

IDEAS AND PERSPECTIVE

From low to high gear: there has been a paradigm shift in our understanding of evolution

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Abstract

Experimental studies of evolution performed in nature and the associated demonstration of rapid evolution, observable on a time scale of months to years, were an acclaimed novelty in the 1980–1990s. Contemporary evolution is now considered ordinary and is an integrated feature of many areas of research. This shift from extraordinary to ordinary reflects a change in the perception of evolution. It was formerly thought of as a historical process, perceived through the footprints left in the fossil record or living organisms. It is now seen as a contemporary process that acts in real time. Here we review how this shift occurred and its consequences for fields as diverse as wildlife management, conservation biology, and ecosystems ecology. Incorporating contemporary evolution in these fields has caused old questions to be recast, changed the answers, caused new and previously inconceivable questions to be addressed, and inspired the development of new subdisciplines. We argue further that the potential of contemporary evolution has yet to be fulfilled. Incorporating evolutionary dynamics in any research program can provide a better assessment of how and why organisms and communities came to be as they are than is attainable without an explicit treatment of these dynamics.

Keywords

Conservation biology, contemporary evolution, eco-evo dynamics, ecosystems ecology, evolution, fisheries biology, genetics of adaptation, invasive species, pest management, wildlife biology.

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INTRODUCTION

Charles Darwin was a great experimentalist long before experiments became the hallmark of modern science. He conducted experiments on why plants grow towards light, whether worms can hear, how seeds can colonise oceanic islands, and many other topics. Yet, for his greatest idea, the theory of evolution by natural selection, it appears that Darwin never even considered conducting an experiment. The reason is simple: Darwin believed that evolution was too slow to be observable in a human lifetime, so there was a little incentive to contemplate such an experiment. Darwin held this view because he looked to the fossil record as the history of life. The record told him that evolution is slow.

Darwin's convictions on the pace of change influenced the field for more than a century. Evolution was perceived as a historical process that left footprints in the fossil record or the properties of living organisms, but was not one we could see acting in real time. When experiments were done, they were confined to the laboratory. This view was so entrenched that when experimental studies of evolution in nature were reported in the 1980s and 1990s, they attracted great media attention, as we learned from our own work (Reznick *et al.* 1990; Losos *et al.* 1997).

The clamor about rapid evolution inspired the late Stephen J. Gould to publish an essay entitled 'The Paradox of the Visibly Irrelevant' (Gould 1997). Rather than join the chorus of acclamation, Gould argued that the rapidity of contemporary evolution was so discordant with the fossil record that it

ought to be regarded as a curiosity rather than an important discovery. Gould's argument was delicate. In his earlier work, Gould had argued that the observed character changes in the fossil record were too rapid to be compatible with the slow pace of natural selection. Now he argued instead that the changes documented in the fossil record unfolded too slowly to be compatible with the rapid rates of contemporary evolution. Clearly, the concept of contemporary evolution was a vexing challenge to the traditional paradigm.

Rapid evolution has now been documented so many times that it is far less newsworthy and, instead, has become a bedrock component of some ecological research. Papers including the phrase 'rapid evolution' receive tens of thousands of citations a year, more than an order of magnitude more attention than they were receiving when Gould wrote his essay (Fig. 1).

This shift from extraordinary to ordinary is important. It heralds what Thomas Kuhn defined as a paradigm shift. A paradigm shift is initiated by scientific achievements that are 'sufficiently unprecedented to attract an enduring group of adherents' away from current approaches to science and sufficiently open ended in its implications to define diverse new problems for the 'redefined group of practitioners to resolve' (p. xxii of 'Introductory Essay', by Ian Hacking, to the 4th edition of 'The Structure of Scientific Revolutions'; Kuhn 2012).

The realisation of contemporary evolution has implications that extend far beyond the feasibility of conducting the sorts of experiments which Darwin never considered. The rate at which populations can adapt means that evolution and

