# Eco-Evolutionary Dynamics in Cold Blood

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# SYMPOSIUM PROCEEDINGS: ECO-EVOLUTIONARY DYNAMICS IN COLD BLOOD

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# Eco-Evolutionary Dynamics in Cold Blood

Andrew P. Hendry[1,2] and David M. Green[1]

**Eco-evolutionary dynamics occur when ecological change influences evolutionary change (eco-to-evo) and when evolutionary change influences ecological change (evo-to-eco), both on contemporary time scales. Fishes, amphibians, and reptiles have played important roles as study animals in the empirical study and exploration of these dynamics. We suggest that this primacy stems in part from the sweet-spot that many species of fishes, amphibians, and reptiles occupy on the continuum from experimental convenience to ecological importance, as well as on the particular organismal properties that they share, including indeterminate growth and ectothermy. Yet our overall understanding of eco-evolutionary dynamics remains very limited. In the hope of reducing this information gap, the present symposium proceedings include 12 contributions that speak directly to three critical topics in eco-evolutionary dynamics: the role of human influences, constraints and alternatives, and the context dependence of eco-evolutionary dynamics *in nature*.**

THE study of eco-evolutionary dynamics seeks to integrate ecological and evolutionary patterns and processes to explain how ecological changes lead to evolutionary changes (eco-to-evo) and how those evolutionary changes then feed back to have ecological consequences (evo-to-eco). Although this sequence of effects is rather obvious on long time scales, it is exciting to now consider how these dynamics might play out on “ecological” or “contemporary” time scales ranging from years and decades to centuries (Fussmann et al., 2007; Bailey et al., 2009; Matthews et al., 2011; Strauss, 2014; Hendry, 2017). Fishes, amphibians, and reptiles have figured prominently in the empirical development of this field, including studies of contemporary evolution in response to environmental change and studies of how contemporary evolution influences population dynamics, community structure, and ecosystem function (Post and Palkovacs, 2009; Schoener, 2011; El-Sabaawi, this volume, 2017). What more can fishes, amphibians, and reptiles tell us about eco-evolutionary dynamics? The present symposium proceedings were designed to bring together relevant research on these animals that addresses specific topics of pressing concern in the field.

## ECO-EVOLUTIONARY DYNAMICS IN COLD BLOOD

Some of the earliest eco-to-evo studies confirming that genetically based phenotypic changes in vertebrates can evolve over short time scales came from fishes, including mosquitofish, *Gambusia affinis* (Stearns, 1983; Stockwell and Weeks, 1999), guppies, *Poecilia reticulata* (Endler, 1980; Reznick and Bryga, 1987), and Pacific salmon, genus *Oncorhynchus* (Hendry et al., 1998; Kinnison et al., 1998). Thereafter, similar outcomes were reported for dozens of other fish species, as well as for amphibians (Skelly and Friedenburg, 2000; Räsänen et al., 2003) and reptiles (Sinervo et al., 2000; Stuart et al., 2014). More recently studies have even documented specific genomic changes associated with contemporary evolution, such as in Atlantic killifish, *Fundulus heteroclitus*, adapting to pollution (Reid et al., 2016).

Perhaps the most obvious level of evo-to-eco effects is that contemporary adaptation of populations to changing conditions should enhance their evolutionary fitness and thereby influence their population dynamics (Kinnison and Hairston, 2007). An example from fishes is that the evolution of Chinook Salmon, *Oncorhynchus tshawytscha*, to different migration distances following their introduction to New Zealand has had large effects on their vital rates of survival and fecundity (Kinnison et al., 2008). In amphibians, resistance to the pathogenic chytrid fungus, *Batrachochytrium dendrobatidis*, appears to be evolving in affected populations (Savage and Zamudio, 2016), which must surely improve population growth rates. And in reptiles, short-term evolutionary cycles in lizard life histories shape population dynamics and feed back to influence evolutionary cycles (Sinervo et al., 2000).

Another level of evo-to-eco effects is that contemporary evolution in ecologically important species can influence community structure. These effects can be direct, such as when trait change influences per capita effects of the species, or indirect, such as when trait change influences population dynamics of the species (as above), which then influences community structure (Hendry, 2017). Some of the best examples of direct effects include how prey communities are influenced by the evolution of trophic traits in fishes, including stickleback, *Gasterosteus aculeatus* (Harmon et al., 2009; Matthews et al., 2016), Alewife, *Alosa pseudoharengus* (Palkovacs and Post, 2009), whitefish, genus *Coregonus* (Lundsgaard-Hansen et al., 2014), and guppies (Palkovacs et

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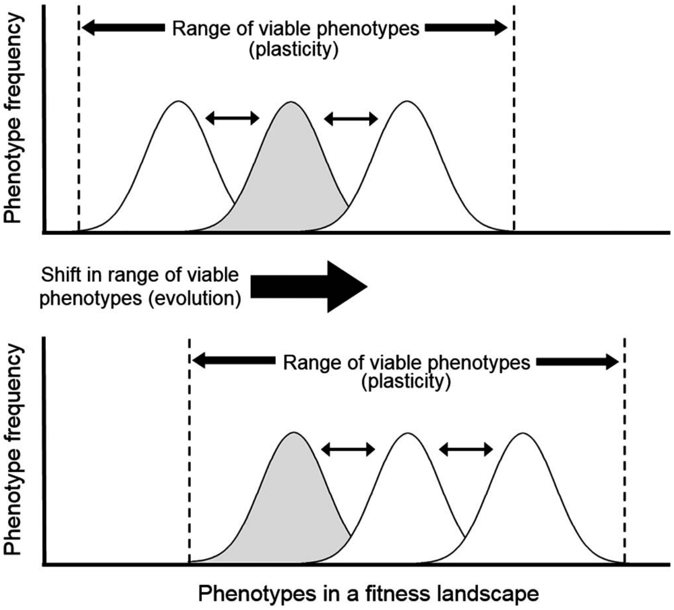


