A way forward with eco evo devo: an extended theory of resource polymorphism with postglacial fishes as model systems

Skúli Skúlason[1,2]*, Kevin J. Parsons[3], Richard Svanbäck[4], Katja Räsänen[5], Moira M. Ferguson[6], Colin E. Adams[7], Per-Arne Amundsen[8], Pia Bartels[9], Colin W. Bean[10], Janette W. Boughman[11], Göran Englund[9], Jóhannes Guðbrandsson[12], Oliver E. Hooker[13], Alan G. Hudson[9], Kimmo K. Kahilainen[14], Rune Knudsen[8], Bjarni K. Kristjánsson[1], Camille A-L. Leblanc[1], Zophonías Jónsson[12], Gunnar Öhlund[9], Carl Smith[15] and Sigurður S. Snorrason[12]

[1] *Department of Aquaculture and Fish Biology, Hólar University, Sauðárkrókur, 551 Iceland*

[2] *Icelandic Museum of Natural History, Brynjólfsgata 5, Reykjavík, IS-107 Iceland*

[3] *Institute of Biodiversity, Animal Health & Comparative Medicine, University of Glasgow, Glasgow, G12 8QQ, U.K.*

[4] *Animal Ecology, Department of Ecology and Genetics, Science for Life Laboratory, Uppsala University, Norbyvägen 18D, Uppsala SE-752 36, Sweden*

[5] *Department of Aquatic Ecology, EAWAG, Swiss Federal Institute of Aquatic Science and Technology, and Institute of Integrative Biology, ETH-Zurich, Ueberlandstrasse 133, CH-8600 Dübendorf, Switzerland*

[6] *Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada*

[7] *Scottish Centre for Ecology and the Natural Environment, IBAHCM, University of Glasgow, Glasgow G12 8QQ, U.K.*

[8] *Freshwater Ecology Group, Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of Tromsö, Tromsö N-9037, Norway*

[9] *Department of Ecology and Environmental Science, Umeå University, Umeå SE-90187, Sweden*

[10] *Scottish Natural Heritage, Caspian House, Mariner Court, Clydebank Business Park, Clydebank G81 2NR, U.K.*

[11] *Department of Integrative Biology, Michigan State University, East Lansing, MI 48824, U.S.A.*

[12] *Institute of Life and Environmental Sciences, University of Iceland, Reykjavik 101, Iceland*

[13] *PR statistics LTD, 53 Morrison Street, Glasgow, G5 8LB, UK*

[14] *Inland Norway University of Applied Sciences, Department of Forestry and Wildlife Management, Campus Evenstad, Anne Evenstadvei 80, Koppang NO-2480, Norway*

[15] *School of Biology, University of St Andrews, St. Andrews, Fife KY16 9AJ, U.K.*

ABSTRACT

A major goal of evolutionary science is to understand how biological diversity is generated and altered. Despite considerable advances, we still have limited insight into how phenotypic variation arises and is sorted by natural selection. Here we argue that an integrated view, which merges ecology, evolution and developmental biology (eco evo devo) on an equal footing, is needed to understand the multifaceted role of the environment in simultaneously determining the development of the phenotype and the nature of the selective environment, and how organisms in turn affect the environment through eco evo and eco devo feedbacks. To illustrate the usefulness of an integrated eco evo devo perspective, we connect it with the theory of resource polymorphism (i.e. the phenotypic and genetic diversification that occurs in response to variation in available resources). In so doing, we highlight fishes from recently glaciated freshwater systems as exceptionally well-suited model systems for testing predictions of an eco evo devo framework in studies of diversification. Studies on these fishes show that intraspecific diversity can evolve rapidly, and that this process is jointly facilitated by (*i*) the availability of diverse environments promoting divergent natural selection; (*ii*) dynamic developmental processes sensitive to environmental and genetic signals; and (*iii*) eco evo and eco devo

* Author for correspondence (Tel: +354 455 6300; Fax +354 455 6301; E-mail: skuli@holar.is).

feedbacks influencing the selective and developmental environments of the phenotype. We highlight empirical examples and present a conceptual model for the generation of resource polymorphism – emphasizing eco evo devo, and identify current gaps in knowledge.

Key words: divergent evolution, epigenetics, genetics, niche construction, non-genetic inheritance, phenotype, phenotypic plasticity, natural selection, polymorphic fishes, speciation.

CONTENTS

I. INTRODUCTION

Many key advances in evolutionary biology over the last century, such as the modern synthesis, have resulted from synergies among fields. Yet, our understanding of what drives the evolution of biological diversity is still limited – not least because we often adopt a discipline-specific focus. For instance, the fields of evolutionary ecology and population genetics have both yielded strong empirical evidence for the role of natural selection in the evolution of biological diversity (Endler, 1986; Schluter, 2000), but they have done so from somewhat disparate perspectives. Evolutionary ecology has focused on relationships among the phenotype, environment and fitness, thus documenting selection, but rarely identifies how phenotypic variation arises (e.g. Danchin *et al.*, 2011) or the agents of selection (e.g. MacColl, 2011). On the other hand, most applications of population genetics theory have focused primarily on changes in allele frequencies at loci that do not necessarily underlie the phenotypic targets of selection. Although this situation is now changing with the opportunities offered by second- and third-generation sequencing (reviewed in Andrew *et al.*, 2013), we still need

greater insight into how phenotypic variation is generated and maintained (Hendrikse, Parsons, & Hallgrímsson, 2007; Minelli, 2015) and how it influences ecological and evolutionary processes (Pigliucci, 2008). This need is of fundamental importance because natural selection acts on the phenotype, which in turn is determined by a complex array of interacting mechanisms (Sultan, 2015).

The origins of phenotypic variation have been a focus of the field of evolutionary developmental biology (evo devo; see Table 1 for a glossary of terms used herein) (Parsons & Albertson, 2013; Moczek *et al.*, 2015). Evo devo takes a 'phenotype first' approach in that it seeks to determine the developmental mechanisms that underlie phenotypic variation. The nature of these mechanisms is now being re-evaluated because of the realization that nucleotide variation (genetic) is not the only source of heritable variation underlying the phenotype (reviewed in Danchin, 2013). One emerging theme is that development itself is a progenitor of phenotypic variation as it responds to environmental cues (in the present and past), thereby determining what heritable phenotypic variation is exposed to selection (West-Eberhard, 2003; Gibson & Dworkin, 2004). The

recognition that inherited variation can also arise through non-genetic mechanisms (e.g. epigenetics) (Danchin, 2013; Bonduriansky & Day, 2018), is re-invigorating research that seeks to understand how phenotypic variation is fuelling the capacity of populations to evolve (Kirschner & Gerhart, 1998; Hendrikse *et al.*, 2007). Despite this shift in focus, the evo devo approach has only recently considered how development interacts with the environmental conditions experienced by organisms (Gilbert & Epel, 2015; Sultan, 2015).

Ecological conditions have traditionally been thought of as the arena within which natural selection operates. Natural selection itself does not generate heritable phenotypic variation but rather sorts it to alter phenotypic and genetic distributions across generations. Our understanding of what determines the strength and nature of selection regimes has been facilitated by the recent integration of ecological and evolutionary processes in the field of eco-evolutionary dynamics (Hairston *et al.*, 2005; Hendry, 2009, 2017). Importantly, this approach has demonstrated that ecologically driven adaptive phenotypic changes can feed back directly to ecology [e.g. population growth and ecosystem function (Thuiller *et al.*, 2013; Raffard *et al.*, 2019)] – illustrating the reciprocity between ecological and evolutionary processes (Metz, Nisbet, & Geritz, 1992; Post & Palkovacs, 2009; Kinnison, Hairston, & Hendry, 2015). Studies of eco-evo dynamics recognize that substantial evolutionary changes can occur at ecological time scales (i.e. within a few generations), thereby confirming that contemporary evolutionary and ecological processes can be strongly coupled. This coupling is particularly relevant for ecosystems facing environmental change (Hendry & Kinnison, 1999; Hairston *et al.*, 2005; Hendry *et al.*, 2009; Matthews *et al.*, 2011; Schoener, 2011).

The need for eco evo integration is further highlighted through the concept of niche construction, a process whereby an organism can influence selective environments by altering its own niche or the niches of other members of the community (Odling-Smee *et al.*, 2013; Matthews *et al.*, 2014; Laland, Matthews, & Feldman, 2016). This concept is closely related to that of eco-evolutionary feedbacks (see Post & Palkovacs, 2009; Sultan, 2015). However, a key difference between the two concepts is that research in eco-evolutionary feedbacks to date has primarily focused on the effects of genetically inherited traits, while niche construction also includes the effects due to phenotypic plasticity (Matthews *et al.*, 2014; Sultan, 2015). The niche construction concept also differs from that of the 'extended phenotype' because the latter is restricted to the environmental effects of genetically inherited traits (Dawkins, 1982). Niche construction theory also emphasizes (more so than eco-evolutionary feedback) a role of inherited environments as a parallel route of inheritance (Danchin, 2013; Odling-Smee *et al.*, 2013). Niche construction can also cause plastic phenotypic responses, thereby influencing phenotypic variation available for selection and the evolution of reaction norms (Badyaev & Uller, 2009; Donohue, 2014; Moczek, 2015; Sultan, 2015; Wolinsky & Libby, 2016; Hendry, 2017). Eco evo theory has,

however, largely ignored the fact that phenotypic variation is shaped by ecological conditions through development and that developmental outcomes can reciprocally influence ecological conditions (e.g. Gilbert, Bosch, & Ledon-Rettig, 2015; Sultan, 2015). Therefore, both evo devo and eco evo require an integrated understanding of the effect of ecological variation on development (and *vice versa*) and how this affects evolution (see Lundsgaard-Hansen *et al.*, 2013; Laland *et al.*, 2015).

We argue that to understand how phenotypic variation originates, evolves and feeds back on ecological processes, it is necessary to integrate the fields of evo devo and eco evo into a 'eco evo devo' framework where all disciplines are on an equal footing (Fig. 1). Previous discussions of the eco evo devo concept have most often considered this integration from the perspective of evo devo (see Section II). Here, we take a step forward to demonstrate how ecology (and its multitude of abiotic and biotic factors) affects organismal development, how developmental processes can in turn feed back on ecosystem-level effects, and that these interactions can themselves evolve as well as feedback to shape the speed and direction of phenotypic evolution (Fig. 1). Given that the integration of fields often results in synergies that can lead to novel hypotheses and implementation of new methodologies, we apply the proposed eco evo devo framework to an existing theory of adaptive divergence – the theory of resource polymorphism (Skúlason & Smith, 1995).