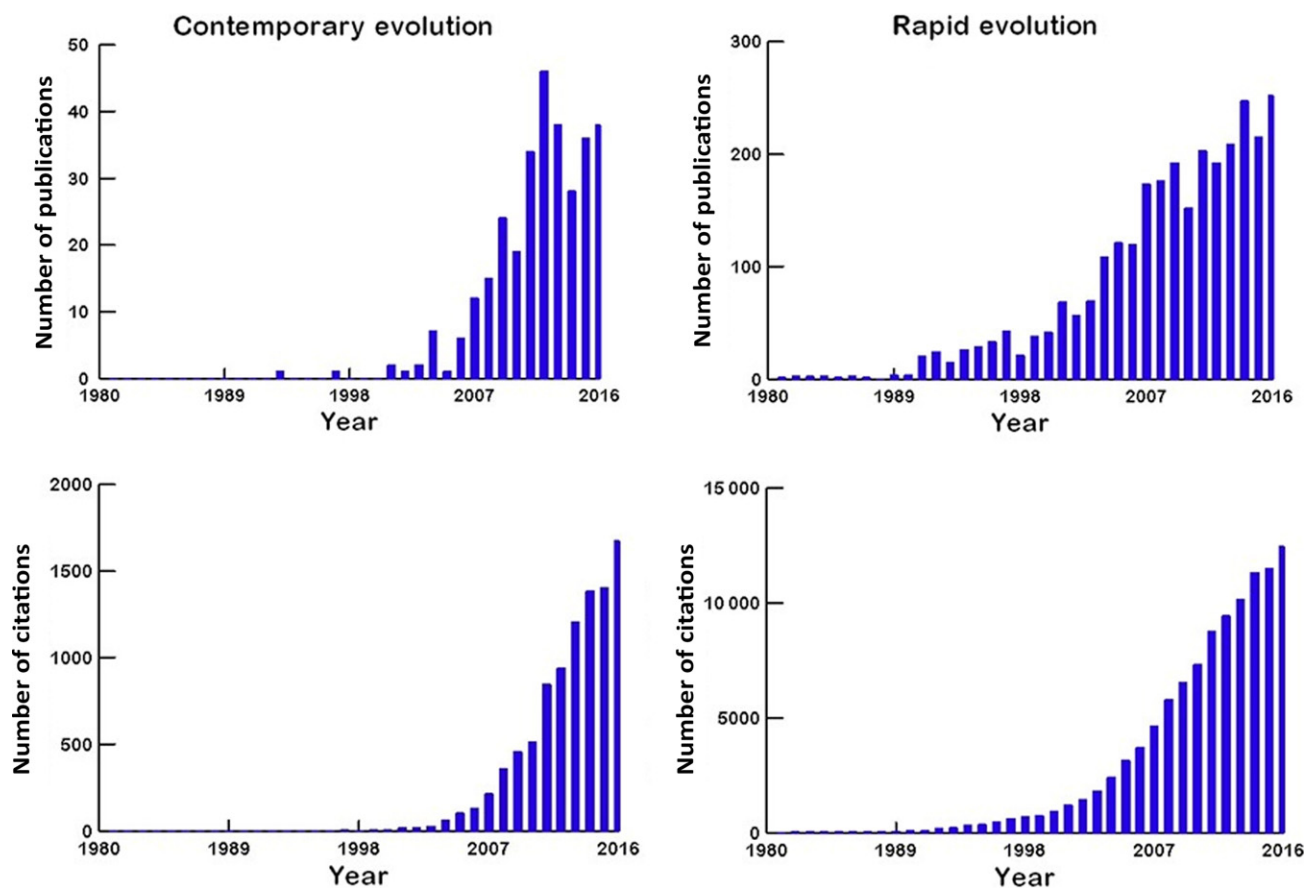


Figure 1 Annual number of publications and citations that use the keywords ‘contemporary evolution’ and ‘rapid evolution’.

ecology can occur on commensurate timescales. In turn, this means that many areas of inquiry that traditionally ignored evolution, from ecosystem science to conservation biology, now incorporate contemporary evolution into their research programs.

Our goals are to outline how this paradigm shift happened then illustrate how the appreciation for contemporary evolution has changed research in ecology and evolution.

THE DISCOVERY OF CONTEMPORARY EVOLUTION

The entrenched idea that evolution is slow was a paradox even before 1980. While the fossil record suggested that evolution was slow, there was empirical evidence that said otherwise; however, this evidence was juxtaposed by respected theory that said rapid evolution was impossible.

The earliest empirical evidence for rapid directional evolution was provided by studies of plant and animal responses to anthropogenic effects. In his presidential address to the Linnaean Society in 1898, H. F. R. Weldon reported on changes in the shell shapes of the crab *Carsinus moenas* over a period of a few years in response to the pollution of Plymouth Sound by china clay, effluent from towns, and shipping activity (Weldon 1899). Other studies of rapid evolution became iconic examples: industrial melanism in the peppered moth, *Biston betularia*, and other lepidoperans (Kettlewell 1955a,b;

Ford 1971), and the evolution of heavy metal tolerance in the grass *Agrostis tenuis* (McNeilly & Antonovics 1967; Antonovics 1971). However, it was easy to consider these examples as special cases driven by artificially strong selection.

Other evidence was also dismissed as unrepresentative. Ecological geneticists like E. B. Ford, Philip Sheppard, and colleagues documented strong selection and visible changes in allele frequencies in a variety of visible genetic polymorphisms (Ford 1971). Dobzhansky and colleagues documented strong selection on inversions of the third chromosome of *Drosophila pseudoobscura* (e.g. Dobzhansky 1943). Lewontin (1974) suggested that these and similar studies were special cases because the variation under scrutiny, visible polymorphisms, and chromosomal inversions, was not typical of the type of genetic variation molded by natural selection.

At the same time, theory, developed initially by Haldane (1957), argued that directional evolution was so costly that sustained rapid evolution was impossible. Haldane began with the example of industrial melanism and Kettlewell’s observation that the relative abundance of the morph that did not match the color background was being reduced by as much as half in a day (Kettlewell 1956). To compensate for this loss and sustain the population, the favoured morph would have to produce twice as many surviving offspring as the disadvantaged morph. While this might be feasible, the situation grew untenable as the number of loci under selection increased:

'Now, if the change of environment had been so radical that ten other independently inherited characters had been subject to selection of the same intensity as that for color, only $(1/2)^{10}$, or one in 1024, of the original genotype would have survived' (p. 511). If the favoured genotype could not produce the required 1024-fold increase in offspring, the population would go extinct. In Haldane's view, the only solution was that selection must be weak and directional evolution slow, proceeding one allelic substitution at a time. He predicted that genetic variation would be scarce and consist primarily of deleterious alleles in the process of being eliminated.

The scarcity of adaptive genetic variation was belied by the data, first and most obviously in the older work of Ford (1971) and, in the 1960s, by new discoveries of variation in an entirely different sort. Hubby & Lewontin (1966), Lewontin & Hubby (1966), and Harris (1966) described widespread polymorphisms at the molecular level for genes of all types in *Drosophila* and humans; results soon followed for hundreds more species (Lewontin 1974; Koehn & Eanes 1978). These results prompted a burst of new theory that explored ways either to reconcile these observations with Haldane's arguments (neutral theory: Kimura & Ohta 1974) or to revisit Haldane's arguments in the light of more sophisticated schemes of fitness and selection (reviewed in Ewens 2004).

