Editorial

How Plasticity and Evolution Work in the Real World

Populations confronted with novel environments have three general strategies to maintain viability: 1) they can tap into their plastic capacity to express different phenotypes using their existing genetic makeup; 2) they can adapt by genetic change over time (evolution); or 3) they can move to a more suitable environment. Although some species can shift their distributions rapidly enough to keep pace with the velocity of climate change (Pinsky et al. 2013; Poloczanska et al. 2013), many others cannot, either because of inherently low dispersal capability or because anthropogenic changes have fragmented suitable habitats and created barriers to dispersal. For these species, evolution or plasticity represent the only real options for persistence.

A great deal has been written recently about contemporary evolution and plasticity, but many treatments consider only plasticity (and not evolution), or vice versa. In most cases, however, these two phenomena will occur simultaneously, so it is important to consider their joint effects and how they interact to determine patterns in the distribution and abundance of species. A little reflection suggests a number of subthemes, including: For how many species will evolution and/or plastic responses substantially help in responding to rapid environmental changes? Can we identify any generic rules/patterns as to which species will and will not be helped much by adaptive responses? Do species generally respond first with plasticity and then with evolution only if plasticity is exhausted, or do both occur simultaneously? Can thermal tolerance evolve fast enough to keep up with global warming? Is this species- or taxon-specific? How about ocean acidification? How rapidly can evolution of reaction norms occur? What are the limits of plasticity? In what species have these limits been empirically demonstrated? And finally, What is the role of epigenetics (a type of cross-generational plasticity) in all this?

These and related questions were tackled at the American Genetic Association Presidential Symposium, “Evolution and plasticity: adaptive responses by species to human-mediated changes to their ecosystems,” held in June 2014 at the University of Washington, Seattle. Belying the new-world name of the AGA, the speakers and poster presenters hailed from 11 different countries on four continents (for a complete list, see http://www.theaga.org/aga-evolandplasticity.htm). Particularly impressive were strong contributions from the many bright, young, and energetic researchers who are interested in how a better understanding of evolution and plasticity can help inform real-world problems in conservation and management of natural populations. A presentation by Michael Skinner (see Kaiser 2014) and a special brown-bag lunch discussion highlighted the emerging interest in the role of epigenetics. A collection of nine papers derived from presentations made at the 2014 AGA meeting comprise this special issue of Journal of Heredity.

David Reznick, who began his research on contemporary evolution in Trinidad guppies long before such studies were in vogue, kicked off the meeting (and this special issue) with the AGA Key Distinguished Lecture, “Hard and soft selection revisited: how evolution by natural selection works in the real world.” After a nice review of the development of ideas about genetic load, he explains why his empirical work has led him to the view that soft selection (i.e., selection that is density-dependent and frequency-dependent) is primarily responsible for shaping how organisms adapt to natural environments. In this view, nature presents ecological vacancies that will be filled one way or another, so absolute fitness is not as important as fitness relative to other individuals that co-occur in time and space. His research has also led Reznick away from Hutchinson’s concept of an ecological stage and an evolutionary player in favor of Pimental’s concept of ecology and evolution as two actors on the same stage, with regular feedback loops in both directions.

A theoretical paper by Len Nunney (this issue) uses a novel definition of phenotypic plasticity to examine the extent to which plasticity can help buffer the probability of extinction for small populations. Otherwise, these small populations cannot maintain sufficient genetic variability to allow adaptive evolution to keep pace with directional environmental change (e.g., through evolutionary rescue). Broader plasticity helps a population buy time in its struggle to adapt, but this can come at a long-term cost in fitness as it reduces the effectiveness of natural selection in promoting adaptation. Nunney’s model shows that this trade-off produces an inherent conflict between short-term individual fitness and long-term population viability, unless the key trait(s) are controlled by only a few gene loci.

Andrew Hendry (this issue) explores the interactions between plasticity and evolution in more detail in a review of key unresolved questions regarding the role of plasticity in eco-evolutionary dynamics. He begins by reviewing methods commonly used to draw inferences about reaction norms and how they might evolve over time. Despite the wealth of empirical data amassed in recent years, Hendry concludes that existing information is insufficient to determine whether plasticity is more likely to help or hinder ecological speciation. However, he also argues that plasticity is essential to consider in empirical investigations of eco-evolutionary dynamics at the levels of communities and ecosystems, as well as populations.