We begin by presenting a brief historical account of the use of the term eco evo devo better to understand the development of the ideas presented in our proposed conceptual framework. We then provide an overview of resource polymorphism theory and argue that freshwater fishes inhabiting recently de-glaciated systems (see reviews by Robinson & Wilson, 1994; Smith & Skúlason, 1996; Robinson & Schluter, 2000) are particularly well suited to the investigation of adaptive divergence using an integrated eco evo devo approach. Next, we review how studies of extrinsic factors (a focus on ecology) and intrinsic factors (a focus on development) have contributed to our understanding of the evolution of biological diversity and present specific examples from resource-polymorphic fishes. Finally, we will come full circle and use the eco evo devo approach to update resource polymorphism theory and highlight research foci that require additional attention. We will make two key arguments: first, that ecological effects on development (as a major progenitor of phenotypic variation) and, ultimately, evolution need to become a greater focus of research on adaptive divergence (e.g. Pfennig *et al.*, 2010) and, second, that adaptive divergence of populations can influence ecosystem processes not only through eco-evo feedbacks (e.g. Post & Palkovacs, 2009; Kahilainen *et al.*, 2011) but also eco-devo feedbacks (Sultan, 2015; Matthews *et al.*, 2016). Finally, we will emphasize the need to pay increased attention to how the environment can impact adaptive divergence through non-genetic modes of inheritance (Danchin & Wagner, 2010; Danchin *et al.*, 2011).

Table 1. Glossary

Ecological inheritance	The legacies of change, in both biotic and abiotic environments, caused by niche-constructing organisms to subsequent populations, which modify selection pressures on descendant organisms.
Evo devo	An integrative discipline dedicated to understanding how evolution and development reciprocally shape each other. The focus of the field is broad and encompasses various time scales. On a generation time scale, a key focus is how phenotypic variation arises from a developmental process as well as explaining its mechanistic basis.
Eco devo	The study of how ecological and developmental processes reciprocally shape each other
Eco-evo dynamics	The study of how ecological factors interact with evolution. Research is broadly motivated but tends to focus on revealing what ecological factors determine the strength and direction of natural selection, and how evolution influences ecology.
Epigenetics	Broadly defined as the factors above the level of the genotype that contribute to developmental variation. More specifically, epigenetics focuses on the stable heritable phenotypes that result from structural changes in chromatin (e.g. DNA methylation or histone modification) without alterations in the DNA sequence itself. Such changes can be stable and cause long-term changes in gene transcription which ultimately affect the phenotype.
Morph	A phenotypic variant within a population. Morphs can be discrete and easily identifiable, but many examples exist where phenotypic variation is subtler, and specializations are part of a continuum.
Ontogenetic plasticity	The changes phenotypes undergo during ontogeny in response to environmental cues.
Niche construction	Organism-mediated environmental modifications that influence selection pressures on a recipient (populations of the focal species itself or other community members). A recipient can respond developmentally and evolutionarily to the environmental modification of the niche constructor. Developmental niche construction occurs when phenotypic transitions during ontogeny influence niche construction.
Phenotypic plasticity	The ability of an individual to produce different phenotypes under different environmental conditions. Often used synonymously with developmental plasticity.
Parental effects	The effect of a parent's phenotype or environment on offspring phenotype or performance. These can include paternal (e.g. *via* paternal care) and maternal effects (e.g. *via* egg size or oviposition site) and can be genetically determined and/or environmentally induced.
Resource polymorphism	The occurrence of discrete intraspecific morphs showing differential niche use, usually through discrete differences in feeding biology and habitat use.
Selection regime	The strength and type of natural selection faced by a population. Selection regimes may favour a single phenotype or divergent phenotypes and may also be considered strong while favouring different phenotypes across populations.
Transgenerational plasticity	A type of non-genetic inheritance whereby the environment experienced by parents influences offspring reaction norms (different phenotypes expressed by the same genotype in different environments) and is manifested as a parent environment × offspring environment interaction.

II. THE HISTORY AND USE OF THE TERM ECO EVO DEVO

The term 'eco evo devo' was first put forward as a recognition that a more complete understanding of the evolution of biodiversity (in this case the morphology and phylogeny of plants) requires the integration of more than two approaches (Givnish, 2003). Subsequent use of this term comes primarily from the field of evo devo, which emphasizes that the environment (eco) plays a central role in intra- and intergenerational processes of phenotypic and genetic change (e.g. Moczek, 2012; Abouheif *et al.*, 2014; Gilbert & Epel, 2015; Moczek, 2015). This focus on 'eco' has been motivated by studies of phenotypic plasticity (e.g. Gilbert *et al.*, 2015; Sultan, 2015) and by the appreciation that genetic accommodation and assimilation can play roles in evolutionary change (Waddington, 1957a; West-Eberhard, 2005). The current rise of ecological evolutionary developmental biology reflects the statement by Van Valen (1973, p. 488) that '*A plausible argument could be made that evolution is the control of development by ecolog*y'.

The notion that the field of eco evo devo provides a framework for novel integration and organization of concepts for evolutionary theory is promoted in recent publications (Ledon-Rettig & Pfennig, 2011; Bassaglia *et al.*, 2013; Benitez, Azpeitia, & Alvarez-Buylla, 2013; Abouheif *et al.*, 2014; Gilbert *et al.*, 2015; Santos *et al.*, 2015; Pfennig, 2016) and many suggest that such a framework should become more widely appreciated and applied (Ghalambor, Martin, & Woods, 2015; Svensson, 2018). Our proposed eco evo devo framework is an attempt to motivate such developments.

III. RESOURCE POLYMORPHISM IN THE CONTEXT OF ECO EVO DEVO

(1) Resource polymorphism

Resource polymorphism is defined by the occurrence of intraspecific morphs that show differential resource use, usually through differences in feeding biology and habitat use (Skúlason & Smith, 1995; Smith & Skúlason, 1996;
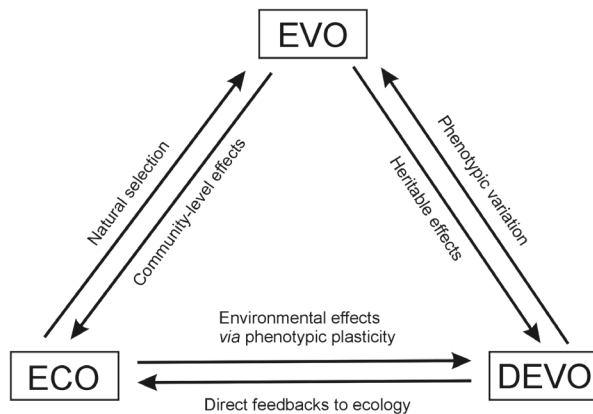
Fig. 1. A conceptual model exploring the interactions among ecological (ECO), evolutionary (EVO) and developmental (DEVO) processes. The key interactions and pathways within this ECO EVO DEVO model can be summarized as follows. In ECO EVO, the environment influences the evolution of populations through natural selection; in EVO ECO, evolutionary responses (i.e. phenotypic changes across generations) influence ecological processes in an ecosystem (often referred to as ECO–EVO feedbacks or niche construction); in ECO DEVO, the environment affects developmental processes of individual organisms (broadly encompassing any form of individual plasticity and parental effects); in DEVO ECO, within-generation developmental responses of individuals influence the response of populations and, subsequently, ecosystems to environmental change; in EVO DEVO, evolutionary processes across generations provide inherited signals (e.g. direct genetic and epigenetic variation) that influence phenotypic development; and in DEVO EVO, selection acts on phenotypic variation from development. In nature, ECO EVO DEVO processes interact and are likely to act dynamically, that is *via* reciprocal feedback responses.

Pfennig & Pfennig, 2012). While ecologically mediated adaptive divergence is a central topic in evolutionary biology (Endler, 1986; Schluter, 2000; Nosil, 2012), emphasis on the role of developmental processes in generating phenotypic variation differs. For example, the predominant 'ecological speciation' view focuses on the evolution of reproductive isolation associated with adaptive ecological divergence (Schluter, 2000; Nosil, 2012), a narrative that often sidesteps the importance of variation generated by developmental processes. By contrast, resource polymorphism theory posits that developmentally mediated phenotypic changes can underlie adaptive change, which ultimately can facilitate reproductive isolation (Smith & Skúlason, 1996; Nonaka *et al.*, 2015).

The evolution of resource polymorphism has been presented in the form of a conceptual model where divergence, and potentially speciation, can take place in the following temporal sequence (Smith & Skúlason, 1996; Skúlason, Snorrason, & Jónsson, 1999): (*i*) exploitation by a monomorphic population of a new or unexploited environment – often with high levels of intraspecific competition; (*ii*) rapid phenotypic shifts, especially in behaviour, morphology and life history, primarily mediated

through phenotypic plasticity; (*iii*) divergent selection and the evolution of specialized and more distinct morphological groups, accompanied by reduced phenotypic plasticity and, finally; (*iv*) reduced gene flow and the evolution of prezygotic and potentially postzygotic reproductive isolation (Smith & Skúlason, 1996). Given that the model hypothesizes that adaptive divergence is initiated by phenotypic plasticity (a developmental phenomenon) in response to ecological variation, and that resource polymorphism has ecosystem consequences (Lundsgaard-Hansen, Matthews, & Seehausen, 2014; Thomas *et al.*, 2017), integration with the evo devo and eco evo fields, through eco evo devo is timely.

(2) Postglacial freshwater fishes as model systems

Resource polymorphism has been identified in a number of animal species (Smith & Skúlason, 1996) and has featured prominently in studies of northern freshwater fishes inhabiting recently de-glaciated systems, including charrs (genus: *Salvelinus*), whitefish (genera: *Coregonus* and *Prosopium*), three-spined stickleback (*Gasterosteus aculeatus*) and Eurasian perch (*Perca fluviatilis*) (Fig. 2; and see reviews in Smith & Skúlason, 1996; Skúlason *et al.*, 1999; Robinson & Schluter, 2000; Snorrason & Skúlason, 2004; Hendry, 2009; Hendry *et al.*, 2009). These fishes typically play a key role in their ecosystems and are particularly well-suited model organisms for the investigation of adaptive divergence using an integrated eco evo devo approach. Their ecological, genetic and developmental tractability (*sensu* Pfennig, 2016) allows rigorous testing of key hypotheses to help establish generality in nature.

