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Stickleback research: the now and the next

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ABSTRACT

Background: Stickleback fishes are an outstanding model for understanding evolution and ecology. Celebrating successes and identifying new questions, the Seventh International Conference on Stickleback Behaviour and Evolution was held 29 July to 3 August 2012 near Seattle, Washington, USA.

Questions: How has research on stickleback shaped our understanding of phenotypic variation, genomic variation, speciation, and eco-evolutionary dynamics? How is future research on stickleback likely to advance these topics?

Phenotypic variation: Stickleback show exceptional variation at a diversity of spatial scales, which has yielded insights not only into how natural selection shapes evolutionary diversification, but also how the influence of natural selection can be constrained. Future research would profit from examining temporal variation in selection and the multifarious nature of selection.

Genomic variation: Stickleback adapted to different environments show widespread, but heterogeneous, genomic differentiation that is often associated with variation in recombination rate and that shows both parallel and non-parallel patterns. Profitable areas for future research include identifying the links between genotype–phenotype–fitness, the processes generating genomic patterns of differentiation, the mechanisms underlying variation in recombination, and the spread of chromosomal inversions.

Speciation: Stickleback research has shaped our understanding of ecological speciation, the factors that promote and constrain it, and the traits involved in reproductive isolation. More work is needed in all these areas, as well as in the genomics of speciation and the alternatives to ecological speciation.

Eco-evolutionary dynamics: Stickleback adapted to different environments have differential effects on community and ecosystem variables in mesocosms. Future work should investigate

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* Each author wishes the others had contributed more.

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the strength and form of these effects in nature, the importance of plastic and genetic contributions, and the nature of feedbacks between ecology and evolution.

Keywords: adaptive divergence, adaptive radiation, constraint, ecological speciation, fluctuating selection, gene flow, natural selection, sexual selection.

INTRODUCTION

Institutions and programs periodically subject themselves to progress reports and strategic plans. Flattering summary statistics are compiled, exciting discoveries are trumpeted, and far-reaching and ambitious goals and visions are made flesh. At the risk of stretching an analogy, stickleback have become an institution and research on stickleback has become a program, and so perhaps it is time for a progress report and strategic plan. Our goal here is to provide this assessment – or at least a semblance of it. Although summary statistics are easily compiled ('stickleback' appears in the title of 1846 papers[1] in Web of Science as of 12 March 2013), we prefer to focus on the state and future of the institution and program by selecting and discussing several major discoveries (the now) and postulating areas where stickleback are poised to make important new contributions (the next).

The occasion and excuse for attempting a progress report and strategic plan for stickleback research was the Seventh International Conference on Stickleback Behaviour and Evolution hosted by Katie Peichel in Seattle from 29 July to 3 August 2012. During the course of this meeting, we heard many talks that summarized the state of various research areas and that were on the cusp on new and exciting approaches and discoveries. In discussing these talks, we realized that much could be gained – for us at least – in summarizing the field and in attempting to prognosticate the future. In conjunction, Andrew Hendry and Katie Peichel commissioned and edited the current special issue of *Evolutionary Ecology Research* so as to represent the diverse and exciting ideas emerging from presentations at the Conference.

Research on stickleback covers many disciplines, from ecotoxicology to behaviour to genetics to physiology to ecology to evolution. However, given our expertise and the contributions to the special issue, we here choose to emphasize evolutionary ecology and its intersections with behaviour, genetics, and physiology. In particular, we examine progress and promise in studies of (1) phenotypic variation, (2) genomic variation, (3) speciation, and (4) eco-evolutionary dynamics. In each case, we seek to integrate results from the symposium and special issue into existing knowledge (the now) and discover key new areas on the horizon (the next).

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[1] Just entering 'stickleback*' as a keyword yielded numerous papers not about stickleback, and sorting through them really would have seemed too much like preparing an actual progress report. For papers with 'stickleback*' in the title, the first year with 100 papers is 2012, the oldest paper is Giard (1900), and the five highest cited are Hynes (1950) with 646 citations, Milinski and Bakker (1990) with 461 citations, Colosimo *et al.* (2005) with 423 citations, Milinski and Heller (1978) with 409 citations, and Schluter and McPhail (1992) with 368 citations. These numbers are only for papers found in Web of Science.

PHENOTYPIC VARIATION

The typical way to start developing evolutionary inferences for a group of organisms is to measure phenotypic variation and relate it to various geographical and environmental factors (Endler, 1986; Schluter, 2000). Such endeavours have long been a part of stickleback research (e.g. Bertin, 1925; Heuts, 1947a, 1947b; Münzing, 1959; Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Hagen and Moodie, 1979, 1982; Bell *et al.*, 1993; McPhail, 1994; Reimchen *et al.*, 1995), and they are increasingly backed-up with experiments (e.g. Rundle, 2002; Marchinko and Schluter, 2007; Marchinko, 2009; Barrett *et al.*, 2011; Eizaguirre *et al.*, 2012; Zeller *et al.*, 2012; Mobley *et al.*, 2013). In this section, we describe some of the evolutionary inferences that have emerged from this work, and then suggest profitable areas for future exploration.

Phenotypic variation: now

Numerous stickleback studies have explored patterns of geographic variation in phenotypic traits, with just a few examples including bony armour (Reimchen *et al.*, 1985, 2013; Baker *et al.*, 2013a; Klepaker *et al.*, 2013), body size (MacColl *et al.*, 2013; Reimchen *et al.*, 2013), body shape (Walker, 1997; Spoljaric and Reimchen, 2007; Kaeuffer *et al.*, 2012; Hendry *et al.*, 2013; Ravinet *et al.*, 2013), trophic traits (Schluter and McPhail, 1992; Caldecutt and Adams, 1998; Kristjánsson *et al.*, 2002a; Berner *et al.*, 2009; Matthews *et al.*, 2010), life history (Baker *et al.*, 1998, 2013b; Karve *et al.*, 2013), sexual dimorphism (Reimchen and Nosil, 2006; Kitano *et al.*, 2007, 2012; Cooper *et al.*, 2011), parasite loads (Kalbe *et al.*, 2002; MacColl, 2009; Konijnendijk *et al.*, 2013), physiology (Tudorache *et al.*, 2007; Kitano *et al.*, 2010; Barrett *et al.*, 2011; Dalziel *et al.,* 2012a; Kitano and Lema, 2013), swimming performance (Taylor and McPhail, 1986; Blake *et al.*, 2005; Hendry *et al.*, 2011; Dalziel *et al.*, 2012b), coloration (Hagen and Moodie, 1979; Reimchen, 1989; Boughman, 2001; Yong *et al.*, 2013), lateral line characteristics (Wark and Peichel, 2010), learning (Girvan and Braithwaite, 2000; Kozak and Boughman, 2008, 2009; Odling-Smee *et al.*, 2008; Kozak *et al.*, 2013; Park, 2013), and various other aspects of behaviour (Foster *et al.,* 1998; Bell *et al.*, 2010; Wark *et al.*, 2011; Kozak and Boughman, 2012; Hughes *et al.*, 2013). This research has revealed that populations in different environments (e.g. benthic vs. limnetic, freshwater vs. anadromous, lake vs. stream, mud vs. lava, etc.) show more or less consistent differences in phenotype, and are thus often referred to as 'ecotypes' (McPhail, 1994; McKinnon and Rundle, 2002; Hendry *et al.*, 2009). In the following sections, we explain how this variation is structured at different scales, how it has informed the power of selection, and how it has revealed the presence of constraints.