**Fig. 1.** An example of phenotypic plasticity in the context of evolutionary change. In the top panel, a population may express differing ranges of phenotypes depending on different environmental conditions. The distributions of these phenotypes (normal curves) vary but remain within the limits (dashed lines) of what is genetically possible. In the lower panel, an evolutionary change in the genetic structure of the population has shifted the range of possible phenotypes along the fitness landscape. The evolution of the population may be masked by phenotypic plasticity and appear to be unchanged (gray-filled curves) depending on conditions.

al., 2009; Bassar et al., 2010). Similar results have been found for Spotted Salamanders, *Ambystoma maculatum*, from nearby ponds with or without predatory Marbled Salamanders, *Ambystoma opacum* (Urban, 2013). Also, invasive Cane Toads, *Rhinella marina*, in Australia are evolving reduced levels of toxicity (Phillips and Shine, 2005), which surely decrease their hitherto massively negative effects on naïve native predators. Indirect effects acting through population dynamics are less well studied, although Bassar et al. (2010) showed that the densities of different guppy ecotypes, which are partly evolutionarily determined, influence aquatic community structure.

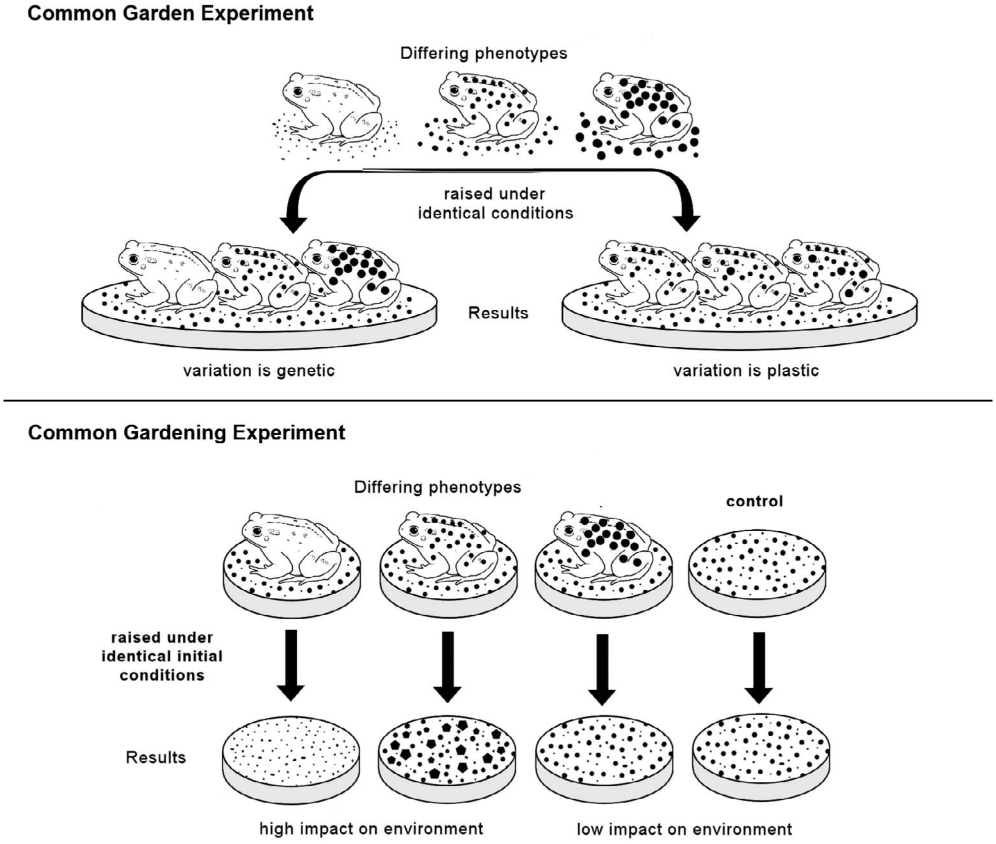
A final level of evo-to-eco effects is that the evolution of ecologically important species could influence ecosystem function. Again, these effects can be direct (per capita) or indirect, such as through effects on population dynamics or community structure (Hendry, 2017). Some direct effects already demonstrated for fishes included the eco-to-evo influence of stickleback on water clarity (Harmon et al., 2009; Matthews et al., 2016), Alewife on phytoplankton abundance (Weis and Post, 2013), whitefish on dissolved organic carbon (Lundsgaard-Hansen et al., 2014), and guppies on periphyton abundance (Palkovacs et al., 2009; Bassar et al., 2010). Nearly all of this work comes from controlled mesocosms; yet, also, selection in nature has been shown to shape salmon-derived nutrient fluxes between lake, stream, and riparian areas (Carlson et al., 2011). In addition, the productivity of fisheries harvest, and the rates of recovery following harvest, are expected to be influenced by evolution in response to the fishery (Dunlop et al., 2015).