The magnitude of phenotypic divergence in postglacial freshwater fishes is associated with variation in ecological conditions (e.g. Hendry, Taylor, & McPhail, 2002; Kaeuffer *et al.*, 2012), genetic connectivity (Gíslason *et al.*, 1999; Lu & Bernatchez, 1999; Hendry *et al.*, 2009) and phenotypic plasticity (Wimberger, 1994; Parsons *et al.*, 2011). These taxa are of diverse phylogenetic origin (see Supporting information, Table S1) and have re-colonized postglacial environments across a broad geographic area in the northern hemisphere within the last 10000–15000 years (Bernatchez & Wilson, 1998; Robinson & Schluter, 2000). Subsequently, many species have undergone rapid adaptive diversification, often within lakes where resource-based morphs can be found at different stages of divergence and, in some cases, have evolved to form new species (Smith & Skúlason, 1996; Robinson & Schluter, 2000); Fig. 2; Appendix S1 and Table S1).

The occurrence of freshwater fishes in species-poor systems with a well-known history (geological, hydrological and potential anthropogenic impacts) makes them ecologically tractable. Their recent evolutionary divergence, and associated incomplete reproductive isolation (i.e. ongoing gene flow), opens a window to evolution where processes facilitating or impeding divergence can be studied along a so-called 'speciation continuum' (e.g. Loh *et al.*, 2008; Via, 2009). Finally, many of these species are highly amenable to both field and laboratory experimentation and now have
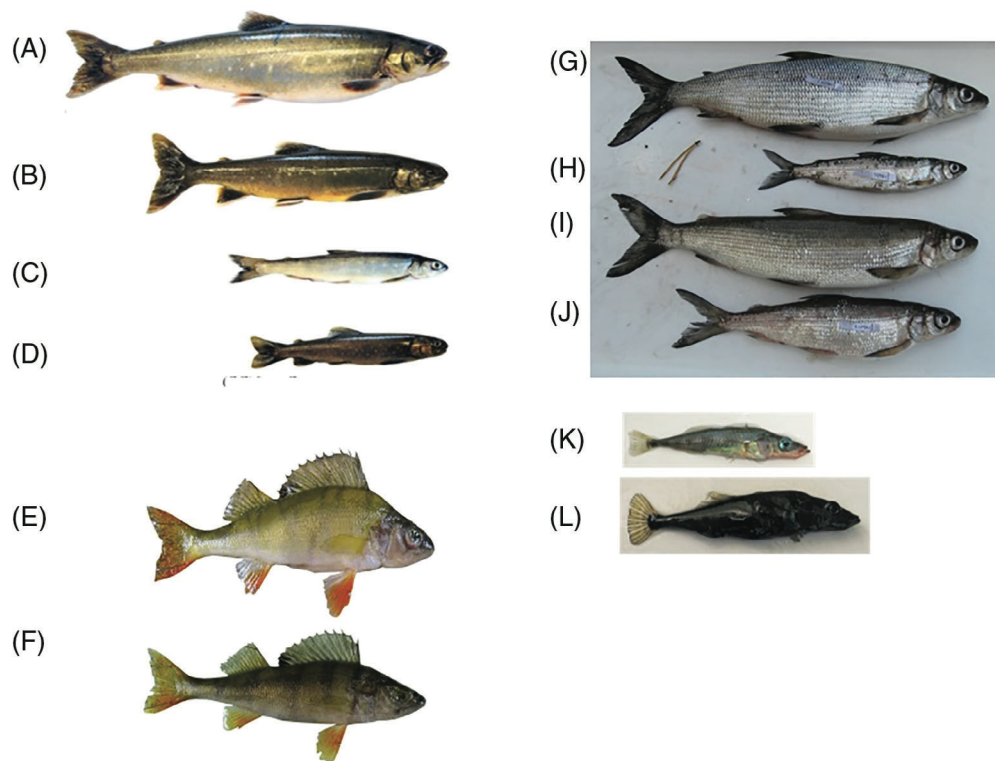
Fig. 2. Examples of sympatric polymorphic fishes in postglacial northern lakes. (A−D) Four Arctic charr (Salmoniformes) morphs (image from Johnston *et al.*, 2004), (E, F) two morphs of perch (Perciformes) (photograph: Phillip Hirsch), (G−J) four whitefish morphs (Salmoniformes) (photograph: Kimmo Kahilainen), (K, L) three-spined stickleback (Gasterosteiformes) morph pair (photograph: Janette Boughman). See Appendix S1 and Table S1 for additional examples.

extensive genomic resources including sequenced genomes (e.g. Christensen *et al.*, 2018), thereby allowing integrated investigation of development- (Robinson & Parsons, 2002), evolution- and ecosystem-level consequences of phenotypic variation.

The presence of substantial phenotypic differences in polymorphic fishes has often led to arguments around the genetic *versus* environmental basis of phenotypes (e.g. Nordeng, 1983). It eventually became recognized that a single species could express regional phenotypic variation, and that such variation could represent local adaptation (Schluter, 2000). Furthermore, in some populations of resource-polymorphic fishes, plasticity-induced phenotypic changes can parallel those typically observed in natural environments (Robinson & Parsons, 2002). For example, laboratory experiments that mimic benthic *versus* pelagic habitats in lakes commonly induce deeper *versus* shallower bodies in offspring (e.g. for Eurasian perch (Svanbäck & Eklöv, 2006). Studies have also shown how different developmental trajectories of these fishes can be shaped by interactions with the environment and internal signalling pathways (Wainwright, Osenberg, & Mittelbach, 1991; Eiríksson, Skúlason, & Snorrason, 1999; Parsons, Skúlason, & Ferguson, 2010; Leblanc *et al.*, 2011; Macqueen *et al.*, 2011; Parsons *et al.*, 2011; Wund *et al.*, 2012; Ahi *et al.*, 2014; Ahi, 2016; Currey *et al.*, 2017). Taken together, this

combination of characteristics offers exciting opportunities to study interacting evolutionary processes in multiple highly tractable systems.

IV. FROM THE OUTSIDE LOOKING IN: EXTRINSIC FACTORS AND THE EMERGENCE OF ECO EVO

Modern evolutionary ecology arguably arose from the need to address the problem of 'adaptive storytelling' (Gould & Lewontin, 1979) and, as a result, has given primacy to demonstrating natural selection as a driving force in evolution (e.g. Endler, 1986). For studies of postglacial fishes, this framework has been especially beneficial as these systems were once mostly relegated to taxonomic arguments that provided little insight into the processes that could explain patterns of inter- and intraspecific variation in phenotypes (Robinson & Parsons, 2002). Over the past two decades, these systems have become paradigmatic examples of adaptive phenotypic divergence and ecological speciation, largely facilitated through the evolution of resource polymorphism (Skúlason *et al.*, 1999; Robinson & Schluter, 2000; Schluter, 2000; Snorrason & Skúlason, 2004) (Fig. 2; see Appendix S1 and Table S1).

Empirical evidence for the role of natural selection in diversification of polymorphic fishes has come from a combination of approaches in the field and laboratory that focus on demonstrating an association among phenotype, fitness and environment (Schluter, 2000; Kingsolver *et al.*, 2001; Bolnick & Lau, 2008; Svanbäck & Persson, 2009). While these approaches do not typically identify the agents of selection (e.g. specific ecological factors) that structure local selection regimes (e.g. MacColl, 2011), they show that a range of biotic and abiotic agents of selection (and their interactions) are associated with phenotypic divergence (Robinson & Wilson, 1994; Smith & Skúlason, 1996; Robinson & Schluter, 2000; Knudsen, Amundsen, & Klemetsen, 2003; Siwertsson *et al.*, 2010; Bartels *et al.*, 2012; Keller & Seehausen, 2012; Woods *et al.*, 2012*a*; Franklin *et al.*, 2018). Biotic factors include low levels of interspecific but high levels of intraspecific competition, as well as interactions with prey, predators and parasites. Abiotic factors include habitat-specific differences in water chemistry, water flow, temperature, light penetration, photoperiod, bedrock composition, and overall habitat availability through variation in lake size and lake depth.

The evolution of resource polymorphism is closely aligned with heterogeneity in the environment. As shown in three-spined stickleback and Eurasian perch, intraspecific competition can cause polymorphism through disruptive selection (Bolnick & Lau, 2008; Svanbäck & Persson, 2009). In this scenario, disruptive selection is frequency dependent, whereby competition is more intense among ecologically similar individuals within a population, while rare types have an advantage due to reduced intraspecific competition with the most common phenotype (Bolnick, 2004; Svanbäck & Persson, 2009). Polymorphism has also arisen as the result of predation avoidance that involves trade-offs that are habitat specific. For example, deeper bodied bluegill sunfish (*Lepomis machrochirus*) and Eurasian perch show greater survival in vegetated littoral habitats, whereas streamlined individuals survive better in open water when exposed to predation (Chipps, Dunbar, & Wahl, 2004; Svanbäck & Eklöv, 2011). Divergence of morphs is also influenced by immunological adaptations to habitat-specific parasites (Knudsen *et al.*, 2003; Eizaguirre *et al.*, 2012; Karvonen *et al.*, 2013) and water clarity that affects visual competence (e.g. in Eurasian perch: Bartels *et al.*, 2012; Bartels *et al.*, 2016). Such interactions draw attention to the dynamic relationship between eco and evo (Fig. 1).