Empirical work took two new directions that again challenged Haldane's view of the world. First, there was a rapid increase in interest in quantitative genetics, inspired by theory by Lande (1976), Bulmer (1976), and others. The data emerging from this effort reflected the same patterns as the studies of molecular variation – substantial levels of additive genetic variance for diverse quantitative traits, including ones closely tied to fitness (Mousseau & Roff 1987; Hansen *et al.* 2011). Second, there was a rebirth of studies of natural selection, not on visible polymorphisms, but on quantitative traits, inspired by Lande & Arnold (1983) paper relating linear statistical models for selection to standard quantitative genetic models for evolution.

In this same period, Endler (1986) presented an encyclopedic summary and synthesis of selection in nature. He found substantial evidence of strong selection on discrete and quantitative traits. The magnitude of the coefficients of selection were often far in excess of the values typically assumed in theoretical population genetics. Endler's compilation suggested that selection would often be strong and directional evolution rapid, even in the absence of anthropogenic influences. The stage was set for a new round of discovery of rapid evolution, discoveries that would be immune to the charge of being special cases.

Those discoveries came rapidly, from observational data (e.g. Boag & Grant 1981; Hairston & Walton 1986) and experiments performed on natural populations (e.g. Endler 1980; Reznick & Bryga 1987; Reznick *et al.* 1990; Losos *et al.* 1997; Reznick *et al.* 1997). By 2001, there were enough compelling examples for three extensive reviews (Thompson 1998; Hendry & Kinnison 1999; Reznick & Ghalambor 2001) that highlighted several ramifications of rapid evolution. From an ecological viewpoint, one was that strong selection and rapid evolution can alter interspecific interaction coefficients from one generation to another. This implies that the parameters

describing interspecific interactions might not be constant for very long, which has profound consequences for our ability to understand ecological dynamics and develop a predictive science around interspecific interactions.

CONSEQUENCES – HOW CONTEMPORARY EVOLUTION CONTRIBUTES TO CONTEMPORARY SCIENCE

There is often a hiatus between new discoveries and their impact on science. Case studies of contemporary evolution date to at least the 1890s (Weldon's work). There have been advocates for and evidence of contemporary evolution since the revitalisation of research on natural selection after the Modern Synthesis; however, we argue here, with examples from diverse areas of research in ecology and evolution, that there was a sea change in the popular perception of evolution as a contemporary process that usually dates to the mid-1990s or later. This sea change is evidence of the paradigm shift in our perception of evolution.

Eco-evo dynamics

Eco-evo dynamics were conceived long before the popularisation of rapid evolution, but did not blossom until after the shift in the perception of evolution. Pimentel (1961) was the first to formally define what we now refer to as eco-evo dynamics in his paper entitled 'Animal population regulation by the genetic feed-back mechanism' – 'Density influences selection; selection influences genetic make-up; and in turn, genetic make-up influences density'. He wrote this paper when the dominant question in ecology was 'what governs the abundance and distribution of organisms?' The answers were the conflicting ideas of density-dependent vs. density-independent population regulation. His is an argument for the predominance of density regulation and how organisms adapt to it, but he goes further in arguing that there will be continuing feedback between density-dependent selection and evolution. He credits the precedent of others, such as Chitty (1960) or Ford & Ford (1930), for contributing to the idea of a feedback between population dynamics, selection and evolution, but his contribution is original in the detail of the definition, marshalling of empirical support, development of models, and formal experimental tests of the concept (Pimentel *et al.* 1963; Pimentel 1968).

One empirical example cited by Pimentel was the extended study of the rabbit-myxomatosis interaction in Australia. The dampening cycles of rabbit abundance were attributed to a complex interaction between the density of rabbits (ecology), evolution of viral virulence, and evolution of resistance by the rabbits. Pimentel's experiments contrasted the population dynamics of a host-parasitoid interaction with treatments in which the host (housefly – *Musca domestica* or blowfly – *Phaenicia sericata*) either did or did not have the opportunity to evolve in response to a parasitic wasp (*Nasonia vitripennis*). He proved that the evolution of the host caused a dampening of the oscillations of abundance in the host and parasite and increased the odds of long-term persistence of both. He thus showed that contemporary evolution changes ecology. The

more general proposition that evolution happens on a similar time frame as ecology and that the two can interact in ways that can cause outcomes different from what is predicted without such interactions is fundamentally important because it holds the promise of improving the predictability of both processes.

With so auspicious a beginning, one would expect Pimentel's pioneering work to be followed by the immediate development of a subfield devoted to the study of the eco-evo dynamics. The idea instead languished for 40 years and we wonder why. We suspect it was because Pimentel was far ahead of his time in treating evolution as a contemporary process. Others had advocated these ideas, albeit from a different perspective than Pimentel's (Antonovics 1992; Endler 1992), yet somehow eco-evo dynamics did not emerge as an active area of inquiry, embraced by a wide variety of investigators, until after 2000.