In all of these examples, eco-evolutionary dynamics are driven by interactions between environmental features and organismal *phenotypes*. Hence, phenotypes, rather than genotypes, are fundamental to understanding the interface between ecology and evolution. Yet, because phenotypes are influenced by both genetic and plastic effects, the potential exists for plastic phenotypic changes (and ecological consequences) to masquerade as genetic effects and for genetically based phenotypic changes (and ecological consequences) to masquerade as plastic effects (Fig. 1). Indeed, many of the above-cited studies of fish influencing aquatic communities and ecosystems used wild-caught fish, and so cannot elucidate what specific effects reflect contemporary evolution (e.g., Harmon et al., 2009; Palkovacs and Post, 2009; Palkovacs et al., 2009; Bassar et al., 2010). To separate genetic versus plastic effects, studies of eco-evolutionary dynamics can employ two types of experiments (Fig. 2), as seen in many of the papers in these symposium proceedings. First, "common garden experiments" take different phenotypes and raise them under identical conditions (sometimes several different such conditions) to tease out plastic and genetic contributions to trait differences. Some examples in this issue are the studies presented by Fitzpatrick et al. (this volume, 2017), Brady and Goedert (this volume, 2017), and Gordon et al. (this volume, 2017). Second, "common gardening experiments" (Matthews et al., 2011) take different phenotypes and place them under identical starting environmental conditions, typically in mesocosms, to measure ecological effects. Experiments of this type are represented in this issue by Fryxell and Palkovacs (this volume, 2017) and Tuckett et al. (this volume, 2017). A study in this issue combining common garden and common gardening approaches is Lundsgaard-Hansen et al. (this volume, 2017).

## WHY FISHES, AMPHIBIANS, AND REPTILES?

Why have certain species of fishes, amphibians, and reptiles been so important in shaping our understanding of eco-evolutionary dynamics? We suggest that the reason partly stems from a "sweet spot" or "Goldilocks position" on the continuum from convenience to importance. For instance, relative to many other vertebrates (apart from some small mammals), numerous species of fishes, amphibians, and reptiles have rather short generation times, are relatively easy to handle in the laboratory, and have ecological effects that can be reasonably approximated in mesocosm settings or studied in the field. Relative to invertebrates and microbes, on the other hand, the per capita effects of individuals are more likely to be large and observable for a number of fishes, amphibians, and reptiles. Relative to plants … well, perhaps animals are simply more interesting to some investigators. Of course, fishes, amphibians, and reptiles are not perfect subjects for the reverse reasons, such as longer generation times than invertebrates and microbes, and smaller per capita effects than at least some birds and mammals.

We further suggest that fishes, amphibians, and reptiles also share additional features that make them particularly interesting from the perspective of eco-evolutionary dynamics. Many fishes, amphibians, and reptiles have indeterminate growth and continue to increase in size with age, although at a decelerating rate. Body size is, of course, a key organismal trait influencing interactions with the environment. From an eco-to-evo perspective, body size is sometimes under strong selection (Kingsolver and Diamond, 2011) and can evolve very rapidly (Gotanda et al., 2015). Yet body size is



Common Garden Experiment

Common Gardening Experiment

**Fig. 2.** Common garden vs. common gardening experiments in eco-evolutionary dynamics. A common garden experiment (top panel) raises different phenotypes, usually taken from nature, under identical conditions to test if the variation is due to genetic differences or due to phenotypic plasticity. A common gardening experiment (bottom panel) places different phenotypes (which can be from a common garden experiment) into identical environments and then monitors how the environment changes.

also a highly plastic trait that is readily influenced by environmental conditions (Yom-Tov and Geffen, 2011; Green and Middleton, 2013). From an evo-to-eco perspective, body size is known to influence a great diversity of ecological processes (Peters, 1986). Hence, changes in the body size of fishes, amphibians, or reptiles—whether as a consequence of changes in age-at-maturity or size-at-age—can be dramatic and can have large ecological effects. The same effects should be much weaker for similar-sized birds or mammals with more determinate growth.

Fishes, amphibians, and reptiles are, with only minor exceptions, ectotherms; and they therefore expend much less energy on maintenance, and consume much less food, than do endothermic birds and mammals. As a result, we might expect the per capita foraging-related impacts of fishes, amphibians, and reptiles to be less than those of birds and mammals, which is interesting given that most studies of fishes have thus far focused on per capita effects. We suggest that the ecological effects of contemporary evolution in a fish, amphibian, or reptile would accrue mainly because these species can sometimes be very abundant. Hence, per capita effects in such species might only be evident at high densities. By contrast, the evolution of foraging traits in birds and mammals might have larger per capita effects at low densities.

## MAJOR THEMES IN ECO-EVOLUTIONARY RESEARCH

The papers in these symposium proceedings employ fishes, amphibians, and reptiles to explore issues in three major areas of present-day research on eco-evolutionary dynamics: human influences, constraints and limits, and dynamics in nature.

***Human influences.***—Humans influence the environment in many ways, and many of those influences can cause evolutionary changes in affected organisms (Palumbi, 2002; Hendry et al., 2008, 2017). Particularly obvious examples include hunting and harvesting (Kuparinen and Festa-Bianchet, 2017), invasive species (Colautti et al., 2017), pollution (Reid et al., 2016; Hamilton et al., 2017), climate change (Merilä and Hendry, 2014), urbanization (Alberti et al., 2017), and habitat fragmentation (Cheptou et al., 2017). In each of these contexts, evolution of the affected organisms might then influence their population dynamics, the structure of their communities, and the functioning of their ecosystems (Hendry et al., 2017). Given that humans derive many ecosystem "services" (both benefits and costs) from these functions, human influences on evolution can feed back to modify the services humans derive from nature (Faith et al., 2010; Rudman et al., 2017). Although human influences on evolution have been well studied, the ecological consequences of that evolution have received far less attention. The present symposium proceedings include several studies working toward that goal.

