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Phenotypic Plasticity

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LAST MODIFIED: 25 OCTOBER 2017

DOI: 10.1093/OBO/9780199941728-0093

Introduction

Phenotypic plasticity (often termed “plasticity”) is generally defined as the capacity of an individual organism to alter its behavior, physiology/gene expression, and/or morphology (i.e., some aspect of its phenotype) in direct response to changing environmental conditions. Plasticity is ubiquitous and many have suggested that it can have important ecological and evolutionary implications. Among other things, plasticity may allow organisms to persist in otherwise unfavorable environments, produce novel, complex traits, and experience altered interactions with other members of their community. In recent decades, the evolutionary power of plasticity has received renewed interest. In particular, the process of genetic accommodation has dominated the literature because of its potential relevance to all aspects of biology. However, there is some skepticism regarding the importance of phenotypic plasticity generally, and genetic accommodation specifically, in evolution. Indeed, despite plasticity being acknowledged for over 100 years, its importance to evolutionary biology has evolved from being a relevant source of phenotypic variation, to being considered just developmental noise, to possibly forming the basis of an extended evolutionary synthesis. While phenotypic plasticity may be viewed as a primarily ecological/evolutionary phenomenon, it touches on such diverse fields as behavior, learning, conservation biology, and human health. Because of its pervasiveness, appreciation for and understanding of phenotypic plasticity would be beneficial to all biologists.

General Overview

Although interest in phenotypic plasticity has increased since the 1980s (Forsman 2014), the resulting proliferation of the literature can make it difficult to keep concepts organized. As a starting point, Whitman and Agrawal 2009 should be the first piece read in this entire bibliography because of its accessibility. A common problem when sifting through literature on phenotypic plasticity is the terminology. The authors of Fusco and Minelli 2010 do a good job of defining and clarifying terms in their review. Stearns 1989 provides a historical perspective in terms of the writing, but also provides a brief history of the field (to that point). While a lot of plasticity research focuses on “higher-order” phenotypes, Callahan, et al. 1997 sets the stage for current work on phenotypic plasticity at the molecular level, which is complemented by Piersma and Drent 2003, which emphasizes how physiological processes are phenotypically plastic. Wund 2012 and Forsman 2014 are particularly useful as introductions to the types of questions being asked by plasticity researchers and how one can test hypotheses relating to plasticity. Finally, Nijhout 1990 provides an excellent introduction to the thinking that drives much of the current research being done on plasticity and evolution—particularly that development is completed by genes alone.

Callahan, H. S., M. Pigliucci, and C. D. Schlichting. 1997. Developmental phenotypic plasticity: Where ecology and evolution meet molecular biology. *BioEssays* 19:519–525.

This review highlights how evolutionary and molecular biology can successfully be married to investigate questions of developmental plasticity. It uses the phytochrome-mediated shade-avoidance and light-seeking responses of flowering plants as a model for this approach.

Forsman, A. 2014. Rethinking phenotypic plasticity and its consequences for individuals, populations, and species. *Heredity* 115:276–284.

The major strength of this review is its emphasis on how to study and test hypotheses relating to phenotypic plasticity. It provides a “whole-organism” rather than “single-trait” perspective for understanding plasticity.

Fusco, G., and A. Minelli. 2010. Phenotypic plasticity in development and evolution: Facts and concepts. In *Special issue: From polyphenism to complex metazoan life cycles*. Edited by G. Fusco and A. Minelli. *Philosophical Transactions of the Royal Society B* 365:547–556.

As an introduction to a special volume in the *Philosophical Transactions of the Royal Society*, this article provides one of the more succinct overviews of phenotypic plasticity, how it evolves, and its role in evolution. It is useful in trying to sort out the myriad of terminology associated with phenotypic plasticity.

Nijhout, H. F. 1990. Problems and paradigms: Metaphors and the role of genes in development. *BioEssays* 12:441–446.

An excellent review of how a gene-driven view of development is flawed. Although it gets a bit technical in places, this generally accessible essay should be read by anyone interested in genetics, development, and/or evolution.

Piersma, T., and J. Drent. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution* 18:228–233.

By focusing on reversible forms of phenotypic plasticity (termed phenotypic flexibility), Piersma and Drent offer a perspective that highlights the ubiquity of phenotypic plasticity. They utilize less frequently noted examples of plasticity, pay particular attention to diet-induced changes in body and organ size and life-cycle staging, and emphasize the role of intra-individual variation.

Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience* 39:436–445.

As an introductory article to a special issue of *BioScience*, this work sets the stage for the rest of its volume, but also introduces readers to terms and concepts used throughout plasticity literature. Among other things, it gives a short, informative history of the reaction norm concept in evolutionary biology.

Whitman, D. W., and A. A. Agrawal. 2009. What is phenotypic plasticity and why is it important? In *Phenotypic plasticity of insects: Mechanisms and consequences*. Edited by D. W. Whitman and T. N. Ananthakrishna, 1–63. Boca Raton, FL: CRC.

This book chapter should be the first piece read by anyone interested in phenotypic plasticity. Although this chapter is in a book on insects, it provides one of the most accessible, comprehensive overviews of phenotypic plasticity available.

Wund, M. A. 2012. Assessing the impacts of phenotypic plasticity on evolution. *Integrative and Comparative Biology* 52:5–15.

This review (in particular Table 1) is a vital resource for those interested in testing hypotheses related to phenotypic plasticity. Almost acting as a “how-to” guide, it outlines approaches and empirical examples for testing eight key hypotheses of plasticity’s role in evolution.

Books

Several books focus on phenotypic plasticity. Those listed in this section can be found on most, if not all, plasticity researchers’ bookshelves. West-Eberhard 2003 is the must-have book in this section because its breadth and depth have served as the foundation for many major advances in plasticity research in recent years. Schlichting and Pigliucci 1998 and Pigliucci 2001 should probably be the first works read in this section because of their ability to highlight the importance of plasticity in evolution in an accessible way. For those that are more theoretically and/or conceptually driven, DeWitt and Scheiner 2004 should be a useful resource. It covers similar topics as the others, but presents them from a slightly different perspective. Actual textbooks on plasticity are somewhat hard to come by. However, Gilbert and Epel 2015 is the closest thing available as a textbook for ecological evolutionary developmental biology. Sultan 2015 could be used as an advanced textbook that features how plasticity is important for ecological development and niche construction and how these processes interact to produce adaptation. Piersma and van Gils 2011 is a useful textbook for physiological ecology. Levins 1968 may be most useful for providing insight onto how plasticity was perceived around fifty years ago, because its major contributions are touched on in the other works of this section.

DeWitt, T. J., and S. M. Scheiner, eds. 2004. *Phenotypic plasticity: Functional and conceptual approaches*. Oxford: Oxford Univ. Press.

DeWitt and Scheiner edit an excellent resource for understanding the breadth of ideas related to phenotypic plasticity using a historical and conceptual approach. More modeling and theory oriented than the other books on this list.

Gilbert, S. F., and D. Epel. 2015. *Ecological developmental biology*. 2d ed. Sunderland, MA: Sinauer.

This book comes the closest to being a textbook for eco-evo-devo. Plasticity is featured throughout. Utilizes both applied and basic research examples to highlight the significance of an eco-evo-devo perspective. Appropriate for upper-level undergraduates and above.

Levins, R. 1968. *Evolution in changing environments: Some theoretical explorations*. Princeton, NJ: Princeton Univ. Press.

An early work that considers the organism–environment relationship and how short-term and long-term environmental changes influence the responses of populations and communities. The first to note that the frequency of environmental encounter is important for evolution.

Piersma, T., and J. A. van Gils. 2011. *The flexible phenotype: A body-centred integration of ecology, physiology, and behaviour*. Oxford: Oxford Univ. Press.

This book focuses primarily on physiological plasticity and pulls from the authors’ research program. It is useful for upper-level undergraduates and above.

Pigliucci, M. 2001. *Phenotypic plasticity: Beyond nature and nurture*. Baltimore: Johns Hopkins Univ. Press.

This could be considered a sequel to Schlichting and Pigliucci 1998 in that it covers many similar topics and themes. It reviews the concept of phenotypic plasticity from the two prior decades and offers insight on potentially fruitful research directions. A good resource for anyone interested in plasticity and how it relates to various biological disciplines. Suitable for advanced undergraduates, graduate students, and professionals.