Key contributions that brought Pimentel's ideas to life were new theory and experiments performed on a model ecosystem by Hairston, Ellner, and colleagues (Fussmann *et al.* 2000; Shertzer *et al.* 2002; Yoshida *et al.* 2003, 2004; Hairston *et al.* 2005). They studied predator-prey oscillations and characterised the differences in dynamics between a rotifer (*Brachionus calyciflorus* – predator) and single-celled algae (*Chlorella vulgaris* – prey) with Pimentel's approach of an evolving vs. non-evolving treatment. They show, as did Pimentel, that the contemporary evolution of the algae causes fundamental changes in the population cycling of both predator and prey, or that evolution changes ecological dynamics. A new challenge is to evaluate the importance of eco-evo dynamics in nature. We are engaged in such research in our respective study system (*Anolis* lizards in the Caribbean and guppies in Trinidad) (Travis *et al.* 2014; Schoener *et al.* 2017). Work by Duffy and colleagues (e.g. Duffy & Sivars-Becker 2007; Duffy *et al.* 2009, 2012) on the way population density and evolution interact to shape disease dynamics between a microcrustacean host (*Daphnia dentifer*) and its yeast parasite (*Metschnikowia bicuspidata*) is one very successful example of the importance of such interactions in natural lakes. The authors show that the evolution of host resistance ends epidemics and allows *Daphnia* populations to recover, but also that whether or not epidemics occur in the first place is a function of lake ecology. Lakes that naturally sustain high *Daphnia* population densities because of high nutrient levels and fewer predators are far more susceptible to epidemics than those with naturally low population densities.

Conservation biology

Conservation biologists have traditionally focused on ecological solutions to species endangerment. However, the realisation that populations can adapt rapidly to changing circumstances implies that populations may be able to adapt to the changed conditions that threaten them—indeed, the famous peppered moth case was an example of species adapting to the consequences of air pollution. Foundational texts in the field of conservation biology took a genetic approach, emphasising the importance of within-population genetic variation both to avoid the deleterious effects of inbreeding and

to preserve evolutionary potential for adaptation to changed circumstances (Soulé & Wilcox 1980; Frankel & Soulé 1981). Initial work focused on the effect of inbreeding, but the importance of adaptive potential has steadily increased. The concept of 'evolutionary rescue' was introduced in 1995 (Gomulkiewicz & Holt 1995). Volumes on the role of evolution in conservation biology appeared early in the twenty-first century and emphasised the significance of rapid evolution and the maintenance of evolutionary potential as a conservation priority (e.g. Ferrière *et al.* 2004; Carroll & Fox 2008). Laboratory studies now have tested hypotheses about what conditions maximise the likelihood of populations adapting to new conditions, in turn leading to prescriptions for conservation practitioners (Carlson *et al.* 2014; Whiteley *et al.* 2015). A topical case in point is global climate change. Many species are negatively affected, either directly or indirectly, by changing climate. A growing number of examples indicate that some species are adapting to new conditions (Muñoz & Moritz 2016). Moreover, new strategies are being proposed to increase the likelihood of adaptive evolution, such as transplanting individuals to new localities to introduce prospectively beneficial genetic variation into populations that otherwise might not be able to adapt quickly enough (Aitken & Bemmels 2016; Smith *et al.* 2017).

Invasive species

Prior to 1995, the explanations for the success of invasive species involved either properties possessed by species or the ecosystem before invasion, which we refer to as 'before hypotheses'. We now also entertain the possibility that success might be attributable to post-invasion evolution. Some dominant 'before' hypotheses are attributed to Darwin (1859). An organism-based hypothesis was that non-native genera will have greater odds of success as invaders because their ecological niches will differ more from native species, increasing the odds of finding a vacancy in the invaded ecosystem. An ecosystem-based hypothesis is 'enemy release'; invaded ecosystems may lack factors that controlled the abundance of the invader in its native homeland, be they predators, competitors, or pathogens. In 1995, Blossey & Notzold (1995) presented the 'evolution of increased competitive ability' (EICA) hypothesis: some plants may become successful as a consequence of how they evolve in response to enemy release. Resources that would otherwise be used for defense are reallocated instead to growth and reproduction. A large number of the 955 papers that cite Blossey and Notzold (Web of Science, 20 September 18) are empirical studies of evolution in invasive plant species. In 1996, Rhymer and Simberloff proposed a novel form of extinction – extinction by hybridisation – which was the genetic swamping of a rare native species by a more abundant invader. Among the 1253 citing articles (Web of Science, 20 September 18) is a growing list of native species endangered by such hybridisation with invaders. In 2000, Ellstrand & Schierenbeck (2000) proposed an evolutionary explanation for three common features of invasions: (1) only a small proportion of introduced species become problematic invaders, (2) often a considerable lag occurs between when invaders are introduced and when they become problematic

invaders, and (3) multiple introductions often precede such invasive outbreaks. They hypothesised that at least some successful invasions are the product of hybridisations, either between genetically distinct allopatric populations from the same species or between closely related but otherwise allopatric species, brought together by joint introductions into new locations. Among the 914 citations of this work (Web of Science 20 September 18) are many studies that present genetic evidence for the multiple origin of invasive species with subsequent hybridisation (e. g. Kolbe *et al.* 2004) and descriptions of new species derived from the hybridisation of two different invasive species (e.g. Heredia & Ellstrand 2014; Welles & Ellstrand 2016). The potential importance of evolution in invasive species began to appear in review papers in 2001 (e.g. Mooney & Cleland 2001; Sakai *et al.* 2001; Prentis *et al.* 2008).

Wildlife and fisheries biology

For most of their scientific lifetimes, fisheries and wildlife science were little influenced by evolutionary biology. Traditional research in these disciplines was purely ecological, revolving around the numerical dynamics of exploited populations (Beverton & Holt 1959) and how population numbers might be managed with interventions like habitat modification (Stoddard 1931), catch or bag limits, and, in fisheries, regulating gear types (Anderson 1998). The appreciation for rapid evolution entered these fields soon after the first discoveries that heavily exploited fish stocks were maturing at earlier ages and smaller sizes (Pauly 1979; Ricker 1980).