Variation at multiple scales

Phenotypic variation in stickleback is present across a diversity of spatial scales, ranging from different parts of a single lake (Reimchen, 1980; Schluter and McPhail, 1992; Boughman *et al.*, 2005; Reimchen and Bergstrom, 2009), to adjacent lake and stream populations (Moodie, 1972; Lavin and McPhail, 1993; Berner *et al.*, 2009; Kaeuffer *et al.*, 2012; Ravinet *et al.*, 2013), to different lakes and streams in a small archipelago (Reimchen *et al.*, 1985, 2013; Reimchen and Nosil, 2006), to different watersheds on a regional scale (Klepaker and Østbye, 2008), to different regions across a continent (Hagen and Gilbertson, 1972), and finally to different continents (Berner *et al.*, 2010). One might expect this phenotypic variation to increase with increasing geographical scale but, remarkably, variation at a small scale can be just as great as that at a larger scale. As just one example, stickleback populations on the Haida Gwaii archipelago of British Columbia, Canada, exhibit phenotypic variation on the same scale as that seen across the entire geographic range of the taxon (Moodie and Reimchen, 1976; Reimchen *et al.*, 1985, 2013). This variation makes stickleback extremely well suited for studying factors that shape evolutionary diversification.

Selection drives diversification

Field surveys have repeatedly documented trait–environment correlations of the sort expected through adaptation to different ecological conditions (Schluter, 2000). As one example, the consumption of zooplankton prey by freshwater populations is strongly predictive of gill raker number (Lavin and McPhail, 1985; Schluter, 1993; Berner *et al.*, 2008; Bolnick *et al.*, 2008; Matthews *et al.*, 2010; Kaeuffer *et al.*, 2012). As another example, bony defensive structures are more pronounced when predation risk from piscivorous fishes is higher (Reimchen, 1980; Bell *et al.*, 1993; Vamosi and Schluter, 2004), but less pronounced when predation risk from invertebrates is higher (Reimchen, 1980; Reimchen *et al.*, 2013) or when the ionic content of the water is lower (Giles, 1983; Bell *et al.*, 1993; Bourgeois *et al.*, 1994). Although the selective causes are often obvious, causation can be difficult to infer from correlation owing to genetic correlations and multiple interacting sources of selection (Wade and Kalisz, 1990; Barrett and Hoekstra, 2011; MacColl, 2011). Inferences are further complicated by the fact that environmentally determined natural selection often interacts with, and is modified by, sexual selection (Kraak *et al.*, 1999; Boughman, 2001; Engström-Öst and Candolin, 2007; Heuschele *et al.*, 2012; Hodgson *et al.*, 2013; Smith and Spence, 2013). Given these complications, inferences from field surveys should be coupled with functional analyses of specific traits (Reimchen, 1992, 1994, 2000), as well as experimental manipulations of putative selective agents. Interestingly, different experiments testing the same selective mechanisms can yield different outcomes (e.g. Marchinko and Schluter, 2007; Marchinko, 2009; Zeller *et al.*, 2012; Mobley *et al.*, 2013).

Constraints on diversification

Although the phenotypic traits of stickleback are often correlated with putative selective factors, as just described, the correlations are never perfect. In particular, phenotypic divergence is sometimes low even when environmental differences suggest that divergent selection should be strong (Bell, 1982; Hendry and Taylor, 2004; Berner *et al.*, 2010). Furthermore, some stickleback lineages have failed to diversify in freshwater (Cassidy *et al.*, 2013). These cases where natural selection seems to fail have been used to infer a number of nuances to, and constraints on, divergence. In particular, weak environmental–trait correlations can reflect (1) limited knowledge of how environmental conditions shape selection (Berner *et al.*, 2008; Kaeuffer *et al.*, 2012), (2) opposing selective pressures (Reimchen and Nosil, 2002, 2004), (3) insufficient time for divergence (Berner *et al.*, 2010; Hendry *et al.*, 2013), (4) limited genetic variation (Leinonen *et al.*, 2012), or (5) maladaptive gene flow (Bell, 1982; Bell *et al.*, 1993; Hendry and Taylor, 2004; Moore *et al.*, 2007). Stickleback are thus not only a good system for examining the power of natural selection but also its limits.

Phenotypic variation: next

Much remains to be learned about how selection and constraints jointly influence phenotypic variation in stickleback. Here we highlight two emerging issues where stickleback research has made some initial progress and shows great potential for the future: temporal variation in selection and multifarious selection.

What are the causes and consequences of temporal variation?

Temporal variation in selection has important consequences for the maintenance of phenotypic variation within populations, for the ability of populations to adapt to local conditions, and for progress towards ecological speciation (e.g. Sasaki and Ellner, 1997; Bell, 2010; Svardal *et al.*, 2011). The magnitude of this variation is currently much debated (Siepielski *et al.*, 2009;

Morrissey and Hadfield, 2011; Kingsolver *et al.*, 2012) and stickleback can make important contributions to the discussion. First, many studies have documented temporal changes in phenotypes during abrupt shifts in environmental conditions, such as colonization of freshwater or the appearance of a new predator (e.g. Klepaker, 1993; Bell *et al.*, 2004; Bell and Aguirre, 2013; Lescak *et al.*, 2013). These results show that stickleback can evolve quickly when selection shifts dramatically owing to abrupt environmental change, but how much does selection vary in more 'natural' situations? The relevant studies are few but informative (Fig. 1). First, seasonal shifts in directional selection have been reported for lateral plate number and spine number, both tied to differences between summer and winter in the relative importance of different predator types (Reimchen, 1995; Reimchen and Nosil, 2002, 2004). Second, inter-annual shifts in directional selection have been tied to shifts in habitat use that influence relative exposure to bird versus invertebrate predation (Reimchen and Nosil, 2002), and to varying levels of maladaptive gene flow (Moore and Hendry, 2009). By contrast, temporal stability in selection has been tied to consistent levels of maladaptive gene flow (Bolnick *et al.*, 2008). Third, inter-annual variation in disruptive selection on trophic morphology has been reported for several British Columbia lakes: compare the results of Bolnick and Lau (2008) to those of Bolnick and Araújo (2011). These studies are too few to allow generalization, but suggest that stickleback are a good system for examining the causes and consequences of temporal variation in selection.

How multifarious is selection and what are the consequences?

The number and nature of selective forces acting on traits can dramatically alter evolutionary trajectories. In particular, increasingly multifarious selection can both constrain and promote adaptive evolution and progress towards ecological speciation (Nosil *et al.*, 2009b). Multifarious selection presumably influences many traits in stickleback, and we here consider lateral plates as an illustrative example. Multiple, independent colonizations of freshwater by oceanic ancestors have repeatedly resulted in reductions in the number of lateral plates (Bell, 2001). This parallel evolution is highly suggestive of a role for natural selection (Schluter, 2000), but it does not identify the specific causal agent (MacColl, 2011) – and these agents could be multifarious given all the features that differ between marine and freshwater environments. One particularly important difference is predation regime (Reimchen, 2000; Vamosi and Schluter, 2004; Marchinko, 2009), but even here the story is complex because bird, fish, and invertebrate predators have different selective effects (Reimchen, 1980, 1994, 1995; Marchinko, 2009; Reimchen *et al.*, 2013). And other selective forces are also likely important, including nutrient availability (McIntyre and Flecker, 2010; El Sabaawi *et al.*, 2012) and ionic concentration (Giles, 1983; Bell *et al.*, 1993). Moreover, lateral plates can experience selection through effects on other traits under selection, including swimming ability (Bergstrom, 2002; Blake, 2004; Hendry *et al.*, 2011), growth rate (Marchinko and Schluter, 2007; Barrett *et al.*, 2009a), and buoyancy (Myhre and Klepaker, 2009). In addition, *Eda*, the major gene influencing plate number (Colosimo *et al.*, 2005), has pleiotropic effects on salinity preference and lateral line morphology (Barrett *et al.*, 2009b; Wark *et al.*, 2012). Once other traits are studied as intensively as lateral plates, it seems likely that selection will prove to be similarly complex. The important question then becomes the extent to which this multifarious selection commonly promotes or hinders divergent adaptation and speciation.

