E., Eshuis, B., Haesler, M.P., Schneider, M.V., van Alphen, J.M. & Seehausen, O. (2008). Color polymorphism and predation in a Lake Victoria cichlid fish. *Copeia*, 2008(3), 621–629. <https://doi.org/10.1643/CE-07-114>
- Mable, B. (2019). Conservation of adaptive potential and functional diversity: integrating old and new approaches. *Conservation Genetics*, 20(1), 89–100. <https://doi.org/10.1007/s10592-018-1129-9>
- Markevich, G., Esin, E. & Anisimova, L. (2018). Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden *Salvelinus malma* from the Lake Kronotskoe Basin. *Ecology and Evolution*, 8(5), 2554–2567. <https://doi.org/10.1002/ece.3806>
- Martínez, C., Chavarría, C., Sharpe, D.M.T. & De León, L.F. (2016). Low predictability of colour polymorphism in introduced guppy (*Poecilia reticulata*) populations in Panama. *PLoS ONE*, 11(2), e0148040. <https://doi.org/10.1371/journal.pone.0148040>
- Mayr, E. (1942). *Systematics and the origin of species*. New York: Columbia University Press.
- Mayr, E. (1949). The species concept: semantics versus semantics. *Evolution*, 3(4), 381–386. <https://doi.org/10.1111/j.1558-5646.1949.tb00038.x>
- Mayr, E. (1960). The emergence of evolutionary novelties. In: Tax, S. (Ed.) *Evolution after Darwin: the evolution of life*. Chicago: University of Chicago Press, pp. 349–380.
- Mayr, E. (1996). What is a species and what is not? *Philosophy of Science*, 63(2), 262–277. <https://doi.org/10.1086/289912>
- McCairns, R.J.S. & Bernatchez, L. (2008). Landscape genetic analyses reveal cryptic population structure and putative selection gradients in a large-scale estuarine environment. *Molecular Ecology*, 17(17), 3901–3916. <https://doi.org/10.1111/j.1365-294X.2008.03884.x>
- Nature Conservancy Council. (1989). *Guidelines for selection of biological SSSIs*. Peterborough.
- Osinov, A.G., Volkov, A.A. & Pavlov, D.A. (2022). Secondary contact, hybridization, and diversification in Arctic charr (*Salvelinus alpinus* (L.) species complex) from lakes of the Norilo-Pyasinskaya water system, Taimyr: how many forms exist there? *Hydrobiologia*, 849(11), 2521–2547. <https://doi.org/10.1007/s10750-022-04869-x>
- Paaby, A.B. & Rockman, M.V. (2014). Cryptic genetic variation: evolution's hidden substrate. *Nature Reviews Genetics*, 15, 247–258. <https://doi.org/10.1038/nrg3688>
- Pabijan, M., Zieliński, P., Dudek, K., Chloupek, M., Sotiropoulos, K., Liana, M. et al. (2015). The dissection of a Pleistocene refugium: phylogeography of the smooth newt, *Lissostriton vulgaris*, in the Balkans. *Journal of Biogeography*, 42(4), 671–683. <https://doi.org/10.1111/jbi.12449>
- Palmé, A., Laikre, L. & Ryman, N. (2013). Monitoring reveals two genetically distinct brown trout populations remaining in stable sympatry over 20 years in tiny mountain lakes. *Conservation Genetics*, 14(4), 795–808. <https://doi.org/10.1007/s10592-013-0475-x>
- Paradis, Y. & Magnan, P. (2005). Phenotypic variation of walleye, *Sander vitreus*, in Canadian shield lakes: new insights on percid polymorphism. *Environmental Biology of Fishes*, 73(4), 357–366. <https://doi.org/10.1007/s10641-005-2261-1>
- Parker, A.D., Stepien, C.A., Sepulveda-Villet, O.J., Ruehl, C.B. & Uzarski, D.G. (2009). The interplay of morphology, habitat, resource use, and genetic relationships in young yellow perch. *Transactions of the American Fisheries Society*, 138(4), 899–914. <https://doi.org/10.1577/T08-093.1>
- Parsons, K.J., Sheets, H.D., Skúlason, S. & Ferguson, M.M. (2011). Phenotypic plasticity, heterochrony and ontogenetic repatterning during juvenile development of divergent Arctic charr (*Salvelinus alpinus*). *Journal of Evolutionary Biology*, 24(8), 1640–1652. <https://doi.org/10.1111/j.1420-9101.2011.02301.x>
- Pfennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D. & Moczek, A.P. (2010). Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology & Evolution*, 25(8), 459–467. <https://doi.org/10.1016/j.tree.2010.05.006>
- Pigliucci, M. (2008). Is evolvability evolvable? *Nature Reviews Genetics*, 9, 75–82. <https://doi.org/10.1038/nrg2278>
- Pigliucci, M., Murren, C.J. & Schlichting, C.D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, 209(12), 2362–2367. <https://doi.org/10.1242/jeb.02070>
- Præbel, K., Knudsen, R., Siwertsson, A., Karhunen, M., Kahilainen, K.K., Ovaskainen, O. et al. (2013). Ecological speciation in postglacial European whitefish: rapid adaptive radiations into the littoral, pelagic, and profundal lake habitats. *Ecology and Evolution*, 3(15), 4970–4986. <https://doi.org/10.1002/ece.3.867>