(1) Eco-evo dynamics and niche construction

The development of the field of eco-evo dynamics has been motivated by the recognition that ecological and evolutionary processes can occur at similar time scales, and by our limited understanding of what defines a selection regime (Hairston *et al.*, 2005; Post & Palkovacs, 2009). Eco-evo dynamics strive to explain both how environmental variables influence phenotypic evolution and how evolution itself acts as an agent of ecological change by creating reciprocal feedbacks between ecological and evolutionary processes (Fig. 1). These

feedbacks may be strong in community-level interactions where, for example, the evolution of predators can influence the evolution of prey (e.g. Walsh *et al.*, 2012; Weis & Post, 2013). The ecological effects of intra- or interspecific interactions often extend beyond the focal species directly affected by those interactions, whereby evolutionary changes of a focal species may alter the environment experienced by the wider community in a given ecosystem. For example, the number of species and their traits are key predictors of many ecosystem-level processes, such as rates of productivity, biomass sequestration and decomposition (Loreau *et al.*, 2001; Schmitz, 2006). Therefore, eco-evo feedbacks and niche construction can, in turn, influence natural selection through 'indirect' ecological interactions (Matthews *et al.*, 2011; Schoener, 2011; Odling-Smee *et al.*, 2013; Matthews *et al.*, 2014). These types of effects can be extrapolated to any number of community members and can involve dynamics that change with population demography and abiotic factors (e.g. temperature, precipitation and nutrients). The sum of these interactions can make up a selection regime, where feedbacks can change or reinforce the present conditions (e.g. *via* niche construction, see Section I).

Importantly, but frequently overlooked, the constructive contribution of species, populations or morphs to the environment can vary during ontogeny (i.e. through a devo to eco process, Fig. 1; Moczek, 2012; Donohue, 2014; Saltz & Nuzhdin, 2014; DiRienzo & Montiglio, 2016). Therefore, in addition to altering selection regimes (Best *et al.*, 2017), niche construction could also change the developmental environment (Ledon-Rettig & Pfennig, 2011; Moczek, 2015). Consequently, the environmental factors that cue development through plastic responses can also be 'constructed' by the ecological feedback of plastic reactions in preceding cohorts (Lundsgaard-Hansen *et al.*, 2014). Such dynamic developmental responses could alter the phenotypic variation available for natural selection and thus influence local adaptation and adaptive divergence (Pfennig *et al.*, 2010; Nonaka *et al.*, 2015).

In postglacial fishes, resource polymorphism can influence eco-evo feedbacks and niche construction. For example, the presence of benthic *versus* limnetic stickleback can strongly affect prey community structure, with cascading effects on total primary production and the nature of dissolved organic matter (DOM) (Harmon *et al.*, 2009). This is important because resource-driven divergence can depend on prey community structure (Hirsch, Eklöv, & Svanbäck, 2013*b*), primary production (Siwertsson *et al.*, 2010; Woods *et al.*, 2012*b*) and the visual environment (Bartels *et al.*, 2012; Hirsch *et al.*, 2013*b*). Spectral properties of light transmission can further influence sexual selection and affect the extent of divergence by altering gene flow (e.g. Boughman, 2001; Candolin, Salesto, & Evers, 2007). The construction of niches by a diverging population may then eventually feed back on its selective landscape. Although understudied, such feedback loops have been observed between zooplankton and planktivorous alewife (*Alosa pseudoharengus*) and whitefish (*Coregonus lavaretus*) (Palkovacs & Post, 2009; Kahilainen *et al.*,

2011). In these systems, selective feeding on different species and sizes of zooplankton induces disruptive selection on gill raker number in the fish. This in turn can affect average size and species composition of zooplankton – and thereby the selective environment for the zooplankton as well as the fish. Furthermore, phenotypic divergence of the focal fish can have a bottom-up effect on the morphology (e.g. chain pickerel, *Esox niger*; Brodersen, Howeth, & Post, 2015) or trophic position (e.g. brown trout, *Salmo trutta*; Thomas *et al.*, 2017) of their predators – which again can feed back as altered predation pressure.

Modifications of the environment by a parental generation can affect the developmental and selective environment of the offspring generation (Matthews *et al.*, 2016). These 'constructed' conditions could prove especially relevant to evolution if they remain across generations, providing a form of ecological inheritance (Danchin, 2013; Odling-Smee *et al.*, 2013). Mesocosm experiments with polymorphic whitefish and three-spined stickleback have shown that intra-generation plastic phenotypic changes affect the environment (Lundsgaard-Hansen *et al.*, 2014; Matthews *et al.*, 2016), influencing the selective and developmental conditions of the offspring (Sultan, 2015; see Section VI). Similarly, phenotypically plastic morphs of Eurasian perch or pumpkinseed sunfish (*Lepomis gibbosus*) (Wainwright *et al.*, 1991; Parsons & Robinson, 2006; Svanbäck & Eklöv, 2006) may have environmental effects that could influence, and even reinforce, selective and developmental processes that maintain and potentially promote the evolution of further divergence (e.g. Matthews *et al.*, 2016).

(2) Resource polymorphism and ecosystem stability

Many natural populations show substantial fluctuations in density over time (Grant, 1986; Grant & Grant, 1992; Mittelbach *et al.*, 1995; Smith *et al.*, 1999; Klemola *et al.*, 2002; Persson *et al.*, 2003) that may be related to environmental factors (e.g. Grant & Grant, 1992) or consumer resource interactions (e.g. Persson *et al.*, 2003). For example, summer temperature determines the growth and strength of a given year-class in many fish species, leading to major impacts on population dynamics. Likewise, predatory or competitive interactions can drive density fluctuations over time (Townsend, Sutherland, & Perrow, 1990; Sanderson *et al.*, 1999; Persson *et al.*, 2003). This can lead to fluctuations in the fitness landscape (Siepielski, DiBattista, & Carlson, 2009; Svanbäck & Persson, 2009; Saether & Engen, 2015) and has the potential to play an important role in the divergence process. The effect of intraspecific heterogeneity, such as seen in polymorphic fish, on population dynamics has been little studied however (Vindenes & Langangen, 2015). In fact, population size for polymorphic fish are known from only a few lakes (Snorrason *et al.*, 1992; Malinen *et al.*, 2014).

Ecosystem stability or predictability will influence phenotypic trait evolution (e.g. Sultan & Spencer, 2002; Tufto, 2015) and *vice versa* (Kinnison *et al.*, 2015), but

also facilitates population divergence and speciation (Snorrason & Skúlason, 2004). For example, sympatric divergence of Arctic charr (*Salvelinus alpinus*) morphs in the sub-Arctic Norwegian lake Fjellfrosvatn was characterized by temporally stable resource use, most likely reflecting predictable ecological conditions (Knudsen *et al.*, 2010, 2011). Furthermore, resource-polymorphic fish are often cannibalistic (Andersson *et al.*, 2007), which may promote divergent resource specialization by stabilizing resource levels (Claessen, de Roos, & Persson, 2000). Ecosystem predictability could be enhanced during the process of diversification *via* stabilized food-web dynamics and niche construction (Rooney & McCann, 2012; Danchin, 2013; Odling-Smee *et al.*, 2013). However, the process of divergence can itself be highly dynamic – at least until reproductive isolation between emerging species is well established. For example, introduction of zebra mussels (*Dreissena polymorpha*) to lakes has led to alterations in the visual conditions and changes in the resource base and, subsequently, to increased phenotypic divergence between littoral and pelagic Eurasian perch (Hirsch *et al.*, 2013b). By contrast, eutrophication has led to breakdown of divergence in whitefish in several European lakes (Vonlanthen *et al.*, 2012; Hirsch *et al.*, 2013a) and in three-spined stickleback in North America (Taylor *et al.*, 2006). Once environmental conditions have returned to broadly pre-perturbation status (e.g. before eutrophication) then divergence may re-commence rapidly and follow similar eco-evolutionary trajectories as before perturbation, as indicated in Lake Constance whitefish following re-oligotrophication (Hirsch *et al.*, 2013a). Such dynamism of divergence may represent what has been identified as Sysiphean evolution, where a species cycles between stages of differentiation without attaining complete reproductive isolation (McKay & Zink, 2015).

The stability or predictability of the environment is likely to interact with the underlying determinants of phenotypic variation. Theoretically, stable ecological environments should favour genetically determined, canalized phenotypes over plastic phenotypes (Hori, 1993; Scheiner, 1993; Smith, 1993), while high levels of phenotypic plasticity should be favoured in temporally unstable or spatially heterogeneous environments (Sultan & Spencer, 2002). Importantly, population density fluctuations (see above) (Svanbäck, Pineda-Krch, & Doebeli, 2009) or other components of ecosystem stability could influence the evolution of plasticity – and plastic as well as genetically derived phenotypic change may influence population and ecosystem stability. Hence, we argue that the relationship between ecosystem stability (and instability) and the evolution of resource polymorphism needs to be examined using an eco evo devo approach, particularly in keystone species of food webs. We will return to this in Section VII when we present an extended theory of resource polymorphism.

V. FROM THE INSIDE LOOKING OUT: INTRINSIC FACTORS AND LEVERAGING EVO DEVO FOR POSTGLACIAL FISHES

While the ecological drivers of resource polymorphism in postglacial fishes have been extensively studied, investigations of the intrinsic factors underlying phenotypic divergence, including the genetic, developmental and physiological underpinnings, have received less attention. Yet, understanding such intrinsic factors, how they interact and are affected by the environment, is key as this will reveal if and how they are 'seen' by selection through their influence on phenotypic development (Houle, Govindaraju, & Omholt, 2010). This is likely to be a complex and cumulative impact stemming from both genetic variation and non-genetic effects (e.g. epigenetic and parental effects) on development across generations (Figs 1 and 3). Apart from affecting responses to natural selection through their interaction with the environment such intrinsic factors can also influence the adaptive landscape through their feedbacks with ecological factors (Saltz & Nuzhdin, 2014). Therefore, we will next focus on research that demonstrates how developmental processes could be influenced by such dynamics and facilitate resource polymorphism in postglacial fishes.

(1) Phenotypic variation results from complex genetic and environmental interactions

The developmental variation underlying phenotypes can differ markedly among populations, species and environments. For example, phenotypic plasticity has long been studied in postglacial fishes and is thought to play a significant role in their ecological divergence, especially during its early stages (e.g. Skúlason, Noakes & Snorrason, 1989; Robinson & Wilson, 1996; Svanbäck & Eklöv, 2006; Parsons et al., 2010, 2011; Kristjánsson et al., 2018). Variation in the magnitude of plasticity varies among populations (e.g. Svanbäck & Schluter, 2012; Oke et al., 2016) and even among morphs within a lake (Parsons et al., 2011). Patterns observed in morphs of Arctic charr, for instance, support the prediction of resource polymorphism theory that plasticity can be reduced in systems that are at an advanced stage of diversification (Parsons et al., 2011). Together, such studies of plasticity have provided some of the best evidence that phenotypic variation originates from complex interactions between the genotype and environment (Houle et al., 2010). Further, knowledge that plasticity is mediated through the sensitivity of developmental systems to environmental variation led to the realization that environmental sensitivity itself can evolve. This in turn has led to insights on the role of plasticity in adaptive divergence from a more mechanistic perspective (e.g. Parsons et al., 2016). For example, plasticity in the expression of genes implicated in the adaptive evolution of three-spined stickleback (e.g. *PPARAa* gene involved in mitochondrial regulation) appears to facilitate colonization of freshwater environments by marine fish (Morris et al., 2014).