The incredible variation that stickleback show at multiple levels, often independently and repeatedly evolved from a common ancestor, positions them well for testing important and general questions about phenotypic variation. Temporal variation and multifarious selection are just two examples, with others including the extent to which evolution is

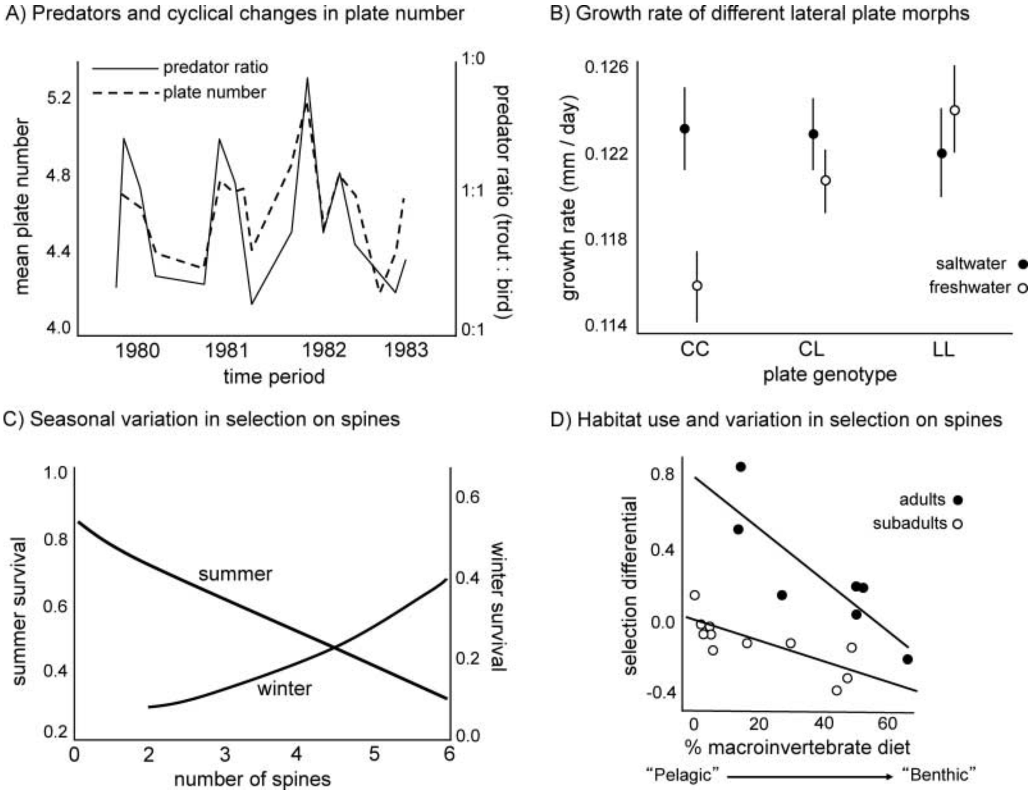

Fig. 1. Variable selection on defensive morphology. (A) Cyclical changes in plate number of subadult stickleback in Drizzle Lake are related to changes in the relative abundance of trout versus bird predators ('predator ratio'). Thus, selection was driven by predators but temporally variable. Modified from Reimchen (1995) with permission of *Behaviour*. (B) Effects of plate morph genotype on the growth rate of stickleback in freshwater (open circles) and saltwater (solid circles) treatments. C = complete morph allele, L = low plate allele. Thus, predation is not the only factor affecting the fitness of different plate morphs. Modified from Barrett *et al.* (2009a) with permission of Wiley-Blackwell. (C) Seasonal variation in selection on spine number in Boulton Lake stickleback. During summer, when avian predators are not prevalent and invertebrate predators are most active, selection favours decreasing spine number. In contrast, during winter when avian predators are prevalent, selection favours increasing spine number. These results are for females in the summer of 1986 and the winter of 1980–1981, but comparable seasonal shifts were observed in multiple years. Modified from Reimchen and Nosil (2002) with permission of Wiley-Blackwell. (D) Yearly variation in selection on spine number in summer. Selection varies according to habitat use (inferred from diet), which affects relative exposure to bird versus invertebrate predators (pelagic vs. benthic biased diet, respectively). Each point represents a different year (i.e. a different summer). Modified from Reimchen and Nosil (2002) with permission of Wiley-Blackwell.

deterministic (Kaeuffer *et al.*, 2012), interactions between plastic and genetic effects (Wund *et al.*, 2008), and the importance of individual variation (Bolnick *et al.*, 2011). All of these topics can be informed through additional field surveys but manipulated experiments, particularly in the field, promise the most novel contributions.

GENOMIC VARIATION

Recent advances in sequencing and computation are revolutionizing our ability to quantify genomic patterns of evolution (Ellegren, 2008). Stickleback research has been at the forefront of these advances. We first summarize new insights into genomic architecture that have emerged from stickleback research, and then discuss outstanding questions that can be addressed through ongoing and future research.

Genomic variation: now

Numerous genomic tools have been developed specifically for stickleback and multiple stickleback genomes have been sequenced (Peichel *et al.*, 2001; Kingsley *et al.*, 2004; Kingsley and Peichel, 2007; Miller *et al.*, 2007b; Baird *et al.*, 2008; Hohenlohe *et al.*, 2010, 2012b; Jones *et al.*, 2012a, 2012b). These developments have made stickleback a leading system for investigating the genomic architecture of adaptation – a so-called 'supermodel' organism (Gibson, 2005). Here we summarize three major findings that have arisen from genomic studies in stickleback.

Widespread and heterogeneous genomic divergence

Much debate has surrounded the extent to which adaptation to new environments proceeds through changes in just a few genomic regions or in many regions spaced throughout the genome (Orr, 2005). Genome scans comparing stickleback populations tend to support the latter expectation in repeatedly documenting widespread and highly heterogeneous genomic divergence (Hohenlohe *et al.*, 2010, 2012a; Deagle *et al.*, 2012; Jones *et al.*, 2012a, 2012b; Roesti *et al.*, 2012). The heterogeneity arises because some genomic regions are much more strongly differentiated than others, a pattern increasingly documented in other organisms (Nosil *et al.*, 2009a; Strasburg *et al.*, 2012). Although the regions of strong differentiation are widespread across the stickleback genome, they are not randomly distributed. In particular, an excess or 'clustering' of loci showing strong differentiation tends to occur near chromosome centres (Roesti *et al.*, 2012), near the *Eda* locus, and in chromosomal inversions (Jones *et al.*, 2012b) (Fig. 2). These patterns allow investigators to consider how genomic divergence is influenced by multiple evolutionary processes, including selection, gene flow, drift, mutation, and recombination. The next section considers some of these potential influences.

The recombination landscape

Population genomic studies in stickleback (Hohenlohe *et al.*, 2012a; Jones *et al.*, 2012b; Roesti *et al.*, 2012), and other organisms (Michel *et al.*, 2010; McGaugh and Noor, 2012; Nachman and Payseur, 2012), are finding that greater divergence tends to occur in regions of reduced recombination. In stickleback, this association is particularly strong for inversions (Jones *et al.*, 2012b) and towards the centres of chromosomes (Roesti *et al.*, 2012). These regions of reduced recombination can bring together suites of alleles at different genes that are important for adaptation (for a review, see Hoffmann and Rieseberg, 2008). In support of this expectation, several genomic regions affecting divergence between marine and freshwater stickleback cluster within an inversion on chromosome XXI (Jones *et al.*, 2012b; Wark *et al.*, 2012) (Fig. 2). More recent theory, however, predicts that such clustering requires special conditions, such as extensively reduced recombination or recent secondary contact (Feder and Nosil, 2009; Feder *et al.*, 2012b; Flaxman *et al.*, 2012). Thus, a logical next step for stickleback is to determine whether recombination rates within inversions are consistent