Human-induced environmental change is altering—usually increasing—the temperatures experienced by many organisms, which can generate contemporary evolution of thermal tolerance and phenology in various fishes, amphibians, and reptiles (Crozier and Hutchings, 2014; Urban et al., 2014). That adaptation will presumably shape the ecological effects of the evolving organisms, often through population dynamic changes. Fryxell and Palkovacs (this volume, 2017) address this question through a common gardening experiment with mesocosms designed to test for differential ecological effects of mosquitofish populations adapted to two different temperature regimes. The two populations did have differential effects on their mesocosm environments, but

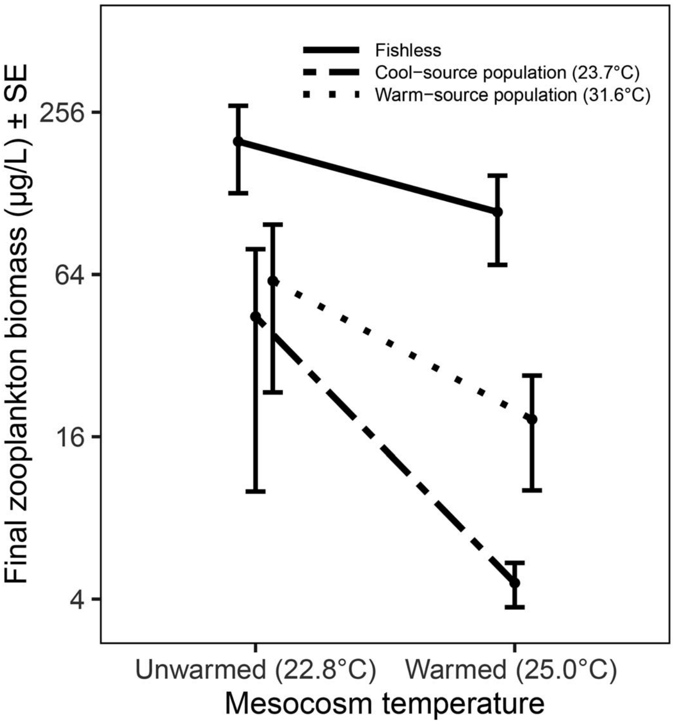


**Fig. 3.** Fryxell and Palkovacs (this volume, 2017) used experimental ponds to test whether thermal context influenced predator intra-specific effects. Warming (warmed relative to unwarmed mesocosms) enhanced top-down fish effects on zooplankton biomass and strengthened ecological effects differences between two recently (<100 years) diverged source populations of mosquitofish. The cool-source population reduced zooplankton biomass more than did the warm-source population in warmed, but not in unwarmed, mesocosms.

only in one of two temperature treatments and only for zooplankton (Fig. 3). Although more work needs to be done, this study suggests that temperature adaptation might not be a critical driver of eco-evolutionary effects in at least some study systems. One possible reason is that the study sought to equalize densities in the mesoscosms, whereas the community and ecosystem effects of adaptation might instead act indirectly through effects on population dynamics (Hendry, 2017).

Climate change is expected to also alter the distributions of various temperature-limited species, especially by expanding high latitude range margins and contracting low latitude range margins (Urban et al., 2016). Expected outcomes are altered patterns of species co-occurrence and altered community compositions. These community changes should generate new species interactions that alter natural selection and thereby shape new evolutionary trajectories and, presumably, cascading ecological effects. In New England, North America, the apex aquatic predator in small ponds, the Marbled Salamander, is expanding northward and encountering populations of Wood Frogs, *Lithobates sylvaticus*, that have long evolved without the salamanders. Urban et al. (this volume, 2017) demonstrate that Wood Frog populations whose tadpoles experience Marbled Salamander predation show local adaptation of plasticity under high risk of predation (Fig. 4). In this system, Wood Frogs seem capable of quickly adapting to the invasive predator, even on very small spatial scales, which should help maintain their existence, abundance, and ecological effects even as climate change modifies patterns of species overlap.

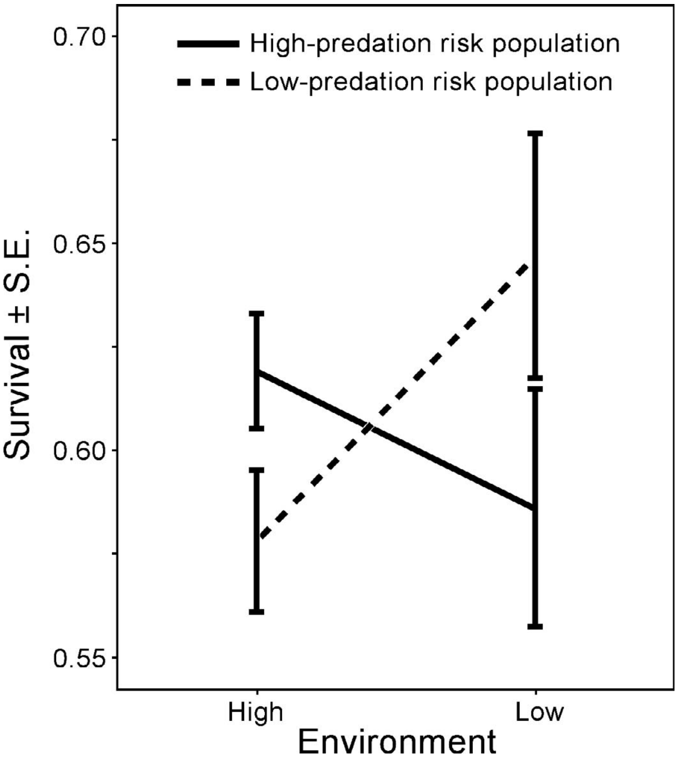


**Fig. 4.** Urban et al. (this volume, 2017) found that Wood Frog tadpoles display adaptive reaction norms in response to Marbled Salamander predation. The survival of Wood Frog tadpoles depended on whether populations came from high-risk sites (solid line) or low-risk sites (dotted line), as well as whether they were raised in high-predation risk or low-predation risk environments.