That selective harvesting could cause evolution was long appreciated (Allendorf & Hard 2009). Observations of widespread reductions in the age and size at maturity in harvested fish stocks (Trippel 1995) and decreases in body and ornament size in hunted populations of male ungulates (Festa-Bianchet 2014) over decadal periods suggested very rapid evolution in response to harvesting. Early arguments for rapid evolution used experimental demonstrations like those in guppies as 'proof of concept' that rapid life-history evolution was possible (Rijnsdorp 1993). Subsequent theory (Law & Grey 1989) and experiments on model systems (Conover & Munch 2002) demonstrated the plausibility of the idea. The accelerating reports of rapid evolution in natural systems bolstered the notion that hunting and fishing pressures were creating evolutionary changes.

There is no doubt that there have been rapid phenotypic changes in harvested populations. How much of this change reflects rapid evolution remains controversial (Hilborn 2006; Traill *et al.* 2014). On the one hand, there has been an explosion of research on the consequences of fisheries induced evolution (Heino *et al.* 2015); the changes in phenotype distribution, regardless of cause, have far-reaching consequences (Travis & Lotterhos 2013). On the other, there are no demonstrations of genetically based changes in fishery stocks (Heino *et al.* 2015), although harvesting has been shown to decrease levels of neutral genetic variation (Allendorf *et al.* 2008). With respect to trophy hunting, not all exploited populations display significant phenotype changes (Buntgen *et al.* 2018) and the single compelling quantitative genetic study in

the literature shows a lower rate of genetic change than phenotypic change (Pigeon *et al.* 2016). A recent theoretical study (Coulson *et al.* 2018) suggested that observed rates of phenotypic change in male ornaments are 1–2 orders of magnitude higher than would be possible with realistic quantitative genetic parameters. While rapid evolution may not be the sole driver of phenotypic change, the possibility has changed the direction of research.

Pest management

The evolution of resistance to pesticides and herbicides may be the paradigmatic example of rapid evolution. Over 550 species of arthropods have evolved resistance to pesticides, most discovered since 1960, and over 400 species of weeds have evolved resistance to herbicides, most discovered since 1970 (Gould *et al.* 2018). Since 1995, over 40 species of weeds have evolved resistance to glyphosate alone (Gould *et al.* 2018). The early dates of these findings carry an interesting message – an appreciation for contemporary evolution in pest management long predates its embrace by other disciplines. We suspect this work had limited impact on other disciplines because the nature of selection was considered to be unnaturally strong, making evolution unnaturally fast.

Today, there is a growing movement to use rapid evolution to counter rapid evolution. In these cases, selfish genetic elements would be used to rapidly spread desirable, genetically engineered traits through a natural population (Kidwell & Ribeiro 1992; Burt 2003). Desirable traits include genes that counteract resistance genes for herbicides and pesticides, lethal genes that would dramatically reduce population sizes of pests or, in the case of mosquitoes and other arthropod disease vectors, genes that interfere with pathogen acquisition or transmission (Esvelt *et al.* 2014). Laboratory experiments have shown that genes edited with CRISPR/cas 9 can be rapidly incorporated into populations with vectors that create a meiotic drive in which the desired gene is transmitted from parent to offspring at a much higher frequency than expected from Mendelian segregation (Gantz *et al.* 2015; Hammond *et al.* 2016).

Deploying rapid evolution against rapid evolution has its risks. The mode of action of the gene editor might provoke mutations to resist the vector carrying the engineered gene (KaramiNejadRanjbar *et al.* 2018). The genetic construct, meaning the vector and its associated engineered gene, might invade non-target populations and spread too rapidly to be controlled (Noble *et al.* 2018). More sophisticated methods are being developed to address these concerns (Burt & Dereced 2018) and the very near future may see rapid evolution deployed for a wide range of human benefits (National Academies of Science, Engineering, and Medicine 2016).

Ecosystems ecology

Ecosystem ecology, with its emphasis on mass-balance relations, stoichiometry, and energy fluxes, developed with essentially no influence from evolutionary biology. Theory for the evolution of ecosystems, defined as systematic changes in the ratio of productivity of biomass, the rate of nutrient cycling,

and the increased efficiency of energy fluxes (Odum 1969, 1983), was fundamentally an argument for group selection among ecosystems, with no role for natural selection among individuals.

The introduction of evolutionary biology into ecosystem ecology followed directly from the discovery of contemporary evolution. Whitham *et al.* (2003) were among the first to argue that genetic differences among individuals can affect ecosystem processes. Subsequent empirical work in many different systems demonstrated that genetic variation within a species can exert very different effects on ecosystem processes, whether that variation was based on individual genotypic differences (LeRoy *et al.* 2007; Compson *et al.* 2016, 2018) or differences between individuals from locally adapted populations (Post *et al.* 2008; Bassar *et al.* 2010, 2012; Urban 2013; El-Sabaawi *et al.* 2015; Rudman *et al.* 2015; Fryxell & Palkovacs 2017; Simon *et al.* 2017).

Given the long path from genetic variation to ecosystem process, it is fair to wonder how the effects of genetic and phenotypic variation compare with those of other drivers of ecosystem dynamics. A recent meta-analysis has shown that the effects of phenotypic variation on ecological parameters like population density, community composition, and ecosystem processes are, generally, at least as strong as replacing one species with another (Des Roches *et al.* 2018).