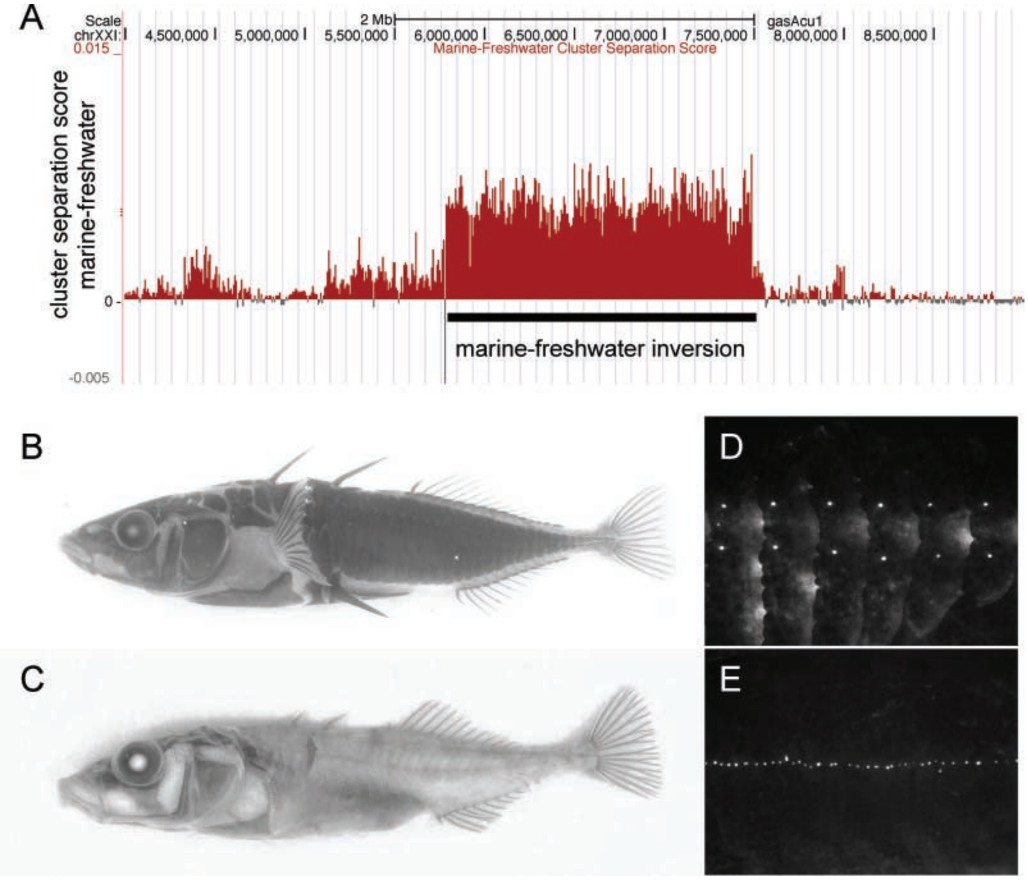

Fig. 2. Strong genomic differentiation and trait clustering within an inversion on chromosome XXI. (A) Screenshot from Sticklebrowser (http://sticklebrowser.stanford.edu; Jones *et al.*, 2012b) of the genomic divergence [measured as the cluster separation score (Jones *et al.*, 2012b)] between 10 marine and 10 freshwater populations across a 5 Mb region of chromosome XXI encompassing a 1.7 Mb inversion between marine and freshwater populations (Jones *et al.*, 2012b). Genes influencing several phenotypic traits map to this region, including QTL influencing body shape (Albert *et al.*, 2008), number of lateral plates (Colosimo *et al.*, 2004; Wark *et al.*, 2012), and lateral line neuromast number and pattern (Wark *et al.*, 2012). (B–E) Comparisons of lateral plate (B, C) and lateral line sensory system (D, E) phenotypes between Japanese Pacific Ocean marine (B, D) and Paxton Benthic freshwater (C, E) stickleback. (B) Alizarin-red stained marine stickleback (Japanese Pacific Ocean) with a complete set of lateral plates. (C) Alizarin-red stained freshwater stickleback (Paxton benthic) with a single lateral plate. (D) Close-up of DASPEI-stained marine stickleback (Japanese Pacific Ocean) highlighting the paired pattern of sensory neuromasts on each lateral plate. (E) Close-up of DASPEI-stained freshwater stickleback (Paxton benthic) highlighting the single line of dense sensory neuromasts found in the absence of lateral plates in this population.

with the theoretical predictions. Finally, these patterns underscore difficulties in interpreting genome scans, because markers showing high divergence might be driven by divergent selection, low recombination, or a combination of the two (Roesti *et al.*, 2012).

Genomic patterns of repeated evolution

Different stickleback populations have repeatedly and independently adapted to similar habitats – but have they done so through similar or different genetic changes? This question is at the heart of continuing debates about the degree to which evolution is 'parallel' or 'convergent' (Arendt and Reznick, 2008; Losos, 2011) and the extent to which it is predictable or idiosyncratic at the genetic level (Conte *et al.*, 2012). To date, the evidence from stickleback points somewhere in the middle – repeated adaptation to similar environments involves a combination of similar and different genetic changes. Supporting parallelism, whole-genome sequencing identified approximately 150 genomic regions that show similar patterns of divergence across 10 marine and 11 freshwater populations from across the world (Jones *et al.*, 2012b). Genomic regions showing parallel divergence were also found in a genome scan of marine and freshwater populations from Alaska (Hohenlohe *et al.*, 2010). Supporting non-parallelism, genome scans of populations that inhabit different freshwater habitats show much less evidence for repeated divergence in the same genomic regions (Deagle *et al.*, 2012; Jones *et al.*, 2012a; Roesti *et al.*, 2012). An important question for the future is the extent to which non-parallel genomic divergence is due to non-parallel divergence at the phenotypic level (as opposed to alternative genetic routes to the same phenotype) and, in either case, the extent to which it reflects repeated mutations at the same locus (e.g. Chan *et al.*, 2010), new mutations at different loci, or selection on standing genetic variation that differs among source populations (e.g. Jones *et al.*, 2012a).

Genomic variation: next

Much remains unknown about the genomics of adaptation (for reviews, see Nosil *et al.*, 2009a; Olson-Manning *et al.*, 2012; Strasburg *et al.*, 2012). Among the many possibilities to discuss, here we only highlight a few where research on stickleback might prove particularly informative. First, we consider ways to better explore the links between divergence in genotypes, phenotypes, and fitness. Second, we discuss improved approaches for inferring the specific evolutionary processes that drive genomic divergence. Third, we discuss the underlying causes of variation in recombination and, finally, factors influencing one of those causes – chromosomal inversions.

What are the links between divergence in genotypes, phenotypes, and fitness?

Genomic divergence is typically examined through genome scans, gene expression assays, and quantitative trait locus (QTL) mapping. All of these approaches are commonly used in stickleback and each has its own limitations. Genome scans (e.g. Hohenlohe *et al.*, 2010, 2012a; Deagle *et al.*, 2012; Jones *et al.*, 2012a; Roesti *et al.*, 2012) have been used to identify genomic regions of accentuated divergence, but they cannot identify the important phenotypic traits. Gene expression assays have revealed hundreds to thousands of genes that are differentially expressed between environments (e.g. Kitano *et al.*, 2010; Greenwood *et al.*, 2012; Lenz *et al.*, 2013; Nikinmaa *et al.*, 2013), but these studies do not discriminate between those changes in gene expression that were the direct targets of selection and those that occurred as a downstream consequence of selected changes. QTL studies have elucidated the genetic basis of a number of divergent traits (e.g. Peichel *et al.*, 2001; Colosimo *et al.*, 2004; Cresko *et al.*, 2004; Shapiro *et al.*, 2004; Kimmel *et al.*, 2005; Coyle *et al.*, 2007; Miller *et al.*, 2007a; Albert *et al.*, 2008; Greenwood *et al.*, 2011; Malek *et al.*, 2012; Rogers *et al.*, 2012; Wark *et al.*, 2012) but have not yet been conducted on many other important traits. What is now needed are integrative studies that combine these approaches, as has been done for other organisms (e.g. Rogers and Bernatchez, 2005, 2007; Yatabe *et al.*, 2007; Stinchcombe and Hoekstra, 2008; Via *et al.*, 2012). For optimal inferences, these analyses should be performed in the same populations and for an extensive suite of phenotypes: morphological, behavioural, physiological, and overall fitness. Genomic regions under selection that are not associated with QTL would suggest 'hidden phenotypes', extensive genetic hitchhiking, epistasis, or a combination of factors (Feder *et al.*, 2012a; Olson-Manning *et al.*, 2012; Via, 2012). Finally, placing genomic divergence and QTL onto maps of recombination rate and structural variation will provide insight into the evolutionary processes underlying the genomics of divergence.