Yet Wood Frogs apparently are not equally capable of adapting to all forms of human-induced environmental change. In particular, roadside populations of Wood Frogs that are exposed to high salinity from road salt run-off seem to be maladapted. That is, performance in roadside ponds is actually worse for frogs from roadside ponds than for frogs from woodland ponds (Brady, 2013), a result directly counter to the usual predictions of local adaptation (Hereford, 2009). However, Brady (2013) had been unable to assess potential contributions of plastic (parental effects) and genetic variation to this puzzling outcome. Therefore, Brady and Goedert (this volume, 2017) test for parental effects on offspring survival in a reciprocal transplant experiment, finding that such effects cannot explain the apparent maladaptation of roadside Wood Frogs. The authors also document substantial genetic variation in the responses of roadside Wood Frogs to roadside conditions (Fig. 5), implying the potential for selection to promote adaptive evolution—the absence of which suggests some constraint hindering local adaptation.

A critical human context for eco-evolutionary dynamics is fisheries. Fisheries generally select against large and old individuals, which frequently leads to shifts in commercial stocks toward earlier age-at-maturity and smaller size-at-age (Darimont et al., 2009; Sharpe and Hendry, 2009). These changes—some of which are genetically based—could feed back to influence population dynamics and thereby, perhaps, influence fisheries yield, population resilience in the face of overfishing, and stock recovery following the cessation of fishing (Dunlop et al., 2015; Kuparinen and Festa-Bianchet, 2017). Yet implications beyond the targeted fish themselves have not been explored. Kindsvater and Palkovacs (this

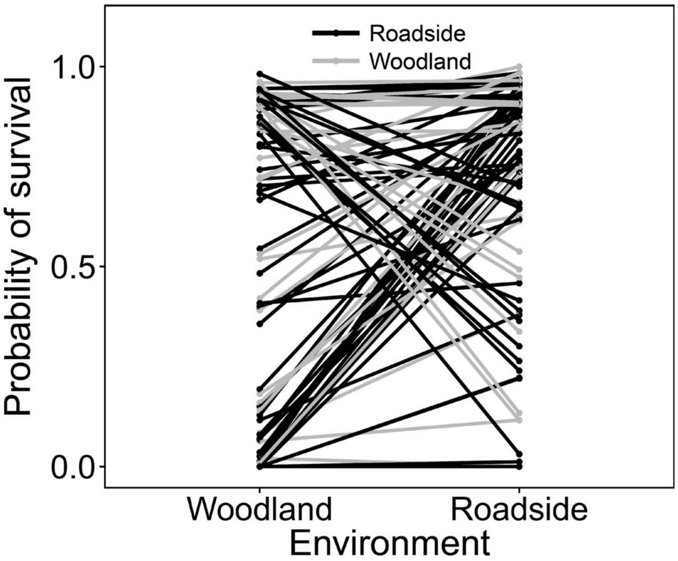


**Fig. 5.** Brady and Goedert (this volume, 2017) documented family-level variation in larval Wood Frog survival across the interaction of population type by environment. Black lines represent roadside populations and gray lines represent woodland populations. Adaptive genotypic variation is present among the roadside populations despite the average pattern of maladaptive survival they exhibit.

volume, 2017) use a modeling approach to ask how fishing, and evolutionary responses to it, shape food web dynamics. The authors predict that fishing reduces the trophic level at which Atlantic Cod would be expected to feed and that evolutionary responses partly offset those decreases in trophic level (Fig. 6).

Human influences have a diversity of effects on the evolution of other organisms, and those evolutionary effects feed back to influence ecological dynamics, including the ecosystem services people derive from nature. Work presented in this volume shows that these eco-evolutionary dynamics likely range from weak to strong, suggesting the need for more work to determine when the different outcomes are most likely.

***Constraints and alternatives.***—Classically, evolution was considered to be too slow to have important effects on short-term, "ecological" time scales (Slobodkin, 1961). Recently, however, the pendulum of opinion might have swung too far to the other side: some authors seem to feel that contemporary evolution is everywhere and is everywhere producing important ecological effects. As is so often the case, the reality certainly lies somewhere in the middle. That is, depending on the specifics of a given system, evolution may plod along slowly and have little immediate consequence or may race quickly ahead and have large ecological effects (Hendry, 2017). It is therefore important for future work to establish the factors that determine where a given system lies on this slow-to-fast and eventual-to-immediate eco-evolutionary continuum. Likely candidates for shifting systems toward the more sedate side of things could include constraints on evolutionary change, alternatives to evolutionary change, and constraints on the translation of evolutionary change into ecological effects. The present