Schlichting, C. D., and M. Pigliucci. 1998. *Phenotypic evolution: A reaction norm perspective*. Sunderland, MA: Sinauer.

This book argues for the importance of considering phenotypic plasticity when thinking about phenotypic evolution. It provides an informative historical overview, assesses the current state of the field (as of 1998), and provides future directions. This work should appeal to graduate students and professionals studying evolutionary biology.

Sultan, S. E. 2015. *Organism & environment*. Oxford: Oxford Univ. Press.

Written as an advanced text for graduate students on the interplay between ecological development and niche construction, *Organism & Environment* would be useful for anyone interested in ecology, evolution, and/or developmental biology. It shows that organisms (through ecological development and niche construction) might have greater ability to influence their evolutionary trajectories than has historically been appreciated.

West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford: Oxford Univ. Press.

This example-rich and comprehensive book covers essentially all aspects of evolutionary biology and how developmental plasticity can contribute to our understanding of them. It is a dense read with lots of information that is best suited for advanced graduate students and professionals. An excellent source for research ideas.

Journals

Studies on phenotypic plasticity could potentially be found in any journal that publishes biological research. However, the four most common journals for plasticity and evolution are *Evolution*, *Proceedings of the Royal Society of London B*, *American Naturalist*, and the *Journal of Evolutionary Biology*. The *Biological Journal of the Linnean Society* is also an important source for plasticity literature, but includes research that is potentially more system specific than the others. *Trends in Ecology and Evolution* is a great resource for easily accessible reviews and opinions on topics at the forefront of the field. *Molecular Ecology* has increased in importance because of the growing ease with which 1) non-model organisms can be studied and 2) the molecular underpinnings of plasticity and its evolution can be explored. Finally, *Ecology* is the leader for more ecologically based articles, but is important because of the ecological basis of phenotypic plasticity.

***American Naturalist*. 1867–.**

Published by the American Society of Naturalists, this journal publishes high-impact articles on ecology and evolution. Theory papers and meta-analyses are not uncommon in this journal.

***Biological Journal of the Linnean Society.* 1969–.**

The descendent of the journal that published the seminal works of Darwin and Wallace in 1858, this journal publishes papers broadly related to evolution. May be more likely to encounter system-specific phenomena than in *Evolution* or the *Journal of Evolutionary Biology*.

***Ecology.* 1920–.**

Published by the Ecological Society of America, this journal is the leader in its field and is focused on generalizable research articles and syntheses. Obviously, most articles are more ecological than evolutionary, but a mixture is certainly present.

***Evolution.* 1947–.**

Published by the Society for the Study of Evolution, this is the leading journal in the field and should be the first place to look for relevant articles. This journal primarily publishes research articles, but perspectives, commentaries, and book reviews are also published.

***Journal of Evolutionary Biology.* 1988–.**

Published by the European Society for Evolutionary Biology, this journal is also a leader in publishing research articles on evolutionary biology. It also publishes review articles.

***Molecular Ecology.* 1992–.**

As the name suggests, this journal is focused on the molecular underpinnings of ecological, evolutionary, and behavioral processes. A useful resource for identifying molecular techniques being used in non-model systems.

***Proceedings of the Royal Society of London B.* 1905–.**

Publishes on topics across biological disciplines, but is often a source of high-impact papers in evolutionary biology and related fields.

***Trends in Ecology and Evolution.* 1986–.**

This journal publishes relatively short reviews and opinion pieces aimed at readers ranging from students to advanced faculty. This is an excellent journal for identifying current issues in the field and obtaining ideas for potentially fruitful research avenues.

Historical Works

Appreciation for the environment's ability to influence development and thereby potentially impact evolution dates back to early

evolutionists such as Jean-Baptiste Lamarck, Erasmus Darwin, Charles Darwin, and August Weismann. However, the works included in this section begin in the late 1800s (Baldwin 1896) and then jump to 1909 (Woltereck 1909) with the conception of the reaction norm—a concept that is fundamental to phenotypic plasticity research. The author of Johannsen 1911 then compares this reaction norm concept with his own idea of “genotype.” A few years later, Nilsson-Ehle 1914 coins the term “plasticity.” Around the time of the Modern Synthesis, Waddington 1942 and Schmalhausen 1949 developed similar concepts of how acquired characters can become heritable and fixed through selection. Despite this work not being explicitly included in the Modern Synthesis, it marks the beginning of modern conceptions concerning plasticity’s possible role in evolution. Although not often noted as a contributor to plasticity, one of the framers of the Modern Synthesis—J. B. S. Haldane—made the case for gene-by-environment (GxE) interactions and indirectly describes the importance of reaction norms (Haldane 1946). Some years later, the review Bradshaw 1965 helped establish plasticity as a legitimate factor in evolution that was more than simply developmental noise. These articles were chosen because they are the most likely to be encountered in contemporary works on plasticity. Nevertheless, many others are important as well. Sarkar 2003 chronicles the history of phenotypic plasticity from 1909 to 1999 and includes the contributions of the other works in this section as well as those not mentioned here.

Baldwin, J. M. 1896. A new factor in evolution. *The American Naturalist* 30:441–451.

Baldwin can be considered one of the founders of phenotypic plasticity research. He proposes a mechanism of evolution in which an acquired character (i.e., a trait induced by the environment) can come under hereditary control via selection. This mechanism reconciles some aspects of Lamarckian and Darwinian ideas of evolution.

Bradshaw, A. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13:115–155.

This seminal review by Bradshaw brought phenotypic plasticity of plants “out in the open,” suggested that plasticity was under genetic control, and helped bridge the gap between the classical view of plasticity as developmental noise and the modern appreciation of its role in ecology and evolution. Despite being over fifty years old, Bradshaw’s comprehensive review remains relevant for those interested in plasticity today.

Haldane, J. B. S. 1946. The interaction of Nature and Nurture. *Annals of Eugenics* 13:197–205.

This work provides an early and influential argument for the significance of the gene-by-environment interaction (GxE). Haldane indirectly describes the significance of plasticity and patterns that reaction norms can take.

Johannsen, W. 1911. The genotype conception of heredity. *The American Naturalist* 45:129–159.

Johannsen introduces and discusses the terms “gene,” “genotype,” and “phenotype” as they relate to inheritance and organismal design. He briefly compares Woltereck’s “Reaktionsnorm” with his own description of “genotype.”

Nilsson-Ehle, H. 1914. Vilka erfarenheter hava hittills vunnits rörande möjligheten av växters acklimatisering? *Kgl. Lantbruksakad. Handl. Tidskr.* 53:537–572.

The use of the term “plasticity” to describe environmentally induced phenotypes began with Nilsson-Ehle in this work. Written in Swedish; English translations may be difficult to find.

Sarkar, S. 2003. From the Reaktionsnorm to the evolution of adaptive plasticity: A historical sketch, 1909–1999. In *Phenotypic plasticity: Functional and conceptual approaches*. Edited by T. J. DeWitt and S. M. Scheiner, 10–30. Oxford: Oxford Univ. Press.

Sarkar's book chapter chronicles the evolution of the norm of reaction (or reaction norm) concept over one hundred years. An excellent resource for finding "classic" literature and the origins of ideas and concepts used today. This work places all the others in the section into their historical context.

Schmalhausen, I. I. 1949. *Factors of evolution: The theory of stabilizing selection*. Chicago: Univ. of Chicago Press.

Schmalhausen solidified the distinction between adaptive and non-adaptive reaction norms (adaptive norms and morphoses, respectively, in his terminology) and described the process of developmental "autoregulation" in which an adaptive norm becomes refined to produce a specific phenotypic outcome. Schmalhausen's autoregulation and Waddington's canalization both describe the same basic phenomenon—that some features of organisms are buffered against large phenotypic changes.

Waddington, C. H. 1942. Canalization of development and the inheritance of acquired characters. *Nature* 150:563–565.

In this landmark paper, Waddington describes how some aspects of organismal development appear buffered against large phenotypic changes and how an environmentally induced phenotype can come under genetic control (this is later termed genetic assimilation; see sections on Genetic Assimilation and Canalization). This process reconciled views of geneticists and naturalists on how traits are acquired and inherited. Waddington's ideas were largely overlooked by his contemporaries and not included in the Modern Synthesis.