(2) Genetic approaches towards a mechanistic understanding of adaptive phenotypes

Understanding the molecular genetic basis of phenotypic change has long been a prevalent theme in research on polymorphic postglacial fishes. Recently, molecular genetic technologies have started to provide more direct insight into the genetic mechanisms underlying resource polymorphism in postglacial fishes than was possible with quantitative genetic approaches alone. For example, quantitative trait locus (QTL) mapping continues to yield valuable information on the genomic architecture (location, number and effect size of loci) of traits involved in phenotypic divergence [e.g. Arctic charr (Küttner et al., 2013), three-spined stickleback (Conte et al., 2015; Glazer et al., 2015), lake whitefish (Laporte et al., 2015)]. In addition, the localization of QTLs (Shapiro et al., 2004; Peichel, 2005) to genomic regions that have undergone divergence in natural populations has partially informed us of the genetic architecture of key traits underlying adaptive diversification (Hohenlohe et al., 2010; Arnegard et al., 2014). However, the dependency of genetic architecture on the environment and the developmental stage at which it is measured is underappreciated. This is key given that different morphs of postglacial fishes frequently develop under different environmental conditions (e.g. benthic/limnetic habitats). In Arctic charr this has resulted in substantial differences in the genetic basis of adaptive phenotypes, with the number and location of QTLs differing between fish reared in benthic or limnetic conditions (Küttner et al., 2014). This suggests that cryptic genetic variation is likely pervasive in postglacial fishes, with genes being 'followers' in evolution through their reliance on environmental conditions for their expression (Gilbert, 2001; Gilbert & Epel, 2009; Gilbert et al., 2015; Sultan, 2015).

While QTL studies have brought us closer to an understanding of the genetic architecture of traits, they are rarely able to pinpoint the exact nucleotide changes that take place during adaptive divergence (e.g. the predominance of gene regulatory changes in the freshwater evolution of stickleback: Jones et al., 2012) nor are they usually combined with functional experiments that would allow us to understand the role of specific loci in phenotypic development. Fortunately, functional genetic studies are now within reach for many postglacial fish species thanks to emerging genomic resources, including fully sequenced genomes (Berthelot et al., 2014; Lien et al., 2016; Peichel et al., 2017; Christensen et al., 2018), and the increasing ease by which genomes can be manipulated [e.g. clusters of regularly interspaced short palindromic repeats (CRISP-R); Ran et al., 2013].

Transcriptomic studies have been particularly helpful in understanding processes involved in adaptive phenotypic divergence of postglacial fishes (Kitano et al., 2011; Hanson et al., 2017) where, for example, genes in bone morphogenetic protein and calcium signalling pathways are involved in the coordinated evolution of traits involved in the divergence of lake whitefish morphs (Filteau et al., 2013). Such functional approaches are used far less in the context of understanding
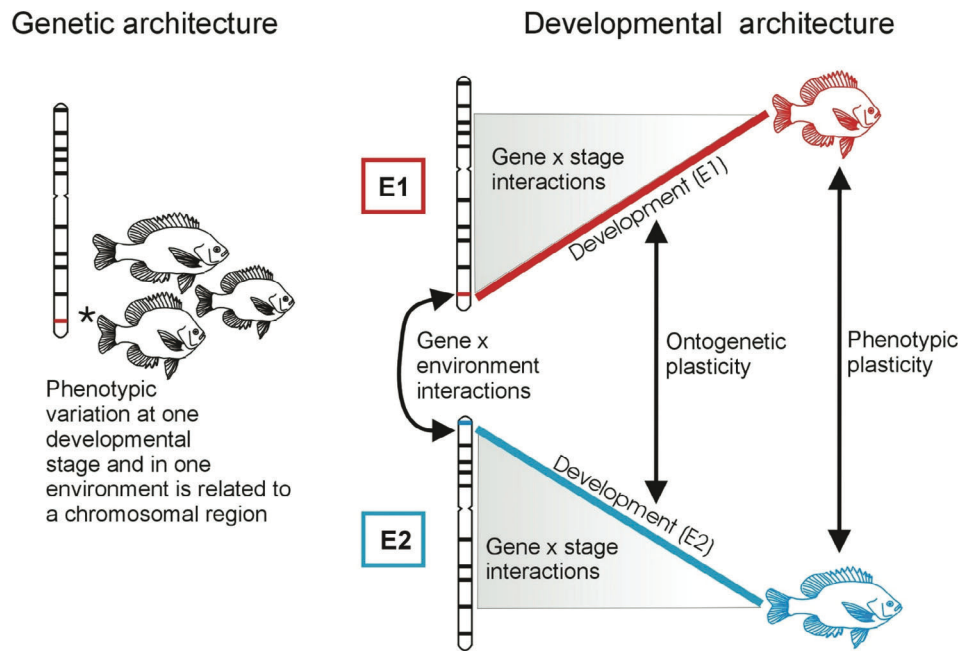
Fig. 3. A visualization of genetic and developmental architecture. Studies on genetic architecture normally only consider relationships between genotypic variation and the phenotype at a single stage of development, and under a single set of environmental conditions. Studies on developmental architecture consider genotype/phenotype relationships that can occur across a range of environments (E1 in red and E2 in blue) and at various stages of ontogeny. Grey shaded areas represent changes in genotype/phenotype relationships that can occur over ontogenetic stages. Empirical measures of ontogenetic plasticity take into account the dynamic nature of genetic and environmental influences over developmental time (occurring from embryonic to adult stages from grey to white shaded area, respectively), which ultimately provides variation for selection at any stage. Ontogenetic plasticity accumulates to be empirically measured as phenotypic plasticity in most studies, but methodological approaches are now emerging that can account statistically for such dynamics. Environmental effects can include external ecological conditions as well as parental effects. Dynamics over ontogeny may further be influenced by epigenetic changes, which may also alter genotype/phenotype relationships and be environmentally induced.

developmental variation (but see Ahi *et al.*, 2014, 2015) even though they could provide a direct link between environmental cues and the developmental response, as well as inform us on eco-evolutionary feedback loops (Becks *et al.*, 2012). For example, in Arctic charr differential expression of genes in the aryl hydrocarbon receptor pathway is associated with developmental variation in craniofacial traits (Ahi *et al.*, 2015).

Ironically, as we learn more about the mechanistic basis of complex phenotypes and their evolution through genomic approaches, we are realizing the limitations of this strategy (Houle *et al.*, 2010). The expectation that the independent evolution of similar phenotypes in similar environments corresponds to the response of similar genomic regions (Gagnaire *et al.*, 2013; Perrier *et al.*, 2013) and the expression of the same genes (Hanson *et al.*, 2017) within them is not always upheld. For instance, in some cases the same signalling pathway, rather than the same loci, may be involved in parallel evolution as observed in the adaptation of poeciliid fishes to hydrogen sulphide springs (Tobler *et al.*, 2018). In addition, most genomic studies have only been able to explain a small proportion of phenotypic variance. The limitations of genomics are made even more poignant by the observation that environmental induction during development can explain similar amounts of phenotypic variation as

do genomic approaches (Hu & Albertson, 2014). Quantitative genetic studies are particularly informative in estimating the relative contribution of different sources of phenotypic variation (e.g. additive genetic, maternal and environmental effects) that is available to selection in quantitative traits (Charmantier, Garant, & Kruuk, 2014). This suggests that the integration of quantitative genetic methodologies with genomic approaches can increase our ability to reveal the relative roles of developmental effects and direct genetic effects on the phenotype (Gienapp *et al.*, 2017). A more systems and developmentally oriented approach that takes into account that genomic structure could impose developmental biases by limiting responses to selection (Uller *et al.*, 2018) might be more fruitful for explaining the origin of diversity.

In polymorphic fishes, we are only just starting to understand the mechanistic basis of traits and how selection acts upon them within a given ecological context. Probably the best understood trait (from a mechanistic perspective) is variation in number of lateral armour plates in three-spined stickleback. The ancestral marine type has bony armour plates along its body, while the derived freshwater types have variably reduced plate numbers (Bell & Foster, 1994; Kristjánsson, Skúlason, & Noakes, 2002*b*; Bell, Aguirre, & Buck, 2004). The alteration of lateral plate number by

manipulating thyroid hormone levels suggests that changes in the timing of developmental events plays a key role in the origin of phenotypes associated with freshwater adaptation (Bolotovskiy *et al.*, 2018). Rapid changes in the frequency and the fixation of a 'freshwater' allele at the ecodysplasin (EDA) locus coincide with the loss of lateral plates (Barrett, Rogers, & Schluter, 2008). The importance of this gene in freshwater adaptation is further supported by strong signatures of selection around the EDA locus in genomic comparisons of marine and freshwater fish (Roesti *et al.*, 2014). The ecological significance of this trait has been demonstrated through evidence for direct selection on lateral plates independent of selection on the EDA locus (Rennison *et al.*, 2015). The discrete nature of this relatively simple trait and its high tractability has enabled consummate studies on the mechanistic basis of natural phenotypic variation.

In reality, most phenotypic changes of polymorphic postglacial fishes, and adaptive radiations more generally, involve quantitative traits (e.g. body size and shape, gill raker length), which are likely to have a complex genetic basis with gene × environment interactions (Edwards, 2013; Parsons & Albertson, 2013). For example, over 130 QTLs for body shape have been detected in normal and dwarf lake whitefish (Laporte *et al.*, 2015), a trait that is also influenced by environmental conditions. For most traits where we have a good understanding of why they 'matter' for adaptation, we usually still have little understanding of their genetic basis and developmental variation. Using complementary molecular approaches such as QTL mapping, transcriptomics and population genomics (termed a selection-signature QTL approach, see Parsons & Albertson, 2013), combined with quantitative genetic analyses (Gienapp *et al.*, 2017; Rudman *et al.*, 2017), in a single study can aid in identifying genotype–phenotype–fitness relationships. However, understanding the relationship between genotype, environment and phenotype will only be achieved with better characterization of the phenotype (Houle *et al.*, 2010).