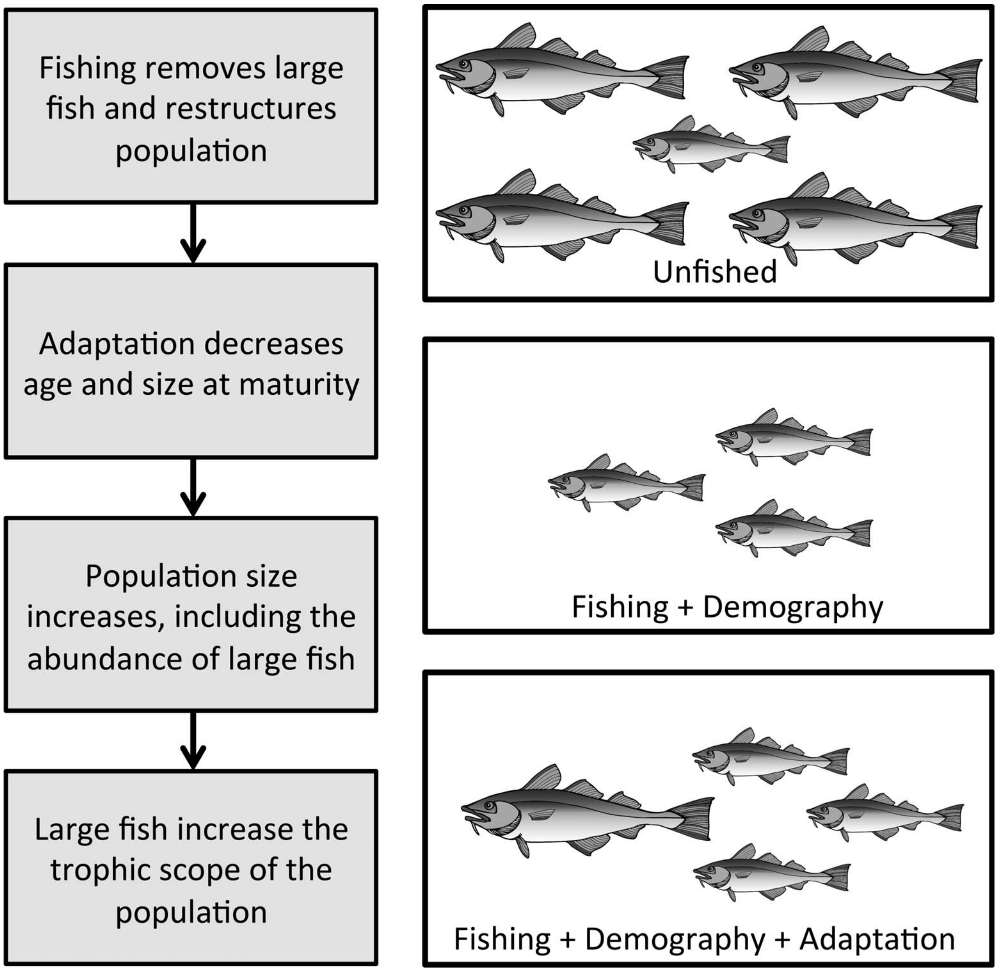


**Fig. 6.** Kindsvater and Palkovacs (this volume, 2017) used models to show how demography and adaptation could interact to shape the abundance, body size distribution, and trophic role of Atlantic Cod.

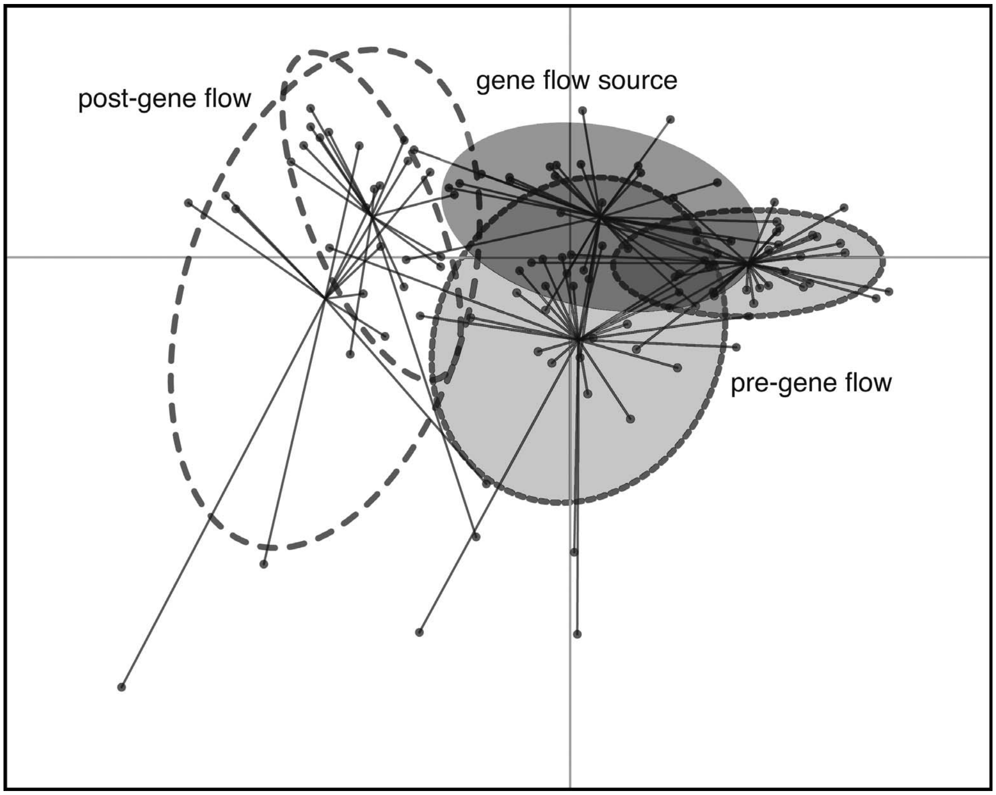


**Fig. 7.** Fitzpatrick et al. (this volume, 2017) explored multivariate trait responses to gene flow in female guppies. Shown are results of discriminant analysis of principal components (DAPC) ordination and 95% confidence ellipses. Two recipient pre-gene flow populations (light fill, small-dashed ellipses) received gene flow from a divergent source population (dark fill). Traits were measured in post-gene flow populations (no fill, large-dashed ellipses) approximately ten generations after gene flow. All traits were measured on second-generation lab-reared guppies in a common environment.

symposium proceedings include several papers that directly address these constraints and alternatives. We here discuss three in this section but also relevant are the studies by Brady and Goedert (this volume, 2017) and Schoener et al. (this volume, 2017).