What processes generate genomic patterns?

Patterns of genomic divergence can be difficult to interpret from an evolutionary perspective because, as described above, multiple interacting factors (selection, drift, mutation, recombination, epistasis) are at play (Nielsen, 2005; Feder and Nosil, 2012; Olson-Manning *et al.*, 2012; Roesti *et al.*, 2012). A resolution to this ambiguity might involve manipulative experiments that measure allele frequency changes across the genome. In such an experiment, one could genotype many individuals, place them into different environments, and then assess their survival and genotype their offspring. Allele frequency shifts within a generation should reflect selection and drift rather than inter-generational processes such as recombination, mutation, or biased-gene conversion. In addition, repeated shifts in particular alleles across experimental replicates would allow one to separate the roles of selection (at least the parallel part) and drift. Coupled with data from natural populations, such experiments could yield strong insights into the relationships between observed genomic patterns and underlying evolutionary processes.

What mechanisms underlie variation in recombination?

As noted earlier, variation in recombination plays a large role in stickleback genomic divergence, but what causes this variation? In many organisms, a major contribution comes from chromosomal rearrangements (Hoffmann and Rieseberg, 2008). The same appears true for stickleback given that large-scale rearrangements are associated with reduced recombination, increased genetic divergence, and variation in phenotypic traits, including those that contribute to reproductive isolation (Ross and Peichel, 2008; Kitano *et al.*, 2009; Jones *et al.*, 2012b; Wark *et al.*, 2012). These rearrangements cannot, however, explain other regions of reduced recombination and increased divergence, such as the centres of chromosomes (Roesti *et al.*, 2012) and on chromosome IV (Hohenlohe *et al.*, 2012a). Perhaps smaller-scale structural variation is also important – it certainly is common. Indeed, whole-genome sequencing of several individuals from a marine population found that structural variation (e.g. inversions, deletions, duplications, translocations) affects at least 7% of the autosomal genome (Feulner *et al.*, 2013). More comprehensive studies of both large- and small-scale chromosomal rearrangements are needed to determine the relationship between structural variation, recombination rate, and genetic and phenotypic divergence.

What governs the spread of chromosomal inversions?

A newly formed inversion is akin to a deleterious mutation because it is present in a single copy and might be selected against due to reduced fitness of heterozygous individuals (Hoffmann and Rieseberg, 2008). How then do these inversions rise to high frequency? Classic theories proposed a role for founder effects and genetic drift in small populations (for a review, see Hoffmann and Rieseberg, 2008) or selection for maintaining linkage between co-adapted sets of alleles (e.g. Dobzhansky, 1970). A more recent model posits that newly formed inversions can capture locally adapted alleles at two or more loci in hybridizing populations, and thus confer a fitness advantage (Kirkpatrick and Barton, 2006). Recent modelling work demonstrated that this effect is increased if inversions originate in allopatry, where they have the highest probability of containing locally adapted sets of alleles and can be present in multiple copies (Feder *et al.*, 2011). Stickleback might be especially well suited for testing these theories given that they exist in a number of geographic contexts (McKinnon and Rundle, 2002; Hendry *et al.*, 2009), show considerable structural variation within and between populations (Jones *et al.*, 2012b; Feulner *et al.*, 2013), and show many instances of hybridization on secondary contact (e.g. Jones *et al.*, 2008).

As the foregoing sections illustrate, the new challenge is to move beyond simply describing patterns of genomic variation to the explicit testing of evolutionary hypotheses. As one example not previously mentioned, Rogers *et al.* (2012) tested factors influencing the distribution of allele effect sizes fixed during adaptation, but comparable studies are lacking and so the generality of these findings is unknown. More studies of this nature are needed, as are integrative approaches and experimental manipulations. Overall, the excellent genomic tools and diverse ecological contexts for stickleback mean that this supermodel is certain to make major contributions to our general understanding of the genomics of adaptation.

SPECIATION

Speciation is the process that converts variation within populations into a diversity of reproductively isolated forms that are henceforth evolutionarily independent (Coyne and Orr, 2004; Nosil, 2012). This process is not a simple march towards inevitability; instead, different populations can be positioned at different places along a continuum that ranges from phenotypic variation within populations, through varying degrees of partial and reversible isolation, to complete and irreversible isolation (Hendry, 2009; Nosil *et al.*, 2009b). Stickleback populations are arrayed across this entire continuum, which has made them particularly useful for the study of speciation (McPhail, 1994; McKinnon and Rundle, 2002; Boughman, 2007; Hendry *et al.*, 2009) (Fig. 3).

Speciation: now

Across their distribution, stickleback populations have repeatedly and independently adapted to a range of different habitats (see above), which has generated reproductive isolation to varying degrees (for reviews, see McPhail, 1994; McKinnon and Rundle, 2002; Boughman, 2007; Hendry *et al.*, 2009). Studies of these population pairs (benthic vs. limnetic, anadromous vs. freshwater, lake vs. stream, mud vs. lava) have informed the factors promoting and constraining progress along the speciation continuum.

Ecological speciation

The theory of ecological speciation posits that divergent adaptation promotes the evolution of reproductive isolation (Schluter, 2000; Rundle and Nosil, 2005; Nosil, 2012). Research on stickleback has been influential in the development of, and in providing support for, this theory – particularly by showing how specific reproductive barriers can result from adaptation to different environments. One key barrier is sexual isolation, which has evolved repeatedly,

Solitary lake population

Lake-stream pair

Benthic-limnetic species pair

Japanese species pair

Fig. 3. The speciation continuum in stickleback. Stickleback populations are found in many different states along the speciation continuum (Hendry *et al.*, 2009), from continuous variation within a population (e.g. solitary lake populations), to discrete variation between ecotypes without the presence of strong reproductive isolation (e.g. lake–stream pairs), to strong variation between ecotypes with the presence of strong (but reversible) reproductive isolation (e.g. benthic–limnetic species pairs), to strong and irreversible reproductive isolation (e.g. Japanese species pair). Thus, stickleback present a remarkable opportunity to identify the factors that promote or constrain progress along the speciation continuum. Photo credits: a solitary lake population (Dan Bolnick); the Misty lake–stream pair (Andrew Hendry); the Paxton benthic–limnetic species pair (Todd Hatfield); and the Japanese species pair (Jun Kitano and Mark Ravinet). Note that pictures are not scaled relative to each other.

and in parallel with ecological conditions, for sympatric limnetic–benthic pairs (Rundle *et al.*, 2000; Boughman *et al.*, 2005), allopatric lake pairs (Vines and Schluter, 2006), and parapatric anadromous–freshwater pairs (McKinnon *et al.*, 2004). Another key barrier is ecologically based selection against hybrids, which has evolved between the limnetic–benthic pairs (Schluter, 1995; Hatfield and Schluter, 1999; Vamosi and Schluter, 1999, 2002; Rundle, 2002; Gow *et al.*, 2007) and probably also between the anadromous–freshwater pairs (Hagen, 1967; Jones *et al.*, 2006). These patterns are unlikely to arise via genetic drift and thus provide strong comparative evidence for ecological speciation (Schluter and Nagel, 1995).