Woltereck, R. 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphnien. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 19:110–173.

Woltereck is credited with creating the reaction norm concept, and in this work he describes the reaction norm as the sum of all the possible phenotypes an organism can express in all the environment's it encounters. Written in German; English translations may be difficult to find.

Proximate Mechanisms of Plasticity

The common theme of changes in gene expression and intra-individual signaling in response to environmental conditions occurs in almost all discussions of the mechanisms underlying plasticity. The transcription factors, RNAs, hormones, etc., involved in eliciting a response are often specific to a particular cue and induced phenotype. Beldade, et al. 2011 and Aubin-Horth and Renn 2009 should act as the first resources from this section because they thoroughly introduce the reader to general mechanisms underlying plasticity and how they can be studied. Dufty, et al. 2002 focuses on the role hormones play in generating plastic responses, and Denver 1997 discusses the hormonal basis of a common example of life history plasticity. Pigliucci 1996 provides a review that sets the groundwork for later research on biased expression of genes and pathways underlying plastic responses. Similarly, Schlichting and Smith 2002 provides a review of plastic mechanisms with particular attention to cellular-level processes. Technological and methodological advances have allowed more detailed exploration of the mechanistic basis of plastic responses. Patalano, et al. 2015 is a great example of how to leverage these advances and demonstrates an integrative approach to uncovering the mechanistic details in a well-known example of phenotypic plasticity.

Aubin-Horth, N., and S. C. P. Renn. 2009. Genomic reaction norms: Using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Molecular Ecology* 18:3763–3780.

This is an invaluable resource for researchers interested in exploring the mechanistic basis of plastic traits. A variety of approaches are described and numerous examples of those approaches are included. Some of the methods described (e.g., microarrays) have become somewhat outdated, but the conceptual approaches still apply.

Beldade, P., A. R. A. Mateus, and R. A. Keller. 2011. Evolution and molecular mechanisms of adaptive developmental plasticity. *Molecular Ecology* 20:1347–1363.

This review is complementary to that of Aubin-Horth and Renn 2009 in this section because it describes cases where developmental plasticity has evolved and discusses current and future approaches for studying the mechanistic basis of plasticity. Another useful resource for potential ways of conducting developmental plasticity experiments.

Denver, R. J. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *American Zoologist* 37:172–184.

One of the best examples of phenotypic plasticity is the ability of organisms to modulate major developmental events. Here, the hormonal basis of one common example—timing of amphibian metamorphosis—is discussed in detail.

Dufty, A. M., J. Clobert, and A. P. Møller. 2002. Hormones, developmental plasticity and adaptation. *Trends in Ecology and Evolution* 17:190–196.

As implied by the title, this concise, yet broad, review explores and emphasizes the role of hormones in generating environmentally induced phenotypes. This is an important resource for those interested in manipulating plastic phenotypes because hormonal alterations may be more feasible than direct genetic or gene expression manipulations in natural systems.

Patalano, S., A. Vlasova, C. Wyatt, et al. 2015. Molecular signatures of plastic phenotypes in two eusocial insect species with simple societies. *Proceedings of the National Academy of Sciences* 112:13970–13975.

Patalano and colleagues utilize a variety of “-omic” techniques to comprehensively explore a widely appreciated example of phenotypic plasticity: eusocial insect castes. Their findings demonstrate that subtle differences in transcriptional network organization, rather than epigenetically mediated (e.g., methylation or microRNA) changes in gene expression, may be responsible for production of alternative phenotypes. This study can serve as a model for advanced graduate students or professionals interested in exploring the mechanistic basis of other plastic phenotypes.

Pigliucci, M. 1996. How organisms respond to environmental changes: From phenotypes to molecules (and vice versa). *Trends in Ecology and Evolution* 11:168–173.

This review utilizes four case studies to demonstrate the biased expression of genetic and physiological pathways for given environmental conditions. In addition, it calls for the unity of molecular and physiological biology with ecological and evolutionary biology that occurs in later works.

Schlichting, C. D., and H. Smith. 2002. Phenotypic plasticity: Linking molecular mechanisms with evolutionary outcomes. *Evolutionary Ecology* 16:189–211.

This thorough review, appropriate for graduate students and professionals, discusses phenotypic plasticity broadly and the general mechanisms of plasticity with a focus on cellular-level responses. Detailed examples from plants highlight some common themes for all plastic responses.

Costs of Plasticity

Starting with the five costs and four limits of plasticity in DeWitt, et al. 1998, the costs, limits, and trade-offs associated with phenotypic plasticity have been an important ongoing area of research. Prior to that, however, Van Tienderen was using models to explore costs associated with being a specialist or a generalist (plastic) (see Van Tienderen 1991). Relyea 2002 empirically demonstrates how such costs can be identified experimentally. Van Buskirk and Steiner 2009 and Auld, et al. 2010 provide meta-analyses and literature reviews of the costs and limits of plasticity and find that they are generally weak, as common as benefits, and hard to detect. Furthermore, Auld, et al. 2010 reduces the number of costs proposed by DeWitt, et al. 1998. The two papers led by Snell-Rood (Snell-Rood, et al. 2010; Snell-Rood 2012) discuss some of the cellular, developmental, and physiological mechanisms that can lead to apparent costs or limits on phenotypic plasticity. Finally, Murren, et al. 2015 highlights that it is probably costs and limits on phenotypes rather than plasticity itself that constrain plasticity's evolution.

Auld, J. R., A. A. Agrawal, and R. A. Relyea. 2010. Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proceedings of the Royal Society B* 277:503–511.

This review suggests that the costs of plasticity are low or nonexistent in most cases, but that co-linearity between trait values and plasticities may obscure accurate measurements of plasticity costs. In addition, the authors reduce the number of possible cost types proposed by DeWitt, et al. 1998 and posit that the distinction between costs and limits of plasticity may not be as clear as other authors suggest.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13:77–81.

This classic work crystallized the concepts of the costs and limits of plasticity. A must-read for anyone interested in plasticity and its evolution.

Murren, C. J., J. R. Auld, H. Callahan, et al. 2015. Constraints on the evolution of phenotypic plasticity: Limits and costs of phenotype and plasticity. *Heredity* 115:293–301.

Argues that costs and limits of phenotypes are more important in the evolution of plasticity than costs of plasticity itself. Various types of constraints on plasticity are discussed, and considerations for moving forward are presented.

Relyea, R. A. 2002. Costs of phenotypic plasticity. *The American Naturalist* 159:272–282.

A good example of how to experimentally test for costs of producing a plastic phenotype.

Snell-Rood, E. C. 2012. Selective processes in development: Implications for the costs and benefits of phenotypic plasticity. *Integrative and Comparative Biology* 52:31–42.

This review puts forth the view that developmental selection—phenotypic sampling and reinforcement during development—is a key mechanism influencing the costs, benefits, and consequences of plasticity. This mechanism is relevant from gene expression to behavior and learning, and it comes with specific, pronounced costs.

Snell-Rood, E. C., J. D. Van Dyken, T. Cruickshank, M. J. Wade, and A. P. Moczek. 2010. Towards a population genetic framework of developmental evolution: The costs, limits, and consequences of phenotypic plasticity. *BioEssays* 32:71–81.

By focusing on relaxed selection, mutation accumulation, and the role of modularity in developmental genetic networks, Snell-Rood and colleagues provide valuable insight on the potential mechanisms leading to constraints on the evolution of plasticity.

Van Buskirk, J., and U. K. Steiner. 2009. The fitness costs of developmental canalization and plasticity. *Journal of Evolutionary Biology* 22:852–860.

This meta-analysis found that the costs of plasticity are generally mild or nonexistent, and that this may potentially be due to the difficulty in detecting them.

Van Tienderen, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* 45:1317–1331.

Van Tienderen uses quantitative genetic models to explore the relative fitness of specialists or generalists (plastic) under hard and soft selection when there is a cost associated with being a generalist. His models demonstrate that strength and type of selection and historical events (i.e., migration, mutation) influence the evolution of specialization and/or phenotypic plasticity.

Modeling Plasticity

Theoretical modeling of phenotypic plasticity has been an important avenue of research for many years because it provides insights that could be difficult to obtain empirically. Further, it helps generate predictions and expectations that can drive empirical research programs. The foundational paper for almost all contemporary models of plasticity is Via and Lande 1985, which uses models to describe how selection can influence the evolution of phenotypic plasticity and the shapes of reaction norms. Another effort at predicting reaction norms based on organismal characteristics was Stearns and Koella 1986. Notably, the authors were able to confirm the efficacy of their models using empirical data. Around that same time, Lively 1986 identified and described the conditions in which an environmentally induced developmental switch should be favored over genetic polymorphism. Gomulkiewicz and Kirkpatrick 1992 expanded on the models of Via and Lande 1985 by considering continuous environments rather discrete patches. Scheiner 1993 provides a review of phenotypic plasticity that is largely focused on modeling and should be the first piece read in this section. A few years later, another review provided a summary of the previous decade of plasticity theory (Via, et al. 1995). The author of De Jong 2005 comes to a conclusion counter to some of her contemporaries—that phenotypic plasticity is not an important factor in evolution (or at least macroevolution). More recently, Lande 2009 is a hallmark paper that showed how the process of Genetic Assimilation can theoretically proceed. This was an extremely important outcome because there has been ongoing skepticism of genetic assimilation as

an important evolutionary process. Finally, Chevin, et al. 2010 demonstrates the importance of including phenotypic plasticity in models of extinction risk and population persistence. This work is timely as numerous species have increased risk of extinction due to ongoing climate change.

Chevin, L. M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology* 8:e1000357.

Chevin and Lande leverage evolutionary models to explore the determinants of extinction risk. They find that phenotypic plasticity and environmental sensitivity of selection are two important parameters that need to be incorporated into models of population persistence. Finally, they show how their approach can be used for predictive purposes.

De Jong, G. 2005. Evolution of phenotypic plasticity: Patterns of plasticity and the emergence of ecotypes. *New Phytologist* 116:101–118.

De Jong uses models to explore the role of plasticity in adapting to novel environments and generating ecotypes. Her conclusion is that Genetic Assimilation does not adequately explain observed patterns and that phenotypic plasticity does not have support as a major mechanism for evolution in terms of invading new niches or macroevolution.

Gomulkiewicz, R., and M. Kirkpatrick. 1992. Quantitative genetics and the evolution of reaction norms. *Evolution* 46:390–411.

Whereas the models of Via and Lande in this section utilize discrete environments, Gomulkiewicz and Kirkpatrick consider environments that vary continuously. Genetic constraints can interact with environmental variation to produce a variety of evolutionary equilibria. This paper provides a framework in which empiricists can test the optimality of their observed reaction norms.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* 22:1435–1446.

Lande showed how the process of Genetic Assimilation can theoretically proceed. First, the mean fitness drops when a new environment is encountered and the mean phenotype jumps toward the new optimum via plasticity. Then rapid evolution increases plasticity and allows the mean phenotype to approach the new optimum. Slowly, plasticity is reduced and compensated by genetic evolution of reaction norm elevation in the ancestral environment.

Lively, C. M. 1986. Canalization versus developmental conversion in a spatially variable environment. *The American Naturalist* 128:561–572.

Lively uses strategy models to investigate the evolution and maintenance of environmentally induced developmental switches. He found three stable states in which a polymorphic (or polyphenic) population can persist—an environmentally induced polyphenism, a genetically determined polymorphism, or a mixture of the two—depending on the conditions.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24:35–68.

Scheiner is one of the leading figures in modeling plasticity and has produced many papers on the subject. This excellent paper

describes three approaches taken when modeling plasticity—optimality models, quantitative genetic models, and gametic models. It should be the first piece read in this section.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.

Stearns and Koella found that the reaction norms for maturation should take one of (at least) four shapes depending on the relationship between changes in growth rate and changes in adult mortality rate and/or juvenile mortality rate. In addition, their predictions are generally supported using nineteen populations of fish and various other species.

Via, S., R. Gomulkiewicz, G. de Jong, S. M. Scheiner, C. D. Schlichting, and P. van Tienderen. 1995. Adaptive phenotypic plasticity: Consensus and controversy. *Trends in Ecology and Evolution* 10:212–217.

This review by Via and colleagues summarizes the previous decade of plasticity theory and provides an accessible synthesis of many of the other works in this section. This would be useful to read before delving more heavily into the strict modeling papers.

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.

This is *the* modeling paper from which almost all subsequent models of phenotypic plasticity stem. It uses a quantitative genetic model to describe how selection can affect phenotypic plasticity and shape reaction norm evolution. The model describes under what conditions the optimal mean phenotype will be obtained in alternative environments and how quickly such optima are reached. Migration and hard and soft selection are both considered.

Plasticity, Local Adaptation, and Gene Flow

The works in this section explore the interaction among phenotypic plasticity, local adaptation, and gene flow. Understanding how these interactions play out is important because it can determine if a lineage will persist in a given environment. An excellent summary of these interactions is found in Crispo 2008 and makes this work the first one that should be read in this section. Sultan 1995 sets the stage for later work comparing the benefits of plasticity versus local adaptation. In particular, Sultan and Spencer 2002 demonstrated that when some gene flow occurs, plasticity should be favored over local adaptation. Alpert and Simms 2002 then discuss more generally under what conditions plasticity should be favored over fixity. Gotthard and Nylin 1995 is an interesting work because it gets into the semantics of what defines adaptive plasticity versus plasticity as an adaptation. This is an important point because plasticity can sometimes be locally adaptive (Lind, et al. 2010), but tracing its origins as an adaptation can be more difficult. Lind, et al. 2010 provides an empirical demonstration of how gene flow, local adaptation, and phenotypic plasticity interact in a natural system of *Rana temporaria*. Scheiner 2013 integrates the effects of gene flow, life history patterns, and spatial and temporal heterogeneity into a comprehensive model of phenotypic plasticity evolution.

Alpert, P., and E. L. Simms. 2002. The relative advantages of plasticity and fixity in different environments: When is it good for a plant to adjust? *Evolutionary Ecology* 16:285–297.

This work discusses, in simple terms, when plasticity should be favored over fixity (local adaptation). It gives particular attention to the

scale, amplitude, and predictability of temporal and spatial environmental heterogeneity as well as the amount of available resources. As noted in the title, the focus is on plants.

Crispo, E. 2008. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation, and gene flow. *Journal of Evolutionary Biology* 21:1460–1469.

This review discusses how plasticity can impede and promote adaptive genetic divergence among populations. Figure 1 and Table 1 provide useful summaries of the potential interactions of phenotypic plasticity, adaptive genetic divergence, and gene flow while also noting the mechanism by which particular outcomes arise.

Gotthard, K., and S. Nylin. 1995. Adaptive plasticity and plasticity as an adaptation: A selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17.

This review focuses primarily on terminology and distinguishes cases where plasticity is adaptive (beneficial function maintained by selection) and cases where the plasticity is an adaptation (its origin is linked to this function). It highlights that, until then, distinguishing between the two empirically had been difficult and infrequently done. It discusses examples in animals regarding the adaptive and adaptation status of various traits.

Lind, M. I., P. K. Ingvarsson, H. Johansson, D. Hall, and F. Johansson. 2010. Gene flow and selection on phenotypic plasticity in an island system of *Rana temporaria*. *Evolution* 65:684–697.

Provided an empirical test of how gene flow, phenotypic plasticity, and local adaptation interact. It highlights the importance of migration and environmental heterogeneity for the evolution of phenotypic plasticity, and it shows that plasticity itself can be locally adaptive.

Scheiner, S. M. 2013. The genetics of phenotypic plasticity. XII. Temporal and spatial heterogeneity. *Ecology and Evolution* 3:4596–4609.

This work contains a comprehensive model that includes not just the effects of gene flow, but also interactions with life history patterns, and spatial and temporal heterogeneity.

Sultan, S. E. 1995. Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica* 44:363–383.

A thorough review of how phenotypic plasticity is adaptive in plants that was written about a decade after the revitalization of plasticity studies. Established a foundation for future work exploring local adaptation and plasticity in plants.

Sultan, S. E., and H. G. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. *The American Naturalist* 160:271–283.

By expanding upon Moran 1992 (cited under Polyphenisms), this study was the first to demonstrate (using a model) that plasticity should be favored over local adaptation in populations where some migration occurs (e.g., metapopulations) and that, in such cases, the plastic response need not be perfect or without cost.

Polyphenisms

Polyphenisms are a particular type of plastic responses that result in two or more discrete phenotypes existing within a population or species. Because of their discrete nature, they are sometimes discussed separately from more continuous or variable plastic responses. Nijhout 2003 should be the first piece read in this section because of its clear overview of the topic and how polyphenisms can arise. Another key work is Moran 1992, which first provided a general framework for understanding the origins and maintenance of polyphenisms. After Mayr 1963 popularized the term polyphenism from Michener's use of "polyphenic" (Michener 1961) its use slowly grew until a book chapter by Shapiro (Shapiro 1976) catalogued numerous examples of seasonal polyphenisms and demonstrated the pervasiveness and importance of the phenomenon. Years later, empirical work by the authors of Abouheif and Wray 2002 highlighted the importance of understanding gene networks in the production of alternate phenotypes. Insects have been (and continue to be) a major resource for studying polyphenisms. Simpson, et al. 2011 surveyed some of the most well-known insect polyphenisms, explored their underlying mechanisms, and discussed their adaptive significance to gain insight on their general features. Finally (and arguably unrelated to other works in this section), Charnov and Bull 1977 discussed the conditions in which an extreme polyphenism—environmental sex determination—should be favored over genetic sex determination (i.e., genetic polymorphism). The authors' general approach could be applied to almost all forms of polyphenism in that costs and benefits to environmental versus genetic determination need to be weighed.

Abouheif, E., and G. A. Wray. 2002. Evolution of the gene network underlying wing polyphenism in ants. *Science* 297:249–252.

This was the first study to look in-depth at the evolution of gene networks for the production of a plastic trait. It demonstrated that both evolutionary lability and conservation of the network underlying trait development may be important for the evolution of polyphenisms. This work highlights the importance of understanding developmental networks and their evolution in order to ultimately understand the evolution of plasticity.

Charnov, E. L., and J. Bull. 1977. When is sex environmentally determined. *Nature* 266:828–830.

This work formalized the conditions in which a major class of polyphenism, environmental sex determination (ESD), is selectively favored. Specifically, ESD is likely to occur where the environment is patchy, different patches favor females or males, and parents and offspring have little control over which patch type the offspring will enter. This work is important because these ideas should apply more generally to other forms of polyphenism.

Mayr, E. 1963. *Animal species and evolution*. Cambridge, MA: Belknap Press of Harvard Univ. Press.

In this important book, Mayr popularized the term "polyphenism" to cover cases where individuals within a population may exhibit a variety of phenotypes, but the differences are not the result of genetic differences. This term was slow to get traction, but is now commonly used to describe cases of phenotypic plasticity that produce discrete alternative phenotypes.

Michener, C. 1961. Social polymorphism in Hymenoptera. *Symposium of the Royal Entomological Society of London* 1:43–56.

In this somewhat obscure work, Michener coins the term "polyphenic" to refer to environmentally determined alternative phenotypes.

Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. *The American Naturalist* 139:971–989.

Moran's highly influential framework showed that ecological, developmental, and genetic factors are all important for understanding the evolutionary maintenance of polyphenisms. In particular, she noted the importance of temporal (compared to spatial) variation, intermediate frequencies of alternative selective environments, and environmental predictability. A strength of this framework is its generalizability and agreement with models that preceded it.

Nijhout, H. F. 2003. Development and evolution of adaptive polyphenisms. *Evolution and Development* 5:9–18.

Nijhout gives a clear introduction to polyphenisms in this review. Importantly, he notes that polyphenisms can arise in two ways—through developmental switches or through environmental discontinuity. He focuses on insects and emphasizes the role endocrine signaling plays in polyphenism development.

Shapiro, A. M. 1976. Seasonal polyphenism. In *Evolutionary biology*. Vol. 9. Edited by M. K. Hect, W. C. Steere, and B. Wallace, 259–333. New York: Springer.

Shapiro's book chapter catalogues numerous examples of seasonal polyphenisms—primarily in insects. By demonstrating how common seasonal polyphenisms are, this chapter solidified the importance of polyphenisms in animal populations.

Simpson, S. J., G. A. Sword, and N. Lo. 2011. Polyphenism in insects. *Current Biology* 21:R738–R749.

This review surveys some of the most well-known insect polyphenisms, explores their underlying mechanisms, and discusses their adaptive significance. In addition, commonalities among these polyphenisms are discussed to highlight general features of the phenomenon.

Evolution of Plasticity

The evolutionary implications of phenotypic plasticity have been discussed for over one hundred years. However, since ~1980s a resurgence in research on phenotypic plasticity has resulted in new appreciation for the role it might play in evolution. This renewed interest has been partially fueled by the acknowledgement that environmentally induced phenotypes may have greater evolutionary potential than mutationally induced ones. Specifically, environmentally induced phenotypes could be powerful evolutionary forces because they occur in response to specific environmental conditions (and in a sense are “directed”), affect multiple individuals at once, and promote the storage and release of cryptic genetic variation under atypical conditions. A common theme of contemporary literature on the evolution of plasticity is that plasticity might precede and facilitate subsequent evolutionary change.

Experimental Evolution

As with all subfields within evolutionary biology, experimental evolution studies have provided some of the strongest support for plasticity's role in evolution and how it itself evolves. Results from experimental evolution studies provided an important step in the recognition of plasticity as a significant evolutionary factor and paved the way for some of the later theoretical and empirical work seen in other sections of this bibliography. A major strength of these kinds of studies is the use of inbred or genetically identical lines (or genotypes) exposed to different environments. Such an approach directly mirrors the classical definition of phenotypic plasticity (i.e., a single genotype giving rise to multiple phenotypes depending on environmental conditions). Although other works have used an experimental evolution approach, they are covered in other sections of this bibliography (e.g., see Waddington 1953 in Genetic

Accommodation and Waddington 1953 and Waddington 1959 in Genetic Assimilation). To become familiar with experimental evolutionary studies of plasticity, Kassen 2002 and then Garland and Kelly 2006 should be read because they are reviews that highlight some of the major insights gained from these types of studies. Then, Hillesheim and Stearns 1991 should be read because it acts as a good guide for how experimental evolution studies can be performed, particularly in *Drosophila*. Similarly, Chippindale, et al. 1993 used *Drosophila* to demonstrate that trade-offs between survival and reproduction can arise via plastic responses as well as evolutionary processes. Prior to either of these studies, Perkins and Jinks 1971 established that the genotype–environment interaction can be artificially selected upon to a desired level and that selection for plasticity in different traits in response to different environmental conditions can occur relatively independently. Likewise, Scheiner and Lyman 1991 found that selection on phenotypic plasticity of a trait can occur relatively independently of selection on the mean of the trait. Spitze 1992 is included as a gateway into the use of *Daphnia* as a model organism for studying the evolution of plasticity and because it provides important insights for this system. Finally, Suzuki and Nijhout 2006 and Sikkink, et al. 2014 address questions related to genetic accommodation and assimilation (see Genetic Accommodation and Genetic Assimilation) in atypical (i.e., non-*Drosophila* and non-*Daphnia*) model organisms for studying plasticity.

Chippindale, A. K., A. M. Leroi, S. B. Kim, and M. R. Rose. 1993. Phenotypic plasticity and selection in *Drosophila* life-history evolution. I. Nutrition and cost of reproduction. *Journal of Evolutionary Biology* 6:171–193.

Chippindale and colleagues demonstrate, using experimental evolution, that dietary manipulation in *Drosophila melanogaster* can mimic *evolutionary* (e.g., dependent on alleles) and *phenotypic* (e.g., dependent on physiology/metabolism) trade-offs between survival and reproduction. Their results suggest that the evolutionary response and the plastic response might share a common physiological basis, but that some discrepancies do exist.

Garland, T., and S. A. Kelly. 2006. Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology* 209:2344–2361.

Garland and Kelly provide a review of studies that used experimental evolution to investigate phenotypic plasticity. Somewhat uniquely, they devote a good amount of space to discussing an example from mice that were selected for wheel-running behavior. Their take-home message/advice was that any selection experiment in which the selective event is more than instantaneous should explore whether plasticity in the appropriate (adaptive) direction has increased as a component of the response to selection.

Hillesheim, E., and S. C. Stearns. 1991. The response of *Drosophila melanogaster* to artificial selection on body weight and its phenotypic plasticity in two larval food environments. *Evolution* 45:1909–1923.

This study is a classical example of how plasticity is studied in an experimental evolution context. Hillesheim and Stearns demonstrated that selection could act on traits in alternative environments, but also on plasticity itself. This work is probably most useful as a guide for how to perform a simple experimental evolution of plasticity study.

Kassen, R. 2002. The experimental evolution of specialists, generalists, and maintenance of diversity. *Journal of Evolutionary Biology* 15:173–190.

Although it is somewhat broader than other works included in this section, this is an excellent resource for finding discussion and references of experimental evolution studies on phenotypic plasticity. This should be the first work read in this section because it helps set the stage for the others and references many other classic pieces of experimental evolution.

Perkins, J. M., and J. L. Jinks. 1971. Specificity of the interaction of genotypes with contrasting environments. *Heredity* 26:463–474.

This work established that the genotype–environment interaction can be artificially selected upon to a desired level and that different genotypes harbor differences in sensitivity to environmental conditions. In addition, it demonstrated that selection for plasticity in different traits (e.g., height versus flowering time) in response to different environmental conditions (e.g., fertilizer versus seasonality) can occur relatively independently. Finally, this work also hints at the potentially significant role plasticity could play in agriculture.

Scheiner, S. M., and R. F. Lyman. 1991. The genetics of phenotypic plasticity. II. Response to selection. *Journal of Evolutionary Biology* 4:23–50.

Scheiner and Lyman found that selection on *phenotypic plasticity of a trait* (thorax size responding to temperature) is possible and that it is partially independent of selection on the *mean of the trait*. In addition, they found that they were able to select for no plasticity, but in these lines genetic variation for plasticity still remained. Finally, the authors suggest that the plasticity of a trait is determined by loci that are separate from those determining the trait mean itself.

Sikkink, K. L., R. M. Reynolds, C. M. Ituarte, W. A. Cresko, and P. C. Phillips. 2014. Rapid evolution of phenotypic plasticity and shifting thresholds of genetic assimilation in the nematode *Caenorhabditis remanei*. *G3: Genes, Genomes, Genetics* 4:1103–1112.

This experimental evolution study of heat shock resistance in nematodes revealed that apparent genetic assimilation (see Genetic Accommodation and Genetic Assimilation) is possible without global changes in gene regulation (e.g., gene expression), but could instead be due to a shift in induction threshold. Thus, before one concludes that genetic assimilation has occurred, a broader environmental context should be explored.

Spitze, K. 1992. Predator-mediated plasticity of prey life history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. *The American Naturalist* 139:229–247.

This study revealed several important features of the well-studied inducible defenses of *Daphnia* species. First, there is inter-genotype variation in the extent of induced defenses. Second, the extent of the induced defense (neck teeth) is not a good predictor of life history changes or fitness gains. Finally, plasticity has different life history consequences depending on genotype. Importantly, this work highlights the need to explore other traits beyond the most visually apparent in order to more fully understand the phenotypic consequences of environmental variability.

Suzuki, Y., and H. F. Nijhout. 2006. Evolution of a polyphenism by genetic accommodation. *Science* 311:650–652.

Suzuki and Nijhout used experimental evolution in the tobacco hornworm (*Manduca sexta*) to demonstrate that selection on a previously cryptic reaction norm (revealed through novel mutation) can lead to the evolution of a polyphenism or loss of plasticity (genetic assimilation). In addition, they suggest that regulators of developmental hormone levels can mask genetic variation and that when they are disrupted they can act as evolutionary capacitors that facilitate the evolution of novelty.

Genetic Accommodation

Genetic accommodation is an important step in the Plasticity-First Evolution process and is the adaptive refinement or extension of an environmentally (or mutationally) induced phenotype. This term was introduced and described at length in West-Eberhard 2003. Three subcategories of genetic accommodation have been described. Crispo 2007 gives a nice description of genetic accommodation and helps clarify the subtleties among these different subcategories. The first—genetic assimilation—involves the loss of plasticity and production of the induced phenotype constitutively (Waddington 1953). Genetic compensation (Grether 2005) occurs when ancestral phenotypes are restored in the presence of phenotype-altering environmental stimuli. The Baldwin effect (Baldwin 1896) is the oldest of the three and has come to be understood as selection favoring increased plasticity (Crispo 2007) and environmentally induced phenotypes coming under greater genetic control. In Simpson 1953, the author coined the term “Baldwin effect” and concluded that it does not contradict the Modern Synthesis. However, he was skeptical of its importance in evolution. This skepticism has continued through the 21st century for all types of genetic accommodation and has spurred increased efforts in testing these ideas experimentally and in nature. Waddington 1953 and Suzuki and Nijhout 2006 both showed that genetic accommodation can occur in the laboratory. However, showing that a process *can* happen is different from showing that it *has* happened in any natural population. Therefore, Schlichting and Wund 2014 sought to assess the strength of the evidence for genetic accommodation and catalogued over a hundred studies that provide some level of evidence for genetic accommodation, many of which are from wild populations. Nevertheless, the significance of genetic accommodation still remains contentious.

Baldwin, J. M. 1896. A new factor in evolution. *The American Naturalist* 30:441–451.

Baldwin proposes a mechanism of evolution in which a character acquired by members of a group of organisms (i.e., induced by the environment) may be reinforced or replaced, via selection, by similar hereditary characters. In 1896, Lloyd Morgan and H. F. Osborn independently developed similar ideas (see Osborn 1896, cited under Learning as Plasticity). Baldwin refined his ideas in later works (e.g., *Development and evolution*. New York: Macmillan, 1902).

Crispo, E. 2007. The Baldwin effect and genetic assimilation: Revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* 61:2469–2479.

In this review, Crispo describes the similarities and differences between the Baldwin effect and genetic assimilation and places both in the broader context of genetic accommodation. This review is particularly useful in that it puts older writings in modern terms. Table 1 is especially useful for identifying predictions of the Baldwin effect and genetic assimilation.

Grether, G. F. 2005. Environmental change, phenotypic plasticity, and genetic compensation. *The American Naturalist* 166:E115–E123.

Grether describes another subcategory of genetic accommodation (in addition to the Baldwin effect and genetic assimilation) that he calls genetic compensation. This term is less frequently used, but is described as the opposite of genetic assimilation—ancestral phenotypes are restored in the presence of phenotype-altering environmental stimuli.

Schlichting, C. D., and M. A. Wund. 2014. Phenotypic plasticity and epigenetic marking: An assessment of evidence for genetic accommodation. *Evolution* 68:656–672.

The first half of this review describes what role epigenetic marks may play in genetic accommodation. The second half focuses on the strength of the evidence for genetic accommodation as an evolutionary process. While the text is beneficial, readers should definitely consult the supplemental tables for over a hundred specific examples with possible links to genetic accommodation.

Simpson, G. G. 1953. The Baldwin effect. *Evolution* 7:110–117.

Simpson coins the term “Baldwin effect” in his discussion of the process and the evidence for it. He concludes that it is not inconsistent with the Modern Synthesis framework, but is doubtful of its importance.

Suzuki, Y., and H. F. Nijhout. 2006. Evolution of a polyphenism by genetic accommodation. *Science* 311:650–652.

This study was the first to show that genetic accommodation can result in polyphenism. In addition, it was the first to show a clear mechanism by which the evolved change happened. The study also found evidence of genetic assimilation.

Waddington, C. H. 1953. Genetic assimilation of an acquired character. *Evolution* 7:118–126.

Waddington provides the first empirical test of genetic accommodation (specifically, genetic assimilation). He demonstrated that selection can favor the loss of phenotypic plasticity and that a previously environmentally induced phenotype can evolve to be constitutively expressed even in the absence of the original inducing stimulus (see also Genetic Assimilation).

West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford: Oxford Univ. Press.

This book is a must-have for anyone interested in evolution and phenotypic plasticity. It is replete with ideas and examples. This book is probably most cited for coining the term “genetic accommodation.” However, genetic accommodation is only a part of the adaptive evolutionary process described by West-Eberhard.

Genetic Assimilation

Genetic assimilation is the adaptive loss of plasticity that leads to constitutive expression of a previously environmentally induced phenotype. The idea that environmentally induced phenotypes can become heritable is often attributed to Lamarck 1809. However, Lamarck’s conception of how this process happens was incorrect. Waddington 1942 and Schmalhausen 1949 (both referenced in Historical Works) independently developed hypotheses on how such environmentally induced traits could come under genetic control. This process was first demonstrated by Waddington 1953 in *Drosophila* wing venation. This work was criticized because it did not show that genetic assimilation could be adaptive. Therefore, in Waddington 1959, the author performed an experiment similar to that in his 1953 work, but focused on an adaptive trait—anal papillae that are responsible for osmotic stress tolerance. Despite the work of Waddington and others, genetic assimilation remained largely a footnote or interesting anomaly in evolutionary biology. The review Matsuda 1982 suggested that genetic assimilation may be important in the wild and provides a schematic for how it might proceed in animals. Still, misunderstandings and skepticism over the significance of genetic assimilation persisted into the 21st century and led to the review Pigliucci, et al. 2006, which seeks to clarify misconceptions and address critiques of the role played by phenotypic plasticity generally, and genetic assimilation specifically, in evolution. Emerging empirical work helped spur the need for such a review because genetic assimilation was being brought into mainstream evolutionary biology again. Chapman, et al. 2000 roughly marks the start of this renewed interest in genetic assimilation and finds evidence consistent with the process of genetic assimilation in the wild. Sixteen years later, Parsons, et al. 2016 provided a compelling example of genetic assimilation at the genetic level. Despite renewed interest in (and evidence for) genetic assimilation, its proximate mechanisms remain poorly understood. Ehrenreich and Pfennig 2016, Schneider and Meyer 2017 (see Speciation and Diversification), and Lande 2009 (cited under Modeling Plasticity) provide insights on the proximate mechanisms of how the process of genetic assimilation may proceed.

Chapman, L. G., F. Galis, and J. Shinn. 2000. Phenotypic plasticity and the possible role of genetic assimilation: Hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecology Letters* 3:387–393.

This study was arguably the first to explicitly investigate genetic assimilation in the wild. Fish from a low-oxygen environment had greater gill surface area than those in a well-oxygenated environment. Importantly, a laboratory experiment also demonstrated that siblings reared in low-oxygen conditions developed greater surface area than their well-oxygenated siblings. However, the way in which greater surface area was achieved differed between the wild and lab groups.

Ehrenreich, I. M., and D. W. Pfennig. 2016. Genetic assimilation: A review of its potential proximate causes and evolutionary consequences. *Annals of Botany* 117:769–779.

The major contribution of this review is its thorough exploration of the proximate genetic, molecular, and physiological mechanisms that may underlie phenotypic plasticity and the process of genetic assimilation.

Lamarck, J.-B. 1809. *Philosophie zoologique*. Paris: Museum d’Histoire Naturelle.

Oftentimes Lamarckism is brought up when discussing genetic assimilation. In this work, Lamarck describes two laws: 1) that use and disuse cause body structures to grow or shrink and 2) these changes are inherited. Such “inheritance of acquired characters” is related to, but distinct from, the process of genetic assimilation. Written in French; English translations may be difficult to find.

Matsuda, R. 1982. The evolutionary process in talitrid amphipods and salamanders in changing environments, with a discussion of “genetic assimilation” and some other evolutionary concepts. *Canadian Journal of Zoology* 60:733–749.

This review was one of the first to explore the extent to which genetic assimilation may be present in the wild as well as providing a hypothetical diagram (Fig. 2) describing the process of genetic assimilation in animal traits. Matsuda suggests that genetic assimilation is responsible for neoteny (reaching sexual maturity while retaining larval characteristics) in salamanders.

Parsons, K. J., M. Concannon, D. Navon, et al. 2016. Foraging environment determines the genetic architecture and evolutionary potential of trophic morphology in cichlid fishes. *Molecular Ecology*.

Using quantitative trait locus (QTL) mapping and hybrid crosses, Parsons and colleagues find evidence for genetic assimilation at a specific locus in cichlid. Specifically, the environment was a better predictor of phenotype than was genotype at this locus, and the ancestral allele had greater environmental sensitivity than the derived allele.

Pigliucci, M., C. J. Murren, and C. D. Schlichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* 209:2362–2367.

Pigliucci and colleagues explore misunderstandings about the role of phenotypic plasticity in evolution. In particular, they address critiques of the role played by phenotypic plasticity and genetic assimilation in evolution and how this role relates to the Modern Synthesis.

Waddington, C. H. 1953. Genetic assimilation of an acquired character. *Evolution* 7:118–126.

Using fruit flies and experimental evolution, Waddington provides the first empirical test of genetic assimilation and demonstrates that temperature-induced changes in wing venation could be selected for constitutive expression in the absence of temperature induction (see also Genetic Accommodation)

Waddington, C. H. 1959. Canalization of development and genetic assimilation of acquired characters. *Nature* 183:1654–1655.

Although this is not the first time Waddington wrote on these topics (see Waddington 1942 in Historical Works and Waddington 1953 in this section and the Genetic Accommodation section), this is the first study to show genetic assimilation of an adaptive trait—anal papillae responsible for osmotic stress tolerance.

Canalization

Canalization is essentially the opposite of plasticity; a canalized trait is produced regardless of environmental conditions. However, for one trait to be canalized, one or more others must be plastically expressed. Various authors have tried to unravel the conditions that favor canalization (Wagner, et al. 1997) and the underlying mechanisms of canalization. In particular, Wilkins 1997 suggested that redundancy due to paralogous genes is key for canalization to arise. This view was challenged by Wagner 2000, which demonstrated (using genomics data in yeast) that interactions of unrelated genes rather than redundancy of paralogous genes are the key to canalization and robustness against developmental perturbations. Furthermore, Siegal and Bergman 2002 used a model to show that canalization might be an inevitable consequence of complex gene regulation networks. That is, the more complex a gene network (i.e., the more interactions it has), the more canalized it will be. However, the more recent work Rünneburger and Le Rouzic 2016 suggests that mutational parameters have greater influence than network size and complexity and that (reminiscent of the view of Wilkins 1997) redundancy in gene regulation is important for the evolution of genetic canalization. Importantly, Hornstein and Shomron 2006 integrates microRNAs (miRNAs) into the canalization framework and adds to our understanding of the complexity that promotes canalization. By focusing on ultimate, rather than proximate, causes of canalization, Masel, et al. 2007 shows how non-selective processes can lead to the loss of plasticity. Finally, another important aspect of canalization not yet mentioned is that it can promote the accumulation of cryptic genetic variation that can be exposed when environmental conditions change. The authors of Rutherford and Lindquist 1998 first showed this to be the case when they found that heat-shock protein 90 (Hsp90) acts as a buffer against phenotypic perturbation and that this buffering not only is a mechanism of canalization but also allows accumulation of cryptic genetic variation.

Hornstein, E., and N. Shomron. 2006. Canalization of development by microRNAs. *Nature Genetics* 38:S20–S24.

This article provides a framework that integrates microRNAs (miRNAs) into current thinking on canalization of development. The importance of miRNAs acting within gene networks is explored and emphasized.

Masel, J., O. D. King, and H. Maughan. 2007. The loss of adaptive plasticity during long periods of environmental stasis. *The American Naturalist* 169:38–46.

Using a mathematical model, the authors show how the loss of plasticity (i.e., canalization) can occur through non-selective processes, such as mutational degradation and random genetic drift.

Rünneburger, E., and A. Le Rouzic. 2016. Why and how genetic canalization evolves in gene regulatory networks. *BMC Evolutionary Biology* 16:239.

Using quantitative genetic models, these authors show that mutational parameters are more important than network topology for the evolution of genetic canalization. Furthermore, they propose a mechanism of canalization that involves shrinkage of mutational targets and redundancy in gene regulation.

Rutherford, S. L., and S. Lindquist. 1998. Hsp90 as a capacitor for morphological evolution. *Nature* 396:336–342.

Rutherford and Lindquist experimentally demonstrate that heat-shock protein 90 (Hsp90) acts as a buffer against phenotypic perturbation. The buffering ability of Hsp90 not only serves as mechanism of canalization, but also provides a means for the accumulation of cryptic genetic variation.

Siegal, M. L., and A. Bergman. 2002. Waddington's canalization revisited: Developmental stability and evolution. *Proceedings of the National Academy of Sciences* 99:10528–10532.

Siegal and Bergman demonstrate that selection toward an optimum phenotype is not necessary for canalization to evolve. Instead, they show (using a model) that canalization might be an inevitable consequence of complex networks of gene regulation. More highly connected networks evolve to be more canalized.

Wagner, A. 2000. Robustness against mutations in genetic networks of yeast. *Nature Genetics* 24:355–361.

Using functional genomics data, Wagner demonstrated that interactions among unrelated genes, rather than redundancy of paralogous genes, is the major cause of canalization and robustness against mutations that affect development.

Wagner, G. P., G. Booth, and H. Bagheri-Chaichian. 1997. A population genetic theory of canalization. *Evolution* 51:329–347.

Wagner and colleagues use various population genetic models of a quantitative trait under stabilizing selection to explore the conditions that favor environmental and genetic canalization. They highlight the importance of genetic variation and the strength and type of selection acting on a population.

Wilkins, A. S. 1997. Canalization: A molecular genetic perspective. *BioEssays* 19:257–262.

This essay discusses the molecular genetic basis for stabilization of development against mutation effects (genetic canalization). Redundancy because of paralogous genes is emphasized as having an important role. Later works challenge this view.

Plasticity-First Evolution

Plasticity-first evolution (PFE) is related to other ideas like Behavioral Plasticity, Genetic Accommodation, Genetic Assimilation, and Novelty. In essence, it posits that phenotypic plasticity may precede and facilitate further evolutionary change, in particular adaptation. Moczek 2007 and Paaby and Rockman 2014 are good introductory reviews of the key terms and processes in PFE, and they should function to orient readers for other works in this section. A major point of contention surrounding PFE is whether or not the evidence is

strong enough to conclude that it is a major contributor to evolutionary change. Two works included here are reviews of how PFE works that also discuss potential cases of PFE from natural populations (Price, et al. 2003; Schwander and Leimar 2011). Levis and Pfennig 2016 serves a similar function, but goes further to present specific predictions and methods that can be used to test this process in natural populations. Badyaev 2005 and Ghalambor, et al. 2007 provide additional insights on how plasticity can contribute to evolutionary changes that are related to PFE, but not explicitly discussed in the context of PFE. In these reviews, Badyaev argues for the importance of stress in revealing variation on which selection can act, and Ghalambor and colleagues discuss the evolutionary potential of adaptive and non-adaptive plasticity in promoting adaptation to novel environments. Both of these insights can inform under what conditions we might expect to see PFE. Finally, Badyaev 2009 provides relatively comprehensive empirical support for PFE (using terminology of the Baldwin effect) in house finches adapting to North America.

Badyaev, A. V. 2005. Stress-induced variation in evolution: From behavioural plasticity to genetic assimilation. *Proceedings of the Royal Society B* 272:877–886.

Badyaev convincingly argues for the importance of stress and stress-induced variation in evolution. In this review, examples of stress-induced genotypic and phenotypic patterns are discussed. The effect of stress on homeostasis is also important.

Badyaev, A. V. 2009. Evolutionary significance of phenotypic accommodation in novel environments: An empirical test of the Baldwin effect. *Transactions of the Royal Society B* 364:1125–1141.

Here, Badyaev provides a review of his research program on house finches (*Carpodacus mexicanus*) within the framework of the Baldwin effect. In doing so, he puts forth four general observations that, if found, would support evolution via plasticity-first evolution and genetic accommodation.

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* 21:394–407.

This influential review thoroughly and clearly discusses evolutionary outcomes of plasticity. In particular, the outcomes of perfect and imperfect adaptive plasticity and non-adaptive and “random” plasticity are described and discussed. This review is also among those that champion comparisons of ancestral versus derived lineages for determining the adaptive value of plasticity and its evolution.

Levis, N. A., and D. W. Pfennig. 2016. Evaluating “plasticity-first” evolution in nature: Key criteria and empirical approaches. *Trends in Ecology and Evolution* 31:563–574.

This article serves as a “how-to” guide for testing predictions consistent with plasticity-first evolution. It acts as an introduction for those unfamiliar with the plasticity-first hypothesis and provides a roadmap for evaluating it in various systems. Explicit predictions, experimental designs, and examples are discussed.

Moczek, A. P. 2007. Developmental capacitance, genetic accommodation, and adaptive evolution. *Evolution and Development* 9:299–305.

This review provides a good introduction to plasticity-first evolution and describes the key components necessary for showing this process in nature. Throughout, the review emphasizes a shift in focus away from strictly genes and mutations to a more in-depth understanding of developmental processes and how they influence evolution.

Paaby, A. B., and M. V. Rockman. 2014. Cryptic genetic variation: Evolution's hidden substrate. *Nature Reviews Genetics* 15:247–258.

While not the first discussion of cryptic genetic variation, this review summarizes and synthesizes the concept and how it can facilitate adaptation in the context of plasticity-first evolution.

Price, T. D., A. Qvarnström, and D. E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B* 270:1433–1440.

Price and colleagues emphasize a simple additive genetic model for describing the process of an environmentally induced phenotype evolving to be constitutively expressed in the absence of the inducing stimulus (i.e., plasticity-first evolution or genetic assimilation). In addition, they argue that moderate levels of adaptive plasticity are necessary for evolution in novel environments. Two case studies using birds are presented in this context.

Schwander, T., and O. Leimar. 2011. Genes as leaders and followers in evolution. *Trends in Ecology and Evolution* 26:143–151.

This analysis finds relatively equal support for cases where genes act as leaders and cases where genes act as followers in evolution, thus suggesting the interchangeability of genetic and environmental inputs during development. However, the evolution of particular types of traits may be more likely to proceed via one path than the other. The examples are restricted to alternative polyphenisms/polymorphisms and are supported by phylogenetic inference.

Macroevolutionary Consequences of Plasticity

The macroevolutionary consequences of plasticity are potentially the most significant but are also the most controversial. By simply allowing species to persist in a new or altered environment, phenotypic plasticity promotes subsequent evolution and diversification. It can also influence what phenotypes are produced during adaptive radiations. Additionally, when a species enters a new environment, the developmental reorganization that happens via phenotypic plasticity may give rise to novel phenotypes.

Speciation and Diversification

The role of plasticity in diversification is among the most controversial (perhaps second only to novelty) among evolutionary biologists. West-Eberhard 1989 and West-Eberhard 2005 provide extensive evidence and discussion of how plasticity can influence diversification. Her works in this section offer abridged versions of the cases she makes in West-Eberhard 2003 (see Books and Genetic Accommodation). Most later works offer pithier and/or clearer explanations of her general ideas. For instance, Pfennig, et al. 2010 hits on many of the same topics as the works by West-Eberhard, but is much easier to digest and should be read first in this section. To lend support to the arguments of West-Eberhard and Pfennig and colleagues, the simulation study Thibert-Plante and Hendry 2011 confirmed that plasticity needs to be considered when investigating ecological speciation and reproductive isolation. Furthermore, Susoy, et al. 2015 found that the appearance of a resource use polyphenism coincided with increased evolutionary rates in nematodes. Finally, Wund, et al. 2008 provided the first explicit test of the “flexible stem” model proposed by West-Eberhard and found evidence that plasticity might precede and bias subsequent divergence of species. Along these lines, the review Schneider and Meyer 2017 discusses the molecular mechanisms that might underlie such plasticity-mediated adaptive radiations. As noted at the beginning of this entry, plasticity's role in diversification has remained controversial. The chapter Futuyma 2015 provides an antithetical view to the

others in this section. While it does not deny that plasticity could be important for evolutionary diversification, it does suggest that our understanding is not revolutionary and that an extended evolutionary synthesis is unwarranted. Pigliucci and Murren 2003 is somewhat light on macroevolutionary discussion, but provides a useful concept map that links various biological ideas and processes to phenotypic plasticity and genetic assimilation. Furthermore, it also helped provide a framework for later discussions of plasticity's role in evolution and diversification.

Futuyma, D. J. 2015. Can modern evolutionary theory explain macroevolution? In *Macroevolution: Explanation, interpretation, and evidence*. Edited by E. Serrelli and N. Gontier, 29–85. New York: Springer.

This book chapter discusses a number of contemporary developments that led some researchers to call for an extended evolutionary synthesis and describes how these developments already fit within the framework of the Modern Synthesis. This work is important in that it provides a contrary viewpoint to other