- Proman, J.M. & Reynolds, J.D. (2002). Differences in head shape of the European eel, *Anguilla anguilla* (L.). *Fisheries Management and Ecology*, 7(4), 349–354. <https://doi.org/10.1046/j.1365-2400.2000.007004349.x>
- Pujolar, J.M., Jacobsen, M.W., Als, T.D., Frydenberg, J., Munch, K., Jónsson, B. et al. (2014). Genome-wide single-generation signatures of local selection in the panmictic European eel. *Molecular Ecology*, 23(10), 2514–2528. <https://doi.org/10.1111/mec.12753>
- Raffard, A., Santoul, F., Cucherousset, J. & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biological Reviews*, 94(2), 648–661. <https://doi.org/10.1111/brv.12472>
- Räsänen, K. & Kruuk, L.E.B. (2007). Maternal effects and evolution at ecological time-scales. *Functional Ecology*, 21(3), 408–421. <https://doi.org/10.1111/j.1365-2435.2007.01246.x>

- Recknagel, H., Hooker, O.E., Adams, C.E. & Elmer, K.R. (2017). Ecosystem size predicts eco-morphological variability in a postglacial diversification. *Ecology and Evolution*, 7(15), 5560–5570. <https://doi.org/10.1002/ece3.3013>
- Rogers, J.G. & Foster, N. (1996). Policy regarding the recognition of distinct vertebrate population segments under the endangered species act. *Federal Register*, 61(26), 4722–4725. <https://www.govinfo.gov/content/pkg/FR-1996-02-07/pdf/96-2639.pdf>
- Rosen, T. (2007). The endangered species act and the distinct population segment policy. *Ursus*, 18(1), 109–116. <https://www.jstor.org/stable/20204073>
- Ryder, O.A. (1986). Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology & Evolution*, 1(1), 9–10. [https://doi.org/10.1016/0169-5347\(86\)90059-5](https://doi.org/10.1016/0169-5347(86)90059-5)
- Schild, D.R., Walsh, M.R., Card, D.C., Andrew, A.L., Adams, R.H. & Castoe, T.A. (2016). EpiRADseq: scalable analysis of genomewide patterns of methylation using next-generation sequencing. *Methods in Ecology and Evolution*, 7(1), 60–69. <https://doi.org/10.1111/2041-210X.12435>
- Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science*, 323(5915), 737–741. <https://doi.org/10.1126/science.1160006>
- Schneider, R.F. & Meyer, A. (2017). How plasticity, genetic assimilation and cryptic genetic variation may contribute to adaptive radiations. *Molecular Ecology*, 26(1), 330–350. <https://doi.org/10.1111/mec.13880>
- Seifert, B. (2014). A pragmatic species concept applicable to all eukaryotic organisms independent from their mode of reproduction or evolutionary history. *Soil Organisms*, 86(1), 85–93. <https://api.semanticscholar.org/CorpusID:54690108>
- Senay, C., Boisclair, D. & Peres-Neto, P.R. (2014). Habitat-based polymorphisms is common in stream fishes. *Journal of Animal Ecology*, 84(1), 219–227. <https://doi.org/10.1111/1365-2656.12269>
- Shoen, L.S., Student, J.J., Hoffman, J.C., Sierszen, M.E. & Uzarski, D.G. (2016). Reconstructing fish movements between coastal wetland and nearshore habitats of the Great Lakes. *Limnology and Oceanography*, 61(5), 1800–1813. <https://doi.org/10.1002/lno.10340>
- Singh, P. & Ahi, E.P. (2022). The importance of alternative splicing in adaptive evolution. *Molecular Ecology*, 31(7), 1928–1938. <https://doi.org/10.1111/mec.16377>
- Skúlason, S., Parsons, K.J., Svanbäck, R., Räsänen, K., Ferguson, M.M., Adams, C.E. et al. (2019). A way forward with eco evo devo: an extended theory of resource polymorphism with postglacial fishes as model systems. *Biological Reviews*, 94(5), 1786–1808. <https://doi.org/10.1111/brv.12534>
- Skúlason, S., Sandberg, O.M., Sigurðsson, S., Guðmundsdóttir R. & Gunnarsson, T.G. (editors) (2023). *Greinargerð í kjölfar málþings um vistkerfisnálgun*. (Report on the outcomes of a symposium on the Ecosystems approach, to the Icelandic Ministry of Food, Agriculture and Fisheries). BIODICE. Available from: https://www.stjornarradid.is/library/01--Frettatengt---myndir-og-skrar/MAR/Fylgiskjol/Greinargerð_Biodice_málþing_210923.pdf
- Skúlason, S. & Smith, T.B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, 10(9), 366–370. [https://doi.org/10.1016/S0169-5347\(00\)89135-1](https://doi.org/10.1016/S0169-5347(00)89135-1)
- Skúlason, S., Snorrason, S.S. & Jónsson, B. (1999). Sympatric morphs, populations and speciation in freshwater fish with emphasis an Arctic charr. In: Magurran, A.E., & May, R. (Eds.) *Evolution of biological diversity*, Oxford: Oxford University Press, pp. 70–92.