If different populations are to have different ecological effects that result from adaptations to their different environments then, by definition, substantial phenotypic divergence must be present. Yet such divergence is not inevitable and, even when present, might be only minor. One factor that might limit adaptive divergence is gene flow, although gene flow can also promote adaptation or have no effect at all (Lenormand, 2002; Garant et al., 2007). Given this ambiguity, we need experimental manipulations of gene flow in nature that assess effects on population divergence (e.g., Riechert, 1993; Nosil, 2009) and any resulting ecological consequences (Farkas et al., 2013, 2015). Toward this end, Fitzpatrick et al. (this volume, 2017) manipulated gene flow between guppy populations that had adapted to different predation regimes. Specifically, low-predation (LP) guppies were experimentally subjected to enhanced gene flow from high-predation (HP) guppies. This enhanced gene flow had effects on a number of phenotypic traits but, importantly, the direction and magnitude of effects were highly variable among traits (Fig. 7). Thus, the effects of gene flow are not only system specific, they are also trait specific, which means that attempts to infer the role of gene flow on eco-evolutionary dynamics will need to consider a diversity of traits that might be ecologically important.

Eco-evolutionary dynamics technically reflect genetic, and therefore evolutionary, change. An alternative is phenotypic plasticity, which also could have important ecological effects (Kovach-Orr et al., 2013; Hendry, 2017). For example, although HP and LP guppies show many genetic differences, they also show plastic differences that reflect immediate responses to perceived predation risk (Ghalambor et al., 2015). One study considering such effects found that guppies from HP and LP environments in the Damier River of northern Trinidad, to which they were introduced seven years previously, had up to 50% higher survival rates in their home environments than did guppies from the ancestral Yarra River population (Gordon et al., 2009). That study, however, did not assess whether the phenotypic differences among populations were genetically based. Gordon et al. (this volume, 2017) report that life history differences between the HP and LP Damier River populations, and between the Damier and Yarra river populations, reflect a combination of genetic change, plasticity, and the evolution of plasticity. Studies of eco-evolutionary dynamics would do well to formally consider plasticity, and its evolution, as a critical part of the eco-evolutionary picture (e.g., Lundsgaard-Hansen et al., 2014).

Another potential limitation on eco-evolutionary dynamics is the potential dependence of ecological effects on the continued presence of the evolving organisms. For instance, anadromous fishes might be present in fresh water for only a short period of time, and so any ecological effects they have might be transitory (Palkovacs and Post, 2009). Lundsgaard-Hansen et al. (this volume, 2017) examine how different species of whitefish in an adaptive radiation influence mesocosm ecosystems when adults are present in the mesocosms versus 14 weeks after the adults are removed. The different species had a diversity of ecosystem effects that differed between the two periods, thus indicating important, but trait-specific, carry-over ecological effects of an adaptive radiation. Similar "after-life" effects have been studied in plants (Genung et al., 2013). Importantly, the overall magnitude of evo-to-eco effects were strong at each time period, but the specific ecological effects differed between the periods.

Eco-evolutionary dynamics will not always be strong and important. Indeed, each of the papers in these symposium proceedings highlight some situations where evolution or its ecological consequences are minimal. Among the many reasons for this, gene flow might constrain adaptive population divergence, organisms might respond to environmental change through plasticity rather than evolution, and the ecological effects of organisms might diminish in the absence of the organism.

***Eco-evolutionary dynamics in nature.***—Nearly all animal-centric studies of the evo-to-eco side of eco-evolutionary dynamics are conducted in artificial settings, although there are notable exceptions (Kinnison et al., 2008; Gordon et al., 2009; Carlson et al., 2011; Turcotte et al., 2011; Farkas et al., 2013). The most common artificial settings are mesocosms such as cattle tanks used for experiment with stickleback and whitefish, experimental stream channels used for work with guppies, and large bags in lakes used for mid-water species such as Alewife. The ecological effects documented in these more-or-less artificial settings could be, and indeed probably are, quite different from those that play out in nature. First, controlled settings often lack important ecological factors that might modify eco-evolutionary dynamics, such as parasites, predators, or competitors (biotic) or habitat structures (abiotic). Second, controlled experiments tend to maximize differences among treatments (often ecotype—sometimes crossed with some other factor) while minimizing variation within treatments. In nature, however, a given causal factor (e.g., predation) likely varies in magnitude among “replicate” locations, as will other non-focal factors (e.g., parasitism or competition), perhaps in association with the focal factor. Third, key external abiotic drivers, such as floods, storms, or droughts, might wash out the ecological effects of evolutionary differences in nature. Of course, removing these confounding and confusing influences is precisely the goal of controlled studies, but the question we really need to answer is just how important a given evolutionary difference is within the context of all the realistic covarying, confounding, and confusing factors found in nature (Hendry, 2017). With this need in mind, the present symposium proceedings include several studies, plus Fitzpatrick et al. (this volume, 2017) discussed above, that specifically focus on eco-evolutionary dynamics in nature.

Context dependence is at the heart of concerns about whether experiments in controlled settings can tell us much about nature. If, for instance, the effects of different ecotypes on community structure are consistent across levels of variation in other environmental factors, then eco-evolutionary effects could be considered “parallel” or “convergent” across settings. In this scenario, studies in mesocosms will accurately depict outcomes in any setting, including nature. Pérez-Jvostov et al. (2012, 2015, 2016) have studied the effects of host-parasite interactions on eco-evolutionary dynamics. Following a series of mesocosm-based studies on guppies and their monogenean ectoparasites, genus *Gyrodactylus*, Pérez-Jvostov et al. (this volume, 2017) set out to consider such effects in a natural setting, taking advantage of the host-specificity of the parasite and the ease which it can be removed from a natural stream after introduction. By experimentally introducing *Gyrodactylus* into two formerly *Gyrodactylus*-free guppy populations, Pérez-Jvostov et al. assessed changes in traits (growth), vital rates (survival), and population dynamics (density) in the guppies as well as in intra-guild predator, the killifish, *Rivulus hartii*. The key finding was remarkable context-dependence: the experiment yielded very different outcomes between the two populations.