In agreement with previous studies demonstrating that broad plasticity can help invasive species cope with novel environments, Tim Horgan-Kobelski et al. (this issue) used a resurrection study to show that reaction norms in the invasive plant (Polygonum cuspidatum) evolved over a period of 11 years to increase photosynthetic rate and delay senescence under hot, dry conditions typical of those
expected in the future under climate change. However, they also found that the same adaptive responses did not occur under Free Air CO2 Enrichment (FACE) conditions with elevated (550 ppm) levels of CO2. This might represent a constraint on adaptive evolution in this species, but it could simply indicate that, to date, cumulative increases in CO2 concentration have not been large enough to trigger the necessary evolutionary response.

The extent to which reaction norms for behavioral traits evolve in human-altered environments can be a crucial issue in applied conservation and management. For example, in the western contiguous United States, about one-third of historic anadromous salmonid populations have been extirpated, and half of those that remain are listed as threatened or endangered species under the US Endangered Species Act (Gustafson et al. 2007). Collectively, hundreds of large dams and thousands of smaller impediments have blocked access by anadromous fish to vast amounts of historic habitat, but resident forms of two species (sockeye salmon, Oncorhynchus nerka, and steelhead, O. mykiss) can complete their life cycle in freshwater and hence maintain populations above these barriers. How long can such resident fish maintain the capability to produce viable anadromous populations in the absence of the ability to express the anadromous phenotype? In the common situation where smolts can leave above-barrier populations and migrate downstream but returning adults are blocked from access, genes promoting migration are lost to the resident population, resulting in active selection against anadromy. Cory Phillips et al. (this issue) studied evolution of smolt reaction norms in one such system in California, where a population of rainbow trout (the resident form of steelhead) has been trapped above a barrier for a century. Using a common-garden approach, they found that the threshold for expressing the behavior to migrate downstream as a smolt to initiate the anadromous part of the life cycle was higher in the above-barrier population than a population below the barrier. Examples like this of evolution of the conditional strategy to migrate in human-altered environments create real challenges for recovery of at-risk species.

Rising temperatures from global warming have clear potential to affect many species that exhibit temperature-dependent sex determination (TSD). Jeanine Refsnider and Fred Janzen (this issue) examine the extent to which the painted turtle can use plastic and/or evolutionary responses to maintain sex ratios consistent with long-term viability. They report moderate heritability for pivotal temperature but relatively low heritability for nesting site choice and nesting phenology. Their results thus suggest that this species has some physiological capacity to adapt to warming temperatures, but that maintaining broad plasticity is the most feasible strategy for behavioral traits. This pattern differs from that found in some migratory species, which can show strong capacity for evolution of phenological traits associated with migration timing (e.g., Reed et al. 2011).

Three papers used RNA-seq or related approaches to examine patterns of gene expression for evidence of adaptations. Melissa De Biasse and Morgan Kelly (this issue) reviewed cases in which comparative transcriptomics has been used 1) to help establish the genetic basis of adaptation to current environmental gradients, and 2) to understand the organismal response to multiple stressors. They found that the few studies that have considered more than one stressor generally evaluate them individually, but this approach fails to elucidate nonlinear, synergistic interactions that commonly occur among the various stressors. They emphasize the importance of rigorous experimental design and call for a greater integration of genomics with transcriptomics. In a study of European grayling, Hannu Mäkinen et al. (this issue) showed that plastic and evolutionary patterns of gene expression are positively correlated, supporting the idea that plastic responses facilitate adaptation in early phases of colonizing new environments. In species with high gene flow, migration slows local adaptation and might prevent it entirely. But if fecundity is high enough, strong, recurrent selection that differs spatially can produce consistent patterns of genetic differentiation based entirely on selective mortality within cohorts. That is the explanation that Laura Eirman and Matt Hare (this volume) find most consistent with their experimental data for the Eastern oyster in Delaware Bay, United States. They found significant spatial divergence in gene expression plasticity for osmoregulation, and they found that osmoregulatory genes were significantly enriched in outlier SNPs (loci with unusually high $F_{ST}$ values).

After hearing for many years that “The genomics revolution is coming! The genomics revolution is coming!” there is no question that it has now arrived. After 2007, next-generation sequencing costs dropped precipitously, with the result that by 2012 the cost per megabase of DNA sequence was three orders of magnitude lower than it would have been if costs had followed Moore’s law (http://www.genome.gov/sequencingcosts/). As noted by Shaw and Mullen (2014), the genomics revolution has helped to blur the distinction between model and non-model species, and this opens up exciting new opportunities for the study of both evolution and plasticity as they occur in wild populations. The next decade or so should produce many novel insights, and undoubtedly a few surprises as well.

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References