(3) Beyond genetics: phenotypic and developmental approaches to understanding adaptive variation through 'developmental architecture'

As we understand better the genetic basis of complex phenotypic variation, we will also need to broaden our thinking to include dynamic gene–environment interactions, such as phenotypic plasticity and transgenerational (e.g. maternal and epigenetic) effects. Cues from the offspring's own environment as well as the parental phenotype (an environmental effect for the offspring; Mousseau & Fox, 1998) have the potential to alter the structure and function of the genome and influence phenotypic variation (Danchin, 2013; Smith & Ritchie, 2013; Schlichting & Wund, 2014). Phenotypic plasticity and transgenerational effects, as well as the associated non-genetic mechanisms of inheritance (Bonduriansky & Day, 2018), are likely to be highly relevant to progressing our understanding under the eco evo devo framework (Bossdorf, Richards & Pigliucci, 2008) proposed here.

In polymorphic fish, studies on plasticity initially documented phenotypic responses to different environmental conditions (Robinson & Schluter, 2000) but became more refined by comparing the phenotypic responses of genotypes/species to environmental variation over ontogeny (e.g. Day, Pritchard, & Schluter, 1994; Parsons *et al.*, 2010, 2011). Particularly relevant in the context of resource polymorphism is that diet-induced changes in phenotype can impact foraging ability (Day *et al.*, 1994; Andersson, 2003; Parsons & Robinson, 2007; Lundsgaard-Hansen *et al.*, 2013), providing a link between ecology, development, and natural selection (Fig. 1). Further, plastic phenotypic responses to diet can mirror larger patterns of trait divergence supporting the idea that plasticity provides a 'flexible stem' upon which further evolution can occur (Gomez-Mestre & Buchholz, 2006; Wund *et al.*, 2008, 2012; Levis, Isdaner, & Pfennig, 2018). Pre-existing plasticity from ancestral populations can release novel phenotypic variation in response to environmental change or colonization of new habitats. According to the theory of phenotypic and genetic accommodation (West-Eberhard, 2003, 2005), natural selection can act on this novel phenotypic variation by either refining the evolution of plastic trait responses of the emerging morphs or by promoting their developmental canalization. In its strongest form, canalization would lead to significant loss of plasticity (i.e. genetic assimilation) in relatively stable environments (West-Eberhard, 2003, 2005; Parsons *et al.*, 2011; Svanbäck & Schluter, 2012; Schlichting & Wund, 2014; Schneider & Meyer, 2017).

The genetic and developmental basis of plasticity in postglacial fishes has been addressed through the study of genes and pathways that are both evolutionarily relevant and whose expression is sensitive to environmental conditions, such as salinity and diet (e.g. McCairns & Bernatchez, 2010; Macqueen *et al.*, 2011). For example, the evolution of small size of Arctic charr morphs in volcanic spring-water systems in Iceland relative to much larger ancestors (Kapralova *et al.*, 2011; Kristjánsson *et al.*, 2012) is associated with the differential expression of nutritionally sensitive genes in the rapamycin (mTOR-signalling) pathway. This altered expression leads to reduced muscle protein accretion even if the fish are reared under growth-favouring conditions (Macqueen *et al.*, 2011). Studies in other fishes have extended these ideas and provided evidence for the evolution of plasticity *via* genetic assimilation. In Malawi cichlids, the induction of benthic and limnetic (pelagic) jaw morphologies by benthic and limnetic food is associated with the effects of a regulatory locus, the patched 1 (*ptch1*) gene, which affects jaw structure through variable mediation of bone deposition around the cartilaginous precursor (Parsons *et al.*, 2016). Bone deposition is associated with variable jaw movements in embryos, which influence the developmental environment leading to changes in mechanical load and ossification (Hu & Albertson, 2017). The sensitivity of the *ptch1* gene to signals from the foraging environment could then lead to selection and a decrease in environmental sensitivity through genetic assimilation (Parsons *et al.*, 2016). Similarly, a study

of the evolution of eye loss in the cave fish (*Astynax mexicanus*) showed that variation in eye and orbit size in surface fish was plastically increased by exposure of embryos to the low water conductivity typical of cave environments (Rohner *et al.*, 2013). Increased plasticity appeared to arise from a failure of the chaperone molecule heat shock protein 90 (HSP90) to facilitate correct protein folding under stressful conditions. These findings suggest that successful colonization of caves by surface fish is facilitated by the release and subsequent selection on cryptic variation resulting in eye loss, i.e. genetic assimilation.

Transgenerational effects *via* maternal and epigenetic mechanisms can also influence diversification. Maternal effects are often prominent, and can influence the direction and speed of evolution at ecological time scales (Räsänen & Kruuk, 2007). In marine three-spined stickleback, maternal rearing temperature affected offspring body size, and this was mediated through mitochondrial respiratory activity and the differential expression of P450 genes (Shama *et al.*, 2014; Shama & Wegner, 2014). Likewise, maternal variation in egg size (correlated with yolk quantity) has large effects on progeny phenotype in salmonid fishes (e.g. Einum & Fleming, 1999; Giesing *et al.*, 2011). In Arctic charr, embryos originating from small eggs tend to allocate energy towards bone development rather than body growth (Eiríksson *et al.*, 1999) and are smaller and less mobile at first feeding than embryos from larger eggs (Benhaïm, Skúlason, & Hansen, 2003; Leblanc *et al.*, 2011). Siblings from large eggs can also survive better than siblings from small eggs (Einum & Fleming, 1999). Such maternally driven differences in developmental trajectories can promote different trophic morphologies in offspring and contribute to the evolution of resource polymorphism. In Arctic charr, there is some evidence for maternally mediated differential expression of genes related to craniofacial development (Ahi *et al.*, 2018; Beck *et al.*, 2019). In brook charr (*Salvelinus fontinalis*), exposure of larger embryos to stressful environments resulted in greater plasticity and a wider developmental trajectory than in smaller embryos (Penney, Beirão, & Purchase, 2018). Although the developmental mechanisms explaining this greater plasticity are unknown in brook charr, studies of mouth-brooding cichlids suggest that embryonic gene expression (in this case a growth hormone receptor gene *GHR*) can respond to signals effected by yolk quantity (Segers, Berishvili, & Taborsky, 2012). Such maternally driven alterations of development could lead to the persistence of maternal effects over generations if, for instance, small fish are competitively inferior and produce smaller eggs, which again leads to small size in the subsequent generation. Such egg-size-mediated size effects in turn should play an important role in determining what genetic variation is exposed to natural selection, and may even influence population dynamics (e.g. Beckerman *et al.*, 2006; Plaistow, Lapsley, & Benton, 2006).

Epigenetics, defined as factors above the level of the genotype that contribute to developmental variation (*sensu* Waddington, 1942, 1957*b*), provides another potential mechanism for transgenerational plasticity. Recent epigenetics studies have focused mostly on stable heritable phenotypes that result from structural changes in chromatin (e.g. DNA methylation or histone modification) without alternations in the DNA nucleotide sequence itself (Berger *et al.*, 2009; Best *et al.*, 2018). Although these changes can be self-perpetuated over generations by the phenotypic outcome of epigenetic responses (Flores, Wolschin, & Amdam, 2013), some environmentally induced epigenetic modifications are repeatable across similar environments (Le Luyer *et al.*, 2017) and stably inherited across generations (Danchin, 2013). Recent studies have identified differentially methylated regions associated with adaptive phenotypic variation in postglacial fishes (Best *et al.*, 2018), such as lateral plate morphs in three-spined stickleback (Smith *et al.*, 2015), migration phenotypes in rainbow trout (*Oncorhynchus mykiss*) (Baerwald *et al.*, 2016) and the degree of behavioural reproductive isolation in tessellated darters (*Etheostoma olmstedi*) (Smith *et al.*, 2016). However, the frequency with which environmentally induced epigenetic variation is inherited is currently unknown (Smith & Ritchie, 2013) and we need to understand how stable heritable phenotypes that result from structural changes in chromatin may feed back to, and influence, genetic variation, ecology, and evolution. As epigenetics involves an understanding of both the extrinsic and intrinsic factors that enable plastic responses, studies of polymorphic postglacial fishes under an eco evo devo framework (Fig. 1) could make a significant contribution to the field of epigenetics as a whole.

Given the above discussion, we advocate that to understand better how phenotypic variation arises and evolves it is necessary to take greater account of the diverse factors affecting development. We suggest that determining the salient 'developmental architecture' (rather than just the genetic architecture) under relevant ecological conditions provides an important empirical focus to help integrate eco evo devo (Fig. 3). Such studies should include the mechanistic basis of phenotypic development in nature, for instance: how molecular genetic variation interacts with internal and external environmental conditions experienced by the organism, how cells and tissues interact to achieve functional integration of the phenotype during development in a given environment (see Young & Badyaev, 2010), what the dynamics of genotype/phenotype/environment and fitness relationships are during ontogeny, and how non-genetic inheritance mechanisms influence the evolution of the phenotype.

VI. EMPIRICAL EXAMPLES OF RESOURCE POLYMORPHISM AND SPECIATION IN FRESHWATER FISH FROM AN ECO EVO DEVO PERSPECTIVE

In certain resource-polymorphic fishes, aspects of the eco evo devo framework have been examined, illustrating the strength of an integrated approach.

(1) Ecological changes facilitate phenotypic divergence: responses of perch to zebra mussel invasions

Littoral and pelagic individuals of Eurasian perch exhibit greater phenotypic divergence in lakes with invasive zebra mussels than in those without zebra mussels (Hirsch *et al.*, 2013*b*). The presence of zebra mussels results in larger zooplankton (Idrisi *et al.*, 2001; Hirsch *et al.*, 2013*b*), a higher density of large benthic invertebrates (Ward & Ricciardi, 2007; Hirsch *et al.*, 2013*b*) and clearer water (Higgins & Vander Zanden, 2010). Foraging on larger zooplankton leads to lower handling costs and higher energy gain for planktivorous perch (Persson, 1986) and zooplankton may also be more conspicuous to foraging fish because of increased water clarity (Ljunggren & Sandstrom, 2007). These factors favour rapid swimming in pelagic fish (Park, Lee, & Park, 2007) and, thus, a more streamlined body is advantageous (Svanbäck & Eklöv, 2003, 2004). Zebra mussels also create physical structure in the benthic habitat. This favours deep-bodied perch which are more efficient at exploiting resources in such environments (Svanbäck & Eklöv, 2003, 2004). Furthermore, the presence of zebra mussels leads to increased densities of larger prey in benthic and pelagic habitats, causing relatively high growth rates of perch (Hirsch *et al.*, 2013*b*). As plasticity is greater with higher growth rates, this facilitates phenotypic divergence (Olsson, Svanbäck, & Eklöv, 2006, 2007). Overall, the presence of zebra mussels changes the selective landscape through changes in resources and the visual environment (eco evo) as well as influencing the plastic response in perch through increased growth (eco devo) (Hirsch *et al.*, 2013*b*).