- Smith, T.B. & Skúlason, S. (1996). Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, 27(1), 111–133. <https://doi.org/10.1146/annurev.ecolsys.27.1.111>
- Strickland, K., Räsänen, K., Kristjánsson, B.K., Phillips, J.S., Einarsson, A., Snorradóttir, R.G. et al. (2023). Genome–phenotype–environment associations identify signatures of selection in a panmictic population of threespine stickleback. *Molecular Ecology*, 32(7), 1708–1725. <https://doi.org/10.1111/mec.16845>
- Thibert-Plante, X. & Hendry, P. (2011). The consequences of phenotypic plasticity for ecological speciation. *Journal of Evolutionary Biology*, 24(2), 326–342. <https://doi.org/10.1111/j.1420-9101.2010.02169.x>
- Tucker, G. (2023). *Nature conservation in Europe: approaches and lessons*, Cambridge: Cambridge University Press. <https://doi.org/10.1017/9781108654647>
- Van Riemsdijk, I., Arntzen, J.A., Bogaerts, S., Franzen, M., Litvinchuk, S.N., Olgun, K. et al. (2017). The near East as a cradle of biodiversity: a phylogeography of banded newts (genus *Ommatotriton*) reveals extensive inter- and intraspecific genetic differentiation. *Molecular Phylogenetics and Evolution*, 114, 73–81. <https://doi.org/10.1016/j.ympev.2017.05.028>
- Verspoor, E. & Cole, L.J. (1989). Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology*, 67(6), 1453–1461. <https://doi.org/10.1139/z89-206>
- Verta, J.-P. & Jacobs, A. (2022). The role of alternative splicing in adaptation and evolution. *Trends in Ecology & Evolution*, 37(4), 299–308. <https://doi.org/10.1016/j.tree.2021.11.010>
- Vonlanthen, P., Bittner, D., Hudson, A., Müller, R., Lundsgaard-Hansen, B., Roy, D. et al. (2012). Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature*, 482, 357–362. <https://doi.org/10.1038/nature10824>
- Waples, R. (2006). Distinct Population Segments. In: Scott, J.M., Goble, D.D., & Davis, F.W. (Eds.) *The endangered species act at thirty, volume 2: conserving biodiversity in human-dominated landscapes*, Washington: Island Press, pp. 127–149.
- West-Eberhard, M.J. (1989). Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, 20, 249–278. <https://doi.org/10.1146/annurev.es.20.110189.001341>
- West-Eberhard, M.J. (2005). Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences*, 102(suppl_1), 6543–6549. <https://doi.org/10.1073/pnas.0501844102>
- Wiegand, M.D., Johnston, T.A., Leggett, W.C., Watchorn, K.E., Ballevena, A.J., Porteous, L.R. et al. (2007). Contrasting strategies of ova lipid provisioning in relation to maternal characteristic in three walleye (*Sander vitreus*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(4), 700–712. <https://doi.org/10.1139/f07-033>
- Wood, J.L.A., Belmar-Lucero, S., Hutchings, J.A. & Fraser, D.J. (2014). Relationship of habitat variability to population size in a stream fish. *Ecological Applications*, 24(5), 1085–1100. <https://doi.org/10.1890/13-1647.1>
- Wright, C.J., Smith, C.W.J. & Jiggins, C.D. (2022). Alternative splicing as a source of phenotypic diversity. *Nature Reviews Genetics*, 23, 697–710. <https://doi.org/10.1038/s41576-022-00514-4>

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