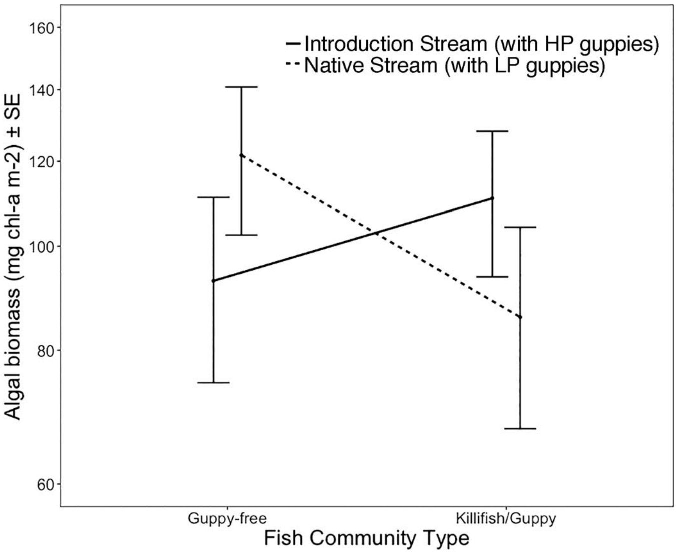


**Fig. 8.** Simon et al. (this volume, 2017) explored the effects of guppy ecotypes on ecosystems in nature. Shown are least square means (±1 standard error) for algal biomass in streams with locally adapted low-predation (LP) guppies or introduced high-predation (HP) guppies. The authors found a significant interaction between fish community type and guppy ecotype for algal biomass, indicating that the effects of guppies depend on the phenotype of the population.

As we noted earlier, numerous empirical insights into eco-evolutionary dynamics have come from comparing HP and LP guppy ecotypes (e.g., Palkovacs et al., 2009; Bassar et al., 2010). However, nearly all of those inferences were quantified in experimental stream channels, leaving open the possibility that observed effects were not representative of nature. Simon et al. (this volume, 2017) tackled this concern head-on by analyzing the ecological effects of natural and experimentally introduced guppy populations in nature. The authors found that excluding different guppy ecotypes (HP or LP) from areas of a stream had different effects on invertebrates and algae (Fig. 8). Moreover, these experimental outcomes were similar to the differences between natural streams containing HP versus LP guppies. The experiment thus showed that effects previously observed in experimental mesocosms can be replicated in natural settings, at least for some variables in some places (see also Urban, 2013).

Yet not all ecological effects in nature are predictable in advance. When Brown Anoles, *Anolis sagrei*, occupy narrow perches in trees, they tend to evolve shorter limbs (Losos et al., 1998). When the predatory curly-tailed lizard, *Leiocephalus carinatus*, is introduced to islands with *A. sagrei*, the anoles move higher in trees to narrower perches, and should therefore evolve shorter limbs (Schoener et al., 1982, this volume, 2017). The ecological outcome is then expected to be a decrease in arboreal arthropods and a corresponding decrease in herbivore damage to the vegetation. Following an experimental introduction of *L. carinatus* to seven small islands with *A. sagrei*, leaving seven *A. sagrei*-only islands as controls, none of the above predicted effects were observed (Schoener et al., this volume, 2017). The main reason appears to be that catastrophic hurricanes effectively reset these island ecosystems, resulting in decreased predation pressure from *L. carinatus* on *A. sagrei*, which reduces the expected selection for shorter limbs in the anoles, which in turn diminishes the corresponding ecological effects. Context, in this case hurricanes, is clearly critical for understanding eco-evolutionary cascades that might occur in nature.

Context dependence also predominates in invasive White Perch, *Morone americana*, adapting to lakes with different productivity levels. Specifically, perch recently adapted to oligotrophic versus euthrophic lakes have different effects on pelagic and benthic communities and on primary productivity when tested in nearly natural experimental ponds (Tuckett et al., this volume, 2017). Importantly, effects of the two perch ecotypes were quite different between experimental ponds that were either oligotrophic or eutrophic, showing dramatic context dependence. Given that perch ecotype influenced primary productivity, this variation has the potential for strong feedback effects that influence the trophic state of lakes and, potentially, regime shifts.

These three studies, and nearly all others in the symposium proceedings, show that context dependence can be extremely strong in eco-evolutionary dynamics, though perhaps not always (see also Urban, 2013). This variation among studies means that we need more experiments in nature, ideally coupled with controlled studies that might be able to inform the causal effects driving patterns observed in nature.

## IMPLICATIONS

At its heart, the study of eco-evolutionary dynamics strives to explain the relationship between ecology and evolution (Hendry, 2017). The nature of this relationship is especially important in today's era of unprecedented, human-caused ecological change. (The lead author is working on these words while tending his sump pumps during the big Quebec flood of 2017.) Quite rightly, human societies are concerned about the conservation of biodiversity, and the increasing frequency and severity of human-animal interactions. Action is necessary, but understanding is even more so. As one example, Population Viability Analyses (PVAs) of endangered and threatened species typically assume that the species in question do not change, and will not change even as conditions are altered. Only the environment is assumed to change. Nearly all considerations of ecosystem services or species habitat models make pretty much the same assumption. Yet, as we have clearly seen via studies of eco-evolutionary dynamics, many organisms have the capacity to evolve rapidly enough to influence their population dynamics (hence PVAs), environments (biodiversity and ecosystem services), and optimal habitat requirements. More such studies are clearly needed in fishes, amphibians, and reptiles; indeed, in all organisms.

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