Experimental studies of guppies adapted to different fish communities yield more precise comparisons of the differences in ecosystem impact caused by fish adapted to different environments. The ecosystem impacts of guppies adapted to diverse, predator rich fish communities vs. guppies adapted to low predation risk headwater streams, where only one other species of fish was present, were assessed in artificial streams. Guppies from low predation risk communities reduced algal biomass to a greater degree, invertebrate biomass to a lesser degree and increased gross primary productivity to a greater degree than guppies adapted to communities where the risk of predation is high. The effects of exchanging ecotypes were at least as large as the effects of doubling population density (Bassar *et al.* 2010), a value chosen because the density of guppies is two times greater in low predation risk localities. In another experiment, the effects of exchanging a high predation risk guppy for a low predation risk guppy were compared to the effects of a four-fold variation in light level (El-Sabaawi *et al.* 2015), so chosen because of the tendency towards much higher light levels in high predation localities because they tend to be larger, wider rivers. The ecotypic effects were as strong or stronger than the effects of light level variation for leaf litter decomposition rates, area-specific gross primary productivity, community respiration, net daily metabolism, total nitrogen flux, and nitrogen recycling rate, while the effects of variation in light level were stronger for mass-specific gross primary productivity, nitrogen excretion rates, and total phosphorus recycling rates. Many of these results have now been replicated in natural streams (Simon *et al.* 2017).

If the effects of genetic variation within species are so large, why have they not always occupied the mainstream of ecosystem science? Ecosystem ecology has focused on nutrient fluxes through functional compartments like producers or primary consumers. Even when individual species are included as

individual compartments, the emphasis has been on the biomass in each compartment, not on the individuals that comprise that biomass. The differences we see among individuals adapted to different environments include changes in physiology (digestive efficiency, metabolic rate), growth rate, and body size. The scaling of variables like consumption rates or metabolic rates on body size means that differences in size distribution in combination with differences in metabolism can cause very different cumulative rates from the same biomass. Representing species by biomass alone does not capture all of these differences among populations because small adaptive changes in combinations of features – e.g. body size, size-specific metabolic rate – can accumulate to large changes at the population level. The available studies of the ecosystem consequences of contemporary evolution tell us that the pace of change is too fast and magnitude of change is too large to neglect if one is to accurately model the ecosystem.

There is a caveat to our argument. Much of the empirical work we have reviewed is based on comparisons among individuals from different locally adapted populations. A role for contemporary evolution is implied because, in most cases, the populations studied are known to have diverged rapidly or at least have been shown capable of rapid divergence. It remains to be directly shown that ecosystem processes change in concert with the evolution of species in those ecosystems.

Two studies, one empirical and one theoretical, provide more direct support for contemporary evolution's importance for ecosystems. On the empirical side, individuals from different populations of the tree *Metrosideros polymorpha*, which have diverged from one another on lava flows in Hawaii since 1858, have different growth patterns with very different effects on soil carbon levels and carbon turnover rates (Mueller *et al.* 2017). On the theoretical side, a model of stoichiometric ratios in a phytoplankton-zooplankton interaction showed that allowing investment patterns in nitrogen and phosphorus to evolve on the same time scale as biomass dynamics produced qualitative changes in the nutrient fluxes when compared to the dynamics in the absence of evolution (Branco *et al.* 2018). This result is similar to the results from models of species interactions that show how contemporary evolution can produce qualitative changes in numerical dynamics and stability regimes (Abrams & Matsuda 1997; Doebeli 1997; Hiltunen *et al.* 2014).

Evolution and the genetics of adaptation

The reality of contemporary evolution can contribute to our ability to answer two big questions in evolutionary biology: 'What is the genetic basis of adaptive evolution?' and 'What is the source of the genetic variation that sustains it?' In a recent perspective entitled 'Can population genetics adapt to rapid evolution?' Messer *et al.* (2016) review how the discovery of rapid evolution has provoked a new look at traditional population genetics. Their reference point is the 'standard model' of population genetics, which applies well to genomic data for large organisms, like humans. It bears a close resemblance to Haldane's view of the world – adaptive allelic replacements are rare and unlikely to be seen in action, deleterious mutations are held in check by purifying selection, most genetic

variation should have minor effects on fitness and genetic drift is the dominant force in evolution. This perspective is not easily reconciled with rapid, contemporary evolution, which requires that the necessary adaptive variation be present at the outset (Barrett & Schluter 2008).

Understanding the maintenance of adaptive genetic variation is one of evolutionary biology's greatest and most enduring challenges (Charlesworth 2015). Messer *et al.* (2016) argue that contemporary evolution in temporally and spatially fluctuating environments offers a robust mechanism for maintaining adaptive variation. To be sure, temporal and spatial variation in fitness among genotypes have long been considered as possible mechanisms for maintaining adaptive variation but, as Messer *et al.* (2016) point out, not the ones that were particularly robust. Messer *et al.* (2016) review how fluctuating environments and strong selection can produce a genetic storage effect, in which the relative fitness of alternative genotypes varies over time and space, sometimes in combination with a life stage (e.g. dormant eggs or seeds) resistant to such fluctuations. Under a broad range of conditions, this storage effect creates negative frequency-dependent selection that can maintain variation, even in a haploid system, in which maintenance of variation under traditional models of heterogeneous environments was considered unlikely (Gulisija & Kim 2015; Dean *et al.* 2017). Under this scenario, populations will have a storehouse of adaptive genetic variation that can respond immediately to altered conditions and new selection pressures.

Reid *et al.*'s (2016) analysis of adaptation by the Atlantic killifish (*Fundulus heteroclitus*) to toxic pollutants in urban estuaries exemplifies the role of such standing variation in rapid evolution. It also highlights the virtues of genomic approaches for identifying the likely genetic mechanisms that underlie adaptation.