Magic traits, imprinting, sexual selection, and reinforcement

These factors have been argued to promote speciation – and each certainly appears important in stickleback. First, some traits involved in divergent adaptation also contribute to premating isolation (Nagel and Schluter, 1998; McKinnon *et al.*, 2004; Boughman *et al.*, 2005; Conte and Schluter, 2013), making them the 'magic traits' thought to be so conducive to speciation (*sensu* Gavrilets, 2004; Servedio *et al.*, 2011). Second, imprinting on the social group and on the father sharpens mating isolation (Kozak and Boughman, 2009; Kozak *et al.*, 2011). Third, divergent sexual selection (as opposed to just divergent natural selection) can cause divergence in mating traits that then confers sexual isolation (Boughman, 2001; Boughman *et al.*, 2005). Fourth, ecologically based selection against hybrids can lead to the 'reinforcement' of sexual isolation in sympatry (Rundle and Schluter, 1998). Thus, many of the ingredients expected to promote rapid and effective ecological speciation are indeed present in a system (stickleback) where ecological speciation is well supported.

Traits generating reproductive isolation

Identifying the traits that influence reproductive isolation promotes insight into the drivers of speciation. For example, traits not under divergent selection imply that speciation has not been 'ecological' (in the above sense), traits that influence mating success suggest an influence (positive or negative) of sexual selection, and traits associated with particular functions (foraging, predator defence, immune response) point towards specific selective factors (diets, predators, parasites). In most taxa, the traits causing reproductive isolation remain poorly understood (Mayr, 1963; Ramsey *et al.*, 2003). In stickleback, however, many traits have been identified that influence one reproductive barrier: sexual isolation. In particular, assortative mating is strongly influenced by body size and shape differences (Nagel and Schluter, 1998; McKinnon *et al.*, 2004; Boughman *et al.*, 2005; Kitano *et al.*, 2009; Conte and Schluter, 2013; Head *et al.*, submitted), nuptial coloration (Boughman, 2001; Boughman *et al.*, 2005), behaviour (Kitano *et al.*, 2009; Kozak *et al.*, 2009), odour (Rafferty and Boughman, 2006), and parasite resistance through MHC genes (Eizaguirre *et al.*, 2012). These results suggest that many traits can influence a single reproductive barrier, but more work is needed to disentangle their relative and potentially interactive effects. Such work will likely be facilitated by the recent development of 3D-animated stickleback models (Veen *et al.*, 2013). Furthermore, additional work is needed to determine the extent to which these barriers are parallel (or not) across replicate population pairs and different environmental contrasts (freshwater vs. anadromous, lake vs. stream, benthic vs. limnetic, mud vs. lava, etc.). Moreover, the traits influencing other reproductive barriers have yet to be elucidated.

Speciation: next

Even though stickleback represent one of the best developed models for studying ecological speciation, many critical questions remain. First, we have not determined the relative importance of different types of isolating barriers. Second, we know almost nothing about the genetic architecture of traits that contribute to reproductive isolation. Third, we cannot yet explain why many populations that experience disruptive or divergent selection have not progressed very far towards speciation (Snowberg and Bolnick, 2008; Berner *et al.*, 2009; Hendry *et al.*, 2009; Bolnick, 2011) (Fig. 3). Fourth, we have inadequately explored how the alternatives to ecological speciation might contribute to the diversification of stickleback.

What are the relative strengths of different reproductive barriers?

Reproductive isolation might result from a single strong and symmetrical reproductive barrier – or it might result from a patchwork of several weaker, and perhaps asymmetric, barriers. The importance of this distinction for progress towards speciation has made cataloguing suites of reproductive barriers a critical component of speciation research (Ramsey *et al.*, 2003; Coyne and Orr, 2004; Nosil, 2012). In stickleback, multiple reproductive barriers have been identified in various instances but other potential barriers have yet to be considered, such as conspecific sperm precedence and gametic isolation. Furthermore, the relative contribution of different barriers to overall reproductive isolation in a particular instance has not been estimated, except for the Japan Sea–Pacific Ocean species pair (Kitano *et al.*, 2009). In this case, pre-zygotic barriers (geographical, temporal, and behavioural) and post-zygotic barriers (hybrid male sterility) were both important. Similar analyses need to be performed for other stickleback systems so as to elucidate the barriers that are important at different stages in the speciation process.

What is the genetic architecture of reproductive isolation?

Critically important for progress towards speciation is the genetic basis of reproductive barriers, including the number of genes and their relative strengths, as well as any physical linkage, pleiotropy, and epistatsis (Coyne and Orr, 2004). As examples, speciation is thought to be easiest when it involves relatively few genes of large effects, when genes under divergent selection have pleiotropic effects on reproductive isolation (i.e. magic traits), and when the same allele causes mating isolation in multiple populations (i.e. one-allele mechanisms) (Felsenstein, 1981; Gavrilets, 2004; Nosil, 2012). In stickleback, most work on the genetics of speciation has focused on the genetics of adaptation, because adaptive divergence is the direct cause of ecologically based barriers such as natural selection against migrants and hybrids (Nosil and Schluter, 2011; Servedio *et al.*, 2011). Beyond adaptation, work on the genetics of reproductive isolation *per se* has only been conducted for the Japan Sea–Pacific Ocean species pair. In this system, two loci have been found on the X chromosome that account for 70% of the variation in sperm number in hybrid males, and several other loci have been found that explain about ~20% of the behavioural isolation (Kitano *et al.*, 2009). All of the above work was based on QTL approaches, which map at a crude level due to few recombination events in laboratory crosses. A useful next step would be to employ genome-wide association mapping in hybridizing populations (e.g. Malek *et al.*, 2012), thus taking advantage of a longer history of recombination to more finely map the genomic regions and traits involved in reproductive isolation.

What limits progress towards speciation?

The preceding sections might give the impression that ecological speciation is common in stickleback. The reality, however, is that strong reproductive isolation between stickleback taxa has evolved in only a handful of instances (Fig. 3). It is instead much more common for stickleback populations to evolve only weak and partial reproductive isolation, even when disruptive or divergent selection is strong (Snowberg and Bolnick., 2008; Hendry *et al.*, 2009; Bolnick, 2011). As just one example, sexual isolation has been tested for, but not yet found, in at least one lake–stream pair (Raeymaekers *et al.*, 2010; Räsänen *et al.*, 2012) and at least one freshwater–anadromous pair (Jones *et al.*, 2008). Moreover, even the strongly isolated benthic–limnetic species pairs can collapse into a hybrid swarm following a change of ecological conditions (Kraak *et al.*, 2001; Taylor *et al.*, 2006). In short, the extent and nature of reproductive isolation varies greatly among stickleback populations, as exemplified by the lake–stream pairs (Berner *et al.*, 2009) and the anadromous–freshwater pairs (Hagen, 1967; McPhail, 1994; McKinnon *et al.*, 2004; Jones *et al.*, 2006, 2008; Karve *et al.*, 2008). Although this variation might be frustrating in its uncertainty, it provides an excellent opportunity to explore the factors promoting and constraining progress towards speciation (Hendry, 2009; Hendry *et al.*, 2009; Nosil *et al.*, 2009b). Such factors potentially include divergence times, gene flow, genetic architecture, sexual dimorphism, phenotypic plasticity, and the strength and dimensionalities of selection (Bolnick and Doebeli, 2003; Hendry and Taylor, 2004; Thibert-Plante and Hendry, 2009, 2011; Berner *et al.*, 2010; Hendry *et al.*, 2013; Boughman *et al.*, submitted).

How important are the alternatives to ecological speciation?