(2) Development and evolution of craniofacial diversity in charrs

Arctic charr provide a classic example of resource polymorphism with the occurrence of multiple morphs that differ in trophic morphology and size associated with resource use. Developmental studies show that differences in head and jaw shape among morphs emerge during embryonic development (Skúlason *et al.*, 1989*a*; Ahi *et al.*, 2015; Kapralova *et al.*, 2015; Guðbrandsson *et al.*, 2018), correlate with variable timing of bone ossification (Eiríksson *et al.*, 1999) and are effected by diet (Parsons *et al.*, 2011), i.e. evo devo and eco devo processes. In the closely related polymorphic Dolly Varden charr (*Salvelinus malma*), differences in adult morphology are related to variable embryonic skull ossification (Esin, Markevich, & Pichugin, 2018). In general, round head structure, blunt snout and short lower jaw – that often characterize adult benthic morphs of charr – indicate retention of embryonic morphological characters (i.e. paedomorphosis; Skúlason *et al.*, 1989*a*). Research on craniofacial transcriptional dynamics in the progeny of benthic and pelagic Arctic charr morphs has identified a gene network, related to glucocorticoid (GC) signalling, that influences bone development and is expressed at higher levels in the benthic than the pelagic progeny (Ahi

et al., 2014). GC signalling has been suggested to regulate Wingless/Integrated (Wnt) signalling, which is an important pathway controlling cranial bone formation (Brugmann *et al.*, 2010; Ahi, 2016). Importantly, in polymorphic Malawi cichlids high levels of Wnt signalling are related to the occurrence of a short lower jaw and blunt craniofacial profile (Parsons *et al.*, 2014). In cichlids, manipulation of Wnt signalling in early larvae showed that its elevation locked in the larval skull morphology resulting in an exaggerated paedomorphic benthic head shape in older progeny (Parsons *et al.*, 2014). Skull development can be sensitive to environmental signals. For example, different diet-related behaviours can mechanically influence the expression of plasticity in the relevant skeletal structures in polymorphic fish (Wainwright *et al.*, 1991; Wimberger, 1994). In Arctic charr, benthic and pelagic diets promoted the development of benthic- and pelagic-like head shapes in juveniles, respectively (Parsons *et al.*, 2010, 2011). Furthermore, when reared on novel prey types, progeny of the pelagic morph showed greater morphological variation during ontogeny than did the progeny of the benthic morph, suggesting that the paedomorphic benthic charr had experienced stronger selection and was relatively more genetically assimilated than the pelagic morph, which was less morphologically divergent from the presumed marine ancestor (West-Eberhard, 2003, 2005; Parsons *et al.*, 2011). Elevated gene-network activity related to skull ossification in progeny of the benthic morph could be related to such canalization (Ahi *et al.*, 2014).

(3) Evo-eco and devo-eco feedbacks in whitefish morphs: genetic divergence and phenotypic plasticity can affect ecosystems

Closely related but phenotypically divergent populations can have different effects on ecosystems (Harmon *et al.*, 2009; Palkovacs & Post, 2009; Bassar *et al.*, 2010). For example, a comparison of lakes with a single morph of European whitefish to lakes with several morphs indicates eco-evolutionary feedbacks between whitefish and zooplankton (Kahilainen *et al.*, 2011), similar to the alewife system in North America (Palkovacs & Post, 2009). Size-selective feeding of whitefish on zooplankton in polymorphic systems in Fennoscandian postglacial lakes reduced the body size and density of zooplankton, leading to disruptive selection on gill raker number of whitefish (Kahilainen *et al.*, 2011). In Lake Lucerne, Switzerland, sympatrically diverged whitefish (a benthic *Coregonus* sp. "Bodenbalchen" and a limnetic *C. zugensis*) species (Hudson, Vonlanthen, & Seehausen, 2011) are genetically differentiated in both feeding-related morphological and behavioural traits (Vonlanthen *et al.*, 2012; Lundsgaard-Hansen *et al.*, 2013) but also show notable phenotypic plasticity in foraging behaviour and efficiency (Lundsgaard-Hansen *et al.*, 2013). Direct tests of the relative contribution of genetic and plastic trait variation showed that ecosystem properties were changed through both processes (Lundsgaard-Hansen *et al.*, 2014). These studies illustrate how both evolution and ecology can

affect the phenotype (evo devo and eco devo, respectively) (Vonlanthen *et al.*, 2012; Lundsgaard-Hansen *et al.*, 2013) and, jointly feed back on ecosystem-level processes (evo eco and devo eco). Thus, polymorphic postglacial fishes may simultaneously construct both their selective and developmental environments, thereby influencing their own adaptive potential both through altered selection and the expression of the phenotypic variation available for natural selection.

VII. AN ECO EVO DEVO FRAMEWORK FOR RESOURCE POLYMORPHISM AND THE ORIGIN OF BIOLOGICAL DIVERSITY

We argue that using an integrative eco evo devo approach will lead to a better understanding of the emergence and role of biological diversity, and promote more focused and detailed hypotheses testing (see also Gilbert & Epel, 2015; Sultan, 2015). To illustrate the power of the eco evo devo framework, we present a conceptual model that expands the existing theory (see Section III) of resource polymorphism (Fig. 4). This model is based on a scenario where populations colonize novel and, in some cases, ecologically unstable habitats (e.g. fish invading freshwater systems emerging from the last glacial period), and undergo diversification into resource-based morphs, which potentially results in the evolution of reproductive isolation (i.e. ecological speciation; Nosil, 2012). The model could also apply to scenarios where organisms are exposed to environments that vary temporally and spatially across their range, such that populations in different locations (i.e. allopatry) encounter different environmental conditions. This then can facilitate the evolution of geographically isolated morphs (e.g. small benthic charr in Iceland: Kapralova *et al.*, 2011; Kristjánsson *et al.*, 2012), whereby plasticity can provide developmental flexibility, i.e. developmental degrees of freedom (Moczek *et al.*, 2011; Kristjánsson *et al.*, 2018), that enables and channels divergence between populations. If such geographically separated populations come into secondary contact, the same mechanisms as in the sympatric scenario could facilitate further evolution of reproductive isolation. The novelty of our extended model of resource polymorphism rests on demonstrating the central role of the eco evo devo processes in divergence, emphasizing the dynamic relationship between ecological and developmental processes.

This extended model highlights the significance of phenotypic plasticity (at an individual and/or transgenerational level) during early divergence in novel environments (see also Wund *et al.*, 2008; Schneider & Meyer, 2017; Matthews *et al.*, 2018; Schwab, Casasa, & Moczek, 2019), followed by potential phenotypic canalization when environments become more structured and stable. Importantly, the model proposes that the continuous interaction of ecological and developmental features, involving eco-evo feedbacks and niche construction,

shapes the environment during the diversification process and can potentially make ecological conditions more predictable. This process is accompanied by modifications of the developmental architecture (Fig. 3) that underlies variable adaptive phenotypes and can also promote reproductive isolation through the evolution of pre- and post-zygotic isolating mechanisms. Thus, the model allies with the theory of phenotypic and genetic accommodation and genetic assimilation (West-Eberhard, 2003, 2005), where plasticity either becomes more structured or is reduced during processes of divergence, but it also emphasizes that the evolutionary process of phenotypic and genetic divergence can be highly dynamic. Thus, if environments become relatively stable over time, as would be expected for northern postglacial fishes after re-colonization, genetic assimilation could emerge. But when ecological factors fluctuate significantly over time, typical of many environments, plastic responses may be favoured and influence performance at diverse points during ontogeny (e.g. Moczek *et al.*, 2011; Parsons *et al.*, 2010, Fig. 3). The responses to selection then depend on the environmental and genetic sensitivity of the underlying regulatory mechanisms (e.g. Parsons *et al.*, 2016; Schneider & Meyer, 2017).

The proposed process of divergence would furthermore be affected by eco-evo and eco-devo feedbacks during divergence (Matthews *et al.*, 2016, 2018), which could influence ecological conditions and thus selective and developmental responses (see earlier discussion and Section VI.3). The scenarios provided by this extended resource polymorphism model are supported by the observed nature and magnitude of phenotypic and genetic divergence seen in many species of postglacial fishes (see Fig. 2, Appendix S1 and Table S1), and not the least by their extensive diversity in spatial and temporal patterns of reproductive isolation, including secondary sexual contact of morphs. However, further research is needed to reveal, examine and test the diverse potential outcomes of the model.