Empirical studies of contemporary evolution reveal two other sources of genetic variation, one predicted and one novel. One is derived from the 40 years of research on the medium ground finch (*Geospiza fortis*) on the island of Daphne Major. The first recorded episode of selection was caused by a drought in which the population shrank from > 1400 to 200 individuals. This decline also generated a 6:1 (male:female) sex ratio because selection favoured larger individuals and males are larger than females (Boag & Grant 1981). The combination of intense selection with small effective population sizes should have purged genetic variation, yet the finches' ability to evolve persisted for the 40-year study period. One reason for this persistence appears to have been the occasional injection of new genetic variation via interspecific hybridisations with *Geospiza scandens* and *Geospiza fuliginosa*. In one sample calculation, hybridisation increased the heritable variation in beak traits by 8–11% and of size-related traits by 19–40% (Table 9.1, p. 171, in Grant & Grant 2014). The role of hybridisation in evolution is well known (e.g. Arnold 1992), but from the historical perspective of morphological and genetic studies of extant populations/species. What is new is seeing the process in action and in association with estimates of the frequency of hybridisation and a quantification of the magnitude of the effect.

A novel and unpredicted source of variation was revealed by the study of repeated adaptation to freshwater

environments by marine sticklebacks. Some of the genetic variation associated with such adaptation is represented by ancient alleles that evolved in the distant past, likely in response to similar episodes of sticklebacks invading and adapting to freshwater environments caused by the repeated ebbing and waning of glaciers. Some of these adaptive alleles are segregating in marine populations and were repeatedly recruited when marine ancestors invaded new freshwater environments created by retreating glaciers. This genetic variation is apparently sustained by the frequent contact and interbreeding between marine and freshwater populations.

This phenomenon was originally discovered in natural freshwater populations created by the most recent glacial retreat (Colosimo *et al.* 2005), but has now been replicated in ponds on islands created by the Great Alaska Earthquake of 1964 (Lescak *et al.* 2015). This discovery raises the possibility that rapid evolution can be fueled by a genetic memory of adaptations past. The scenario at play here – cyclic environmental changes that cause repeated retreat from and recolonisation of a given habitat type by a large number of founders – may seem idiosyncratic but probably applies more widely. All that is required is repeated patterns of change in the environment that impose strong selection and a metapopulation structure that can retain some of the genetic variation among populations adapted to different environments. 'Environment' can be defined by physical factors, like fresh vs. salt water, but can also be defined by biotic factors, such as the presence or absence of species that engage in a strong interaction with the target species.

The divide between microevolution and macroevolution is most often recognised by a distinction between genetic changes within populations and speciation. In his essay, Gould acknowledged the importance of natural selection as a facet of microevolution, but asserted that the pace of natural selection is incompatible with macroevolution. Recent studies show that even this bridge can be crossed by contemporary, adaptive evolution. One example is the origin of the big bird lineage on Daphne Major (Grant & Grant 2014). It began with the arrival of a large male *fortis-scandens* hybrid from nearby Santa Cruz Island. He mated with three *G. fortis* females and spawned a line of descendants larger than the resident *G. fortis* and with distinct vocalisations. They have bred only among themselves for five generations. They occupy the enlarged morphological space between *G. fortis* and *Geospiza magnirostris* induced by the severe drought of 2004. While this example may stand alone as a truly contemporary origin of a 'species in the making,' meaning one observed from the start in a single study, there are many others that detail how natural selection can lead populations down the path to speciation on a time scale of decades to centuries, including sticklebacks (Lescak *et al.* 2015), the mosquitos of the London Underground (*Culex pipiens*) (Byrne & Nichols 1999), or host races of the fruitfly *Rhagoletis pomonella* (Feder *et al.* 2003a,b). Gould's 'visibly irrelevant' is relevant after all.

CONCLUSIONS

Why does the change in our perception of evolution from a historical to contemporary process matter? The general reason

is that treating evolution as a contemporary process can fundamentally change how we approach any topic in ecology and evolution. It causes us to recast old questions, changes the answers to those questions and enables us to ask new questions that were otherwise inconceivable. There is more to recognising this paradigm shift than simply acknowledging a historical event – it can inspire us to identify areas of life sciences where the shift is yet to be realised and hence identify new research questions and opportunities.

Incorporating contemporary evolution into our thinking about the interaction between ecology and evolution holds the promise of increasing the predictability of both ecology and evolution through the incorporation of the interaction between the two. The shift to a higher gear in conservation biology contributed to the development of new concepts, like evolutionary rescue, and new strategies for helping organisms adapt to a changing environment. In invasive species research, prior to the gear shift we only had ‘before’ hypotheses, which postulated that properties of the organism or environment that existed before the invasion are what determine success. Now we have new ‘after’ hypotheses that postulate that the successful invaders are the product of post-invasion evolution.

Adding evolutionary dynamics to fisheries and wildlife management gives us a new understanding of the consequences of exploiting natural populations. In addition to altering the population dynamics of targeted species, we act as agents of selection, causing exploited populations to evolve traits like smaller body size, sometimes to the detriment of their value as a source of protein. Evolution can slow the recovery in response to reduced exploitation. We can develop new strategies of exploitation and management that minimise the evolutionary impact of exploitation plus develop better strategies for engineering the recovery of exploited populations.

Ecosystems ecology perceived the world as being like a jigsaw puzzle comprised of rigid pieces. Each piece was a compartment containing biomass and transferring energy and nutrients to other compartments. Adding contemporary evolution means that all pieces can change shape. The evolution of one species has the same effects as a change in the shape of a puzzle piece, which is that others around it will change in response. The other pieces may be other species, but they also include the features of the physical environment that link the biotic elements together. With changes in how the pieces fit together come changes in nutrient and energy fluxes and, perhaps, a change in the entire picture the puzzle depicts.

The influence of contemporary evolution is yet to be fully realised. To illustrate its potential, we digress a moment to consider the argument Lenski & Travisano (1994) presented for the virtues of their replicated experimental studies of evolution in *Escherichia coli* bacteria. They compared their study with an imaginary fossil record in which each generation of each replicate population can be brought back to life, enabling one to fully assess the ancestors, the path through which descendants evolved from ancestors, and even compare ancestors and descendants side by side. Being able to do so means being able to develop a far better understanding of how and why the target organism evolved than would be the case if all you had was the fossil record or a comparison of two divergent descendants.