In contrast to divergent selection driving ecological speciation, other causes of speciation have received far less attention in stickleback research. For example, reproductive isolation could arise due to the fixation of different and incompatible mutations in separate populations experiencing similar selection pressures (Schluter, 2009; Nosil and Flaxman, 2011). Speciation could also arise owing to divergence driven by conflict between the sexes or between genetic elements within the genome (Presgraves, 2010; Crespi and Nosil, 2013). Thus far, sexual conflict has been implicated in reproductive isolation in the Japan Sea–Pacific Ocean pair where fusion between the ancestral Y chromosome and an autosome has generated a neo-sex chromosome pair (Kitano *et al.*, 2009). Such fusions are proposed to result from selection for linkage between the sex-determination locus and genes with differential fitness effects in males and females (Charlesworth and Charlesworth, 1980). Strikingly, all known traits that contribute to behavioural isolation between the Japan Sea and Pacific Ocean stickleback map to the neo-sex chromosome (Kitano *et al.*, 2009). These results – as well as the fact that all recognized stickleback species differ in sex determination systems (Ross *et al.*, 2009) – suggest the need for an increasing emphasis on alternatives to ecological speciation.

Stickleback are an important model for research on ecological speciation. As the foregoing description illustrates, however, we remain ignorant regarding several key questions, such as the relative contribution of different reproductive barriers and their genetic basis. In addition, it has become clear that (1) different ecological conditions only rarely generate substantial progress towards ecological speciation, and (2) the strongest reproductive barriers in stickleback appear to be unrelated to different ecological conditions. The time is therefore ripe for some serious outside-the-box thinking in stickleback speciation research.

ECO-EVOLUTIONARY DYNAMICS

Rates of evolution were historically assumed to be very slow, whereas recent studies have revealed substantial adaptive evolution on time scales of only years to decades – so-called 'contemporary' or 'rapid' evolution (for reviews, see Hendry and Kinnison, 1999; Reznick and Ghalambor, 2001; Hendry *et al.*, 2008). In addition, it is now well documented that even subtle genetic and phenotypic differences within and among populations and species can have significant effects on ecological processes at the population, community, and ecosystem levels (Fussman *et al.*, 2007; Hughes *et al.*, 2008; Pelletier *et al.*, 2009; Post and Palkovacs, 2009; Matthews *et al.*, 2011a, 2011b; Schoener, 2011). From the convergence of these two realizations emerges the field of eco-evolutionary dynamics: ecology and evolution can strongly influence each other on contemporary time scales.

Eco-evolutionary dynamics: now

Eco-evolutionary dynamics come in two basic flavours: in one, ecological differences drive evolutionary change on contemporary time scales (eco-to-evo) and, in the other, evolutionary change on contemporary time scales drives ecological change on similar time scales (evo-to-eco). And these flavours can be mixed through feedbacks, such as when ecological differences cause evolutionary changes that then cause ecological change, or evolutionary changes cause ecological changes that influence further evolutionary change (Post and Palkovacs, 2009). Research on stickleback has made important contributions to our appreciation of both flavours.

Ecology drives evolution (eco-to-evo)

As previously outlined, stickleback populations in different ecological environments often show dramatic adaptive differences, and these differences sometimes contribute to reproductive isolation. These associations indicate that ecological differences are a primary determinant of evolutionary divergence in stickleback. For these effects to be especially relevant to eco-evolutionary dynamics, they would need to arise quickly – and this appears to be the case for stickleback. For instance, substantial genetic and phenotypic changes often occur almost immediately after the colonization of a new ecological environment

(Klepaker, 1993; Kristjánsson *et al.*, 2002b; Bell *et al.*, 2004; Leaver and Reimchen, 2012; Bell and Aguirre, 2013); and, in at least one instance, these changes have led to assortative mating (Furin *et al.*, 2012). This last result is particularly important because examples of reproductive isolation evolving on contemporary time scales are still relatively rare (Hendry *et al.*, 2007). Stickleback thus provide an exemplar for the growing acceptance that ecological differences can shape evolutionary change on very short time scales, although it is important to recognize that rapid change does not always take place (e.g. Berner *et al.*, 2010; Hendry *et al.*, 2013).

Evolution drives ecology (evo-to-eco)

As noted above, evidence is growing that contemporary evolution can influence population dynamics, community structure, and ecosystem function. Our current understanding of such effects stems from a series of case studies, including one from stickleback. Harmon *et al.* (2009) used mesocosms to show that stickleback populations with different phenotypes (benthic vs. limnetic) have different effects on a broad range of ecological conditions, including the structure of prey communities, primary productivity, and light transmission. This work indicates that phenotypic diversification in stickleback can affect ecological processes, and it points to several new questions that we introduce here and develop further in the next section. First, Harmon *et al.* (2009) studied post-glacially diverged populations, so we don't yet know whether phenotypic diversification of stickleback on more contemporary time scales has similar ecosystem effects. Second, the experiments were conducted in mesocosms, whereas the effects might be quite different in nature. Third, the experiments were conducted with wild-caught fish, and so genetic and plastic effects could not be discriminated. Finally, we don't yet know how stickleback-mediated ecological changes might alter natural selection, generating feedbacks that could either promote or constrain further evolutionary change.

Eco-evolutionary dynamics: next

Important next steps in examining the effects of ecology on evolution (eco-to-evo) were generally considered in the previous sections on phenotypic variation, genetic variation, and speciation. Here we instead focus on important next steps in examining effects of evolution on ecology (evo-to-eco). We focus on five major questions: (i) what is the relative strength of evolutionary effects on ecological processes, (ii) how does the distribution of ecological effects change along the speciation continuum, (iii) what is the role of plastic versus genetic differences in explaining ecological effects, (iv) what is the nature of eco-evolutionary feedbacks, and (v) how do eco-evolutionary dynamics play out in nature.

What is the relative importance of evolution?

A key uncertainty in the study of eco-evolutionary dynamics is the extent to which ongoing ecological processes are influenced by contemporary evolution – as opposed to external drivers such as habitat size, species composition, connectivity, or climate (Hairston *et al.*, 2005; Tack *et al.*, 2012). Stated simply, does contemporary evolution explain 5% or 50% of the variation in population dynamics, community structure, or ecosystem function? Work on stickleback could help to answer this question by quantifying, in both experiments and surveys, the importance (percent variance explained) of phenotypic variation versus other factors. Establishing the distribution of these effect sizes will tell us when ecologists studying contemporary processes should be concerned with evolutionary effects.

How does the distribution of effects change along the speciation continuum?

Evolutionary biologists have long discussed whether speciation is associated with abrupt shifts in phenotype (Futuyma, 1987; Uyeda *et al.*, 2011; Burbrink *et al.*, 2012). Given that phenotypes have ecological effects, speciation therefore might or might not be associated with discontinuous ecological changes. Stickleback are extremely well suited to explore this question given the above-described variation at multiple spatial scales and its association with varying degrees of progress towards speciation. Moreover, many of the traits that vary along this continuum, particularly foraging-related traits (Schluter and McPhail, 1992; Berner *et al.*, 2009; Hendry *et al.*, 2009), are the sorts of traits expected to have effects on aquatic communities. Although we currently have very little understanding of how these dynamics might play out, we venture some hypotheses in Fig. 4. To address these hypotheses, we need a concerted interdisciplinary effort among evolutionary biologists, ecologists, and ecosystem scientists (Matthews *et al.*, 2011b).

What is the role of plastic versus genetic effects?