In practical terms, rigorous tests of the different pathways of such an eco evo devo framework (Figs 1 and 4) are challenging. To facilitate such investigations, we identify some key research topics and hypotheses that are amenable to testing (Table 2). These relate to (*i*) the role of spatial and temporal variability and discreteness of resources; (*ii*) the significance of transgenerational effects; (*iii*) the role of eco-evo feedbacks across generations and eco-devo feedbacks during ontogeny; and (*iv*) structuring of ecosystems and developmental architecture. We strongly advocate that future research should consider explicitly the integration of these processes rather than focusing on the alternatives (such as genes *versus* environment). Thus, we need studies that explore how evolutionary and developmental processes feed back on ecosystems, both in controlled mesocosms and field experiments (e.g. Lundsgaard-Hansen *et al.*, 2014; Matthews *et al.*, 2016) as well as long-term studies in nature (Rudman *et al.*, 2017), and in what way these processes affect selection regimes and developmental environments (Sultan, 2015). In line with this, studies of genotype–phenotype relationships
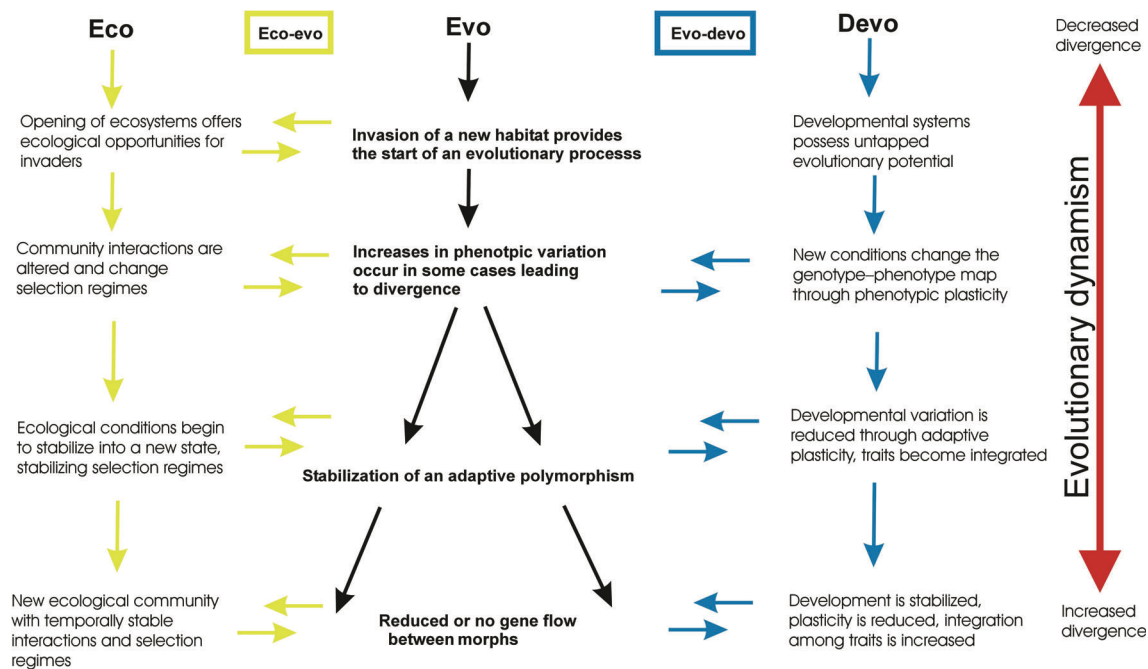
Fig. 4. A schematic illustration of the temporal sequences of interactions that take place during the evolution of resource polymorphism within an eco evo devo framework. In this scenario, we assume colonization of a new habitat and subsequent sympatric diversification. The framework can also be applied to the more common scenario in nature where environmental change (with or without invasion of a new habitat) leads to diversification in allopatry. The series of steps under each heading (Eco, Evo, Devo) are initiated by the immigration of an organism to a new habitat (e.g. immigration of fish into myriad freshwater systems that were formed in the wake of the last glacial epoch). The Eco column shows the initial state and successive predicted ecological changes that both dictate and are influenced by evolutionary processes. This series of steps and interactions can be classified as Eco-evo dynamics (green arrows). The Devo column shows the initial state and successive, predicted processes and changes in development that occur during adaptive divergence. These developmental processes dictate the variation that is made available for natural selection (Evo-devo, blue arrows), but are also influenced by environmental parameters (Eco-devo). As evolution progresses, ecological and, hence, developmental conditions are stabilized resulting in reduced phenotypic variation and more integrated phenotypes (e.g. more stable polymorphisms). Eventually ecological conditions can become stable and development canalized and traits more integrated. As a consequence of habitat matching and/or phenotype assortative mating, gene flow between morphs can be reduced or eliminated. Additionally, as indicated by the red arrow, systems are dynamic with regard to these steps. The patterns of divergence across systems can reflect any of these steps, depending on the nature of the respective processes that have shaped these patterns. Furthermore, due to environmental changes (e.g. in temperature, oxygen or light conditions, habitats, introduction of new species) plasticity can at any stage of divergence continue to provide novel phenotypic variation, such as through its diverse role over ontogeny, trait development, as well as physiological or behavioural alterations – facilitating adaptive responses of morphs. Thus, the process of divergence is dynamic and reversible, unless complete genomic isolation has evolved. The sequence of events and the processes involved with an allopatric scenario are similar to that of the sympatric scenario except that multiple morphs do not evolve as all organisms in a population are exposed to the same eco evo devo mechanisms in time and space.

need to be conducted more often in ecologically relevant settings, e.g. in the field or in mesocosms, rather than in standardized laboratory conditions (e.g. Küttner *et al.*, 2014; Sultan, 2015). Furthermore, developmental studies should examine how environmental conditions affect gene expression, behaviour of cells during development and epigenetic patterns (including their inheritance).

VIII. CONCLUSIONS

(1) We believe that the integration of multiple interacting processes into the eco evo devo framework proposed here (Fig. 1) will allow researchers to understand better how phenotypes arise and are shaped by development. Using empirical examples from polymorphic postglacial fishes we have illustrated how phenotypic change and community-level ecological interactions can be reciprocal (Miner *et al.*, 2005; Lundsgaard-Hansen *et al.*, 2014; Matthews *et al.*, 2014). We also emphasize that phenotypic differences among individuals within and among generations are not fully dictated by differences in the DNA sequence and that a broader understanding from the perspective of developmental architecture is needed (Fig. 3) (see Danchin, 2013; Smith & Ritchie, 2013). We advocate postglacial fishes as model taxa for addressing a wide range of questions within a dynamic eco evo devo framework.

Table 2. Key research questions on an eco evo devo framework of resource polymorphism. The following hypotheses and predictions are examples of research topics that could be examined through field and laboratory studies and experiments applying within- and among-species comparisons. These research topics are naturally connected in a variety of ways differing primarily in the 'starting point' of the respective arguments

Research question	Background	Hypothesis	Prediction
1. How do spatial and temporal variability and discreteness of resources interact in the generation of resource polymorphism?	Spatial and temporal variability and discreteness of niches arise from ecological and geographical features of the environments in which resource polymorphisms occur. The environments of diverging morphs can be subtly different but also highly distinct.	The degree of spatial and temporal resource separation impacts the nature and strength of natural selection and its interplay with phenotypic plasticity and gene flow.	Temporally unstable and unpredictable (often 'novel') ecological conditions favour phenotypic plasticity (especially in behaviour), while more stable and predictable environments promote phenotypically segregated and less-plastic morphs.
2. What are the roles of epigenetic and parental effects?	Non-genetic inheritance mechanisms (e.g. epigenetic effects on DNA methylation) and parental effects (such as mRNA, hormones and yolk in eggs) can strongly influence phenotypic variation, and often in a highly environment-dependent manner. Studies will need to take into account how different transgenerational effects and phenotypic plasticity, in general, operate and interact amongst themselves and with direct genetic mechanisms of inheritance.	Environmental stability influences the relative role of direct genetic and non-genetic inheritance in determining phenotypic variation. Adaptive transgenerational plasticity will be important when environments fluctuate predictably (e.g. because of seasonality and regular population fluctuations), whereas bet-hedging strategies will be favoured in unpredictable environments. Adaptive transgenerational plasticity allows the offspring phenotype to adaptively track favourable conditions (for example through methylation in the same genomic location), whereas bet-hedging strategies maximize the probability of at least some offspring surviving.	Non-genetic inheritance has significant effects during the early stages of adaptive divergence (i.e. when populations have recently invaded post-glacial lakes and rivers) and to reinforce divergence when populations are already segregated in more distinct habitats.
3. How do eco-evo feedbacks and niche construction interact with eco-devo feedbacks during ontogeny?	Eco-evo feedbacks and niche construction originate from phenotypic changes across generations, resulting in ecological responses that can affect both natural selection and plasticity in developmental architecture. Moreover, phenotypic changes during ontogeny can influence the within-generation environment, leading to developmental niche construction.	(1) Niche construction through eco-evo feedbacks of invading populations and, subsequently, diverging morphs will alter the selective environments (e.g. through predator–prey interactions and community and food-web structuring) of the focal species or other community members (2) Niche construction through eco-devo feedbacks, where phenotypes change due to individual or transgenerational plasticity, will influence environmental conditions.	(1) Predator–prey feedback loops, evaluated as reciprocal effects, reinforce phenotypic divergence, and community and food-web structuring (e.g. evaluated as numbers of morphs, species and links in food webs) of diverging morphs facilitates discreteness and temporal stability of ecosystem resources, thereby strengthening divergent selection and potential reproductive isolation of morphs. (2) Eco-devo feedbacks influence selection regimes and the nature of the environmental signalling that causes plastic responses, resulting in more structured or predictable interaction between the environment and the phenotype during ontogeny (ontogenetic niche construction)
4. How does the structuring of ecosystems and developmental architecture interact?	Developmental architecture (see Fig. 3) of diverging morphs and ecosystem characteristics interact at any given time. This interaction is expected to vary during divergence.	The developmental response depends on the spatial and temporal variability of ecosystems, which influences natural selection and the environmental–phenotypic interaction during development.	(1) When populations and morphs experience novel environments (e.g. following colonization), developmental systems are unstable and responsive, and (2) when environmental conditions become more predictable (e.g. when divergence of morphs is more established), developmental responses become more stable and integrated.

(2) We emphasize that an eco evo devo approach is a powerful conceptual framework for understanding the complex integrated processes that ultimately determine the patterns of biological diversity in nature. Thus, we have discussed how natural selection is not an autonomous process that is only driven by factors external to the respective organisms, but also by intrinsic factors whereby organisms can shape their own external environment. The external factors that determine selection can often be the same as those that influence individual development through phenotypic plasticity. Thus, the snapshot of phenotype–fitness relationships we often use to measure natural selection empirically may be a subset of much broader and highly dynamic eco evo devo processes. It follows that these relationships could be viewed as evidence for coordinated variation between dynamic intrinsic developmental factors, which affect the outward phenotype, and current ecological factors. We hope that future advances in evolutionary biology will accommodate more forcefully the role of development and apply a scientific thinking that fully integrates the sub-fields of eco, evo and devo.

IX. ACKNOWLEDGEMENTS

X. REFERENCES

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XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. Examples of empirical evidence for different patterns of resource polymorphism in postglacial freshwater fishes including phenotypic distribution, trait type, ecological axis of divergence, and evidence of reproductive isolation.
Appendix S1. Overview of resource polymorphism in fish in postglacial freshwater systems.