While the virtues of contemporary studies of evolution fall short of these ideals, they capture some of the dynamics in ways that improve our ability to understand why organisms are the way they are. Consider the traditional approach of studying evolution by comparing closely related species. Comparisons among species yield clues about how and why each diverged from a common ancestor, but we miss what the common ancestor was like and all of the intermediate steps between the ancestor and descendants. Such a retrospective view of evolution can only reveal correlations from which we make inferences about why traits evolved.

We face a similar limitation when we compare locally adapted populations of a single species because they are the end products of some unseen process. When populations adapt to different conditions, especially ones with different biotic interactions, they can change their impact on their surrounding community and ecosystem. This means that when we compare the ecological attributes of populations adapted to different environments, what we see may be a confounding of the causes of local adaptation with the consequences of local adaptation. For example, our guppies adapted to headwater streams live in environments that have lower invertebrate abundance than the high predation communities downstream. This difference suggests that headwater streams naturally have fewer invertebrates for guppies to feed on. Guppies from these environments include more algae and abundance in their diets than do guppies downstream, which seems like a natural response to lower invertebrate abundance. However, our experimental studies show that the invertebrate abundance was not lower before the arrival of guppies; as guppies attained higher population densities in response to the reduced risk of predation, they depleted the environment of invertebrates and expanded their diet. Thus, lower invertebrate abundance is an effect of guppy adaptation, not a cause of it.

We illustrate the virtue of a contemporary perspective with an example from evolutionary developmental biology. Alex Badyaev is using contemporary evolution to address alternative hypotheses for the evolution of beak morphology in house finches (Badyaev 2010, 2011). Bird beaks pose the dilemma of being developmentally complex, potentially very different among closely related species, and precisely adapted to different diets. The first hypothesis is that beaks are conventional, polygenic traits that evolve continuously. The alternative is that they are traits whose development is modular, with early development consisting of highly conserved modules common to all vertebrate skulls and later conserved modules more specific to birds. The details of beak architecture are shaped by a small number of regulatory genes acting at different stages of development. The highly conserved nature of the modules suggests they are not directly affected by selection. Phenotypic evolution can instead be attained by changes in the patterns of expression of individual genes that act at different stages in development and by a rearrangement of conserved modules.

How can we discriminate between these two different types of evolution? Badyaev has followed the evolution of beak morphology of house finches as they extended their geographic range through Montana into valleys separated by

high mountain ranges. His long-term data include information on the age of each population and the change in beak morphology each generation as finches adapted to different food sources. He has replicate populations of different ages represented by the progressive colonisation of different valleys. He can now exploit the virtue of replication, archived tissue samples, and populations in different stages of adaptation to discriminate among these alternatives because he can evaluate the joint dynamics of changes in beak morphology and gene expression.

Not all systems offer replicated populations at different stages of contemporary evolution. In these cases, experiments can be deployed to draw the same inferences. One example is Barrett *et al.*'s (2008) experimental study of evolution in the stickleback (*Gasterosteus aculeatus*). An allelic substitution at the Ectodysplasin locus is associated with the reduction in lateral plates seen in freshwater populations relative to their marine ancestors, suggesting a direct causal relationship. Experimental evolution revealed instead selection against the allele for low plate count early in development, before plates formed, in populations adapting to freshwater environments. The reversal of fates of carriers of the low-plate allele, from selection against the allele early in development to selection in favour of the allele later in development, means either that the gene has pleiotropic effects or that other, closely linked genes play a critical role in shaping the evolution of lateral plates and possibly other aspects of the phenotype. Only a dynamic assessment of evolution could have revealed this complexity.

A second example is the study of joint selection on behaviour and morphology in the lizard *Anolis sagrei* by Lapidra *et al.* (2018). While theirs is an experimental episode of selection, rather than evolution, it reveals the virtue of looking at dynamics rather than end products. They were interested in whether behaviour can either accelerate or inhibit morphological evolution. Neither was true. Their experiment showed that selection acted independently on behaviour and morphology. Had they only been able to compare two related descendants adapted to different environments, they would see correlated evolution of behaviour and morphology. Such correlations have been interpreted by others as evidence of causation, but the details of Lapidra *et al.*'s results show that behaviour and morphology are independent traits that make independent contributions to survival. This would be a case in which correlation did not reveal causation.

More generally, studies of contemporary evolution have filled the literature with species, traits and details on the populations that differ in those traits for known reasons. Any investigator can gain entry by capitalising on pre-existing studies of contemporary evolution to design experiments that incorporate evolutionary dynamics and, like those of Badyaev, Barrett and Schluter, and Lapidra *et al.*, recapture the trajectory of selection and evolution.

Evolution has traditionally been viewed as a historical phenomenon. This view emerged naturally from the presumption that evolution unfolds too slowly to be observed in real time. History is studied retrospectively; we attempt to recreate the past by examining its artifacts and making observations about the present. Contemporary evolution frees us from the constraints of retrospection. The ability to observe evolution in

action or study it experimentally can be exploited to test not only hypotheses about how individual traits have evolved, but also about the trade-offs among traits that create constraints on adaptation. Indeed, we can also learn which trade-offs really are constraints and which are the products of adaptive changes in genetic covariances. Bringing this perspective to a variety of ecological areas offers the opportunity to accelerate the progress of both evolution and ecology.

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AUTHOR CONTRIBUTIONS

DR conceived of the manuscript. All three authors contributed to the writing of the manuscript.

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