Eco-evolutionary dynamics are shaped by phenotypes, and phenotypes can be influenced by both genetic and plastic effects (Falconer and MacKay, 1996). The potential contributions of these two effects to ecological dynamics have yet to be disentangled for any fish species because all previous studies have used wild-caught individuals (Harmon *et al.*, 2009; Palkovacs and Post, 2009; Palkovacs *et al.*, 2009; Bassar *et al.*, 2010). Stickleback are appropriate for attempting this disentanglement because the phenotypes of populations in different ecological environments are known to be shaped by both genetic differences and plasticity (Day *et al.*, 1994; Sharpe *et al.*, 2008; Wund *et al.*, 2008). The logical next step is to raise individuals from different populations under common-garden conditions, and then test for their differential effects in 'common gardening experiments' (*sensu* Matthews *et al.*, 2011b). It will also be useful to induce plastic effects, through realistic diet or flow manipulations (Day *et al.*, 1994; Wund *et al.*, 2008), and then test for ecological consequences. Such experiments would be an extremely valuable contribution to our understanding of the phenotypic underpinnings of eco-evolutionary dynamics.

What is the nature of eco-evolutionary feedbacks?

Evolution can drive ecological changes that can either promote (positive feedbacks) or constrain (negative feedbacks) further evolution (Post and Palkovacs, 2009). The specific outcome likely depends on the size, dimensionality, and persistence of ecosystem effects, and the specific traits and ecological variables involved (Fig. 4A). Experiments testing for such feedbacks are virtually non-existent, even though feedbacks themselves are implicit in many models of speciation and adaptive divergence. An obvious approach with stickleback would be to conduct a common-gardening experiment with ecotypes that are expected to differentially shape ecosystem conditions (Matthews *et al.*, 2011b). These gardening fish could then be removed from the experimental arenas and a new set of individuals (e.g. juveniles of different types) could be used as a 'selection probe', to test whether fitness is higher for individuals that are more similar (positive feedback) or less similar (negative feedback) to the type that originally shaped the environment.

How do eco-evolutionary dynamics play out in natural populations?

Most evo-to-eco experiments, including all of those with vertebrates, have been conducted in controlled environments: guppies in experimental stream channels (Palkovacs *et al.*, 2009; Bassar

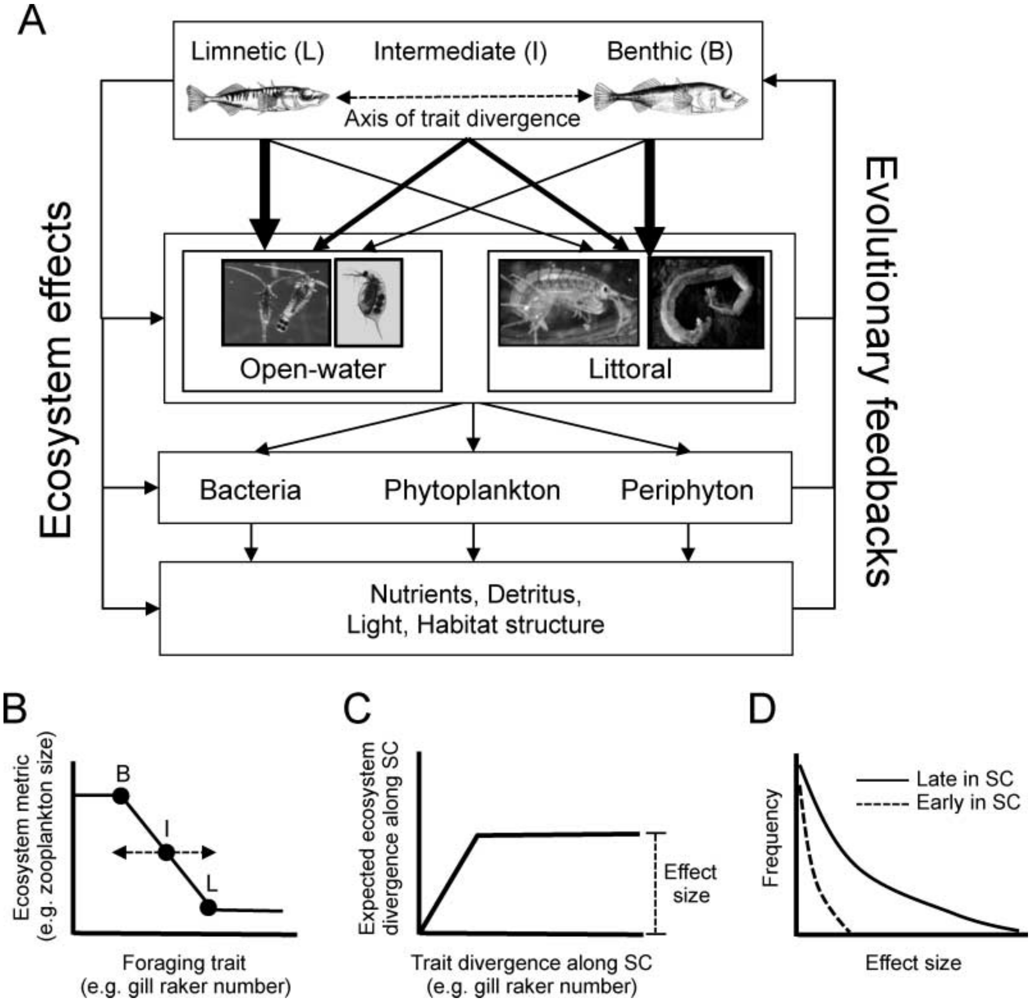

Fig. 4. Eco-evolutionary dynamics in stickleback. (A) Stickleback can influence various aspects of their ecosystems via direct and indirect pathways. The strength of these pathways (indicated by the weight of arrows) can change progressively with increasing phenotypic divergence (weights of arrows at top) of key traits, for example from a limnetic specialist through intermediate forms to a benthic specialist. Such ecosystem effects (downward arrows) could also drive evolutionary feedbacks by changing selection pressures (returning arrows). (B) Hypothesized relationship between gill raker number of a stickleback population and the resulting average body size of plankton in an open-water habitat. (C) Relationship between trait and ecosystem divergence at different places along the speciation continuum (SC), following the predicted relationship in panel (B). Effect sizes can be measured in common-gardening experiments performed with a range of contrasting stickleback phenotypes used as treatments. (D) Predicted change in the effect size distribution measured in common gardening experiments using stickleback at different stages along the SC. This assumes that phenotypic divergence is positively correlated with multiple ecosystem effects. Large effect sizes could be caused either by direct or indirect pathways, as illustrated in panel (A). Stickleback drawings in panel (A) by Laura Nagel.

et al., 2010), alewives in bags in lakes (Palkovacs and Post, 2009), and stickleback in cattle tanks (Harmon *et al.*, 2009). These arenas reveal that evolution can potentially influence ecology, but they do not inform eco-evolutionary dynamics that actually occur in nature – which is the critical question. Stickleback are well suited to address this deficiency. In particular, flow-through (mesh) experimental enclosures in different stickleback environments could be used to assess the role of different stickleback ecotypes in shaping community and ecosystem properties. Such experiments are imminently feasible given that many previous experiments have placed stickleback in such enclosures (Schluter, 1995; Hendry *et al.*, 2002; Rundle, 2002; Bolnick, 2004; Eizaguirre *et al.*, 2012). Field surveys could then be used to see if results from these experiments correspond to broad-scale patterns of covariance between phenotypes and environments.

CONCLUSIONS

What will a progress report for stickleback research look like 10 years from now? As for all programs and institutions, it will likely be able to tout numerous accomplishments originally set out in the previous strategic plan – as well as a number of (probably more important) findings that were not previously envisioned. It seems inevitable that we will be able to say much more about genomic variation given the rapidly advancing methodology. Progress in the other areas (phenotypic variation, speciation, and eco-evolutionary dynamics) will be slower, simply because they require more boots-on-the-ground and eyes-to-the-objective effort that will never show the half-life of genomics. And yet it still seems likely that dramatic advances also will be accomplished in those areas, particularly through the application of established methodologies to an ever increasing number of populations, as well as through the implementation of more controlled experiments, especially in nature. Even more intriguing, however, are the advances that we can't even imagine. It is tempting to list a whole range of possibilities here in hopes that we accidentally hit the future advances, but it seems more honest and interesting to just admit our ignorance. That seems the surest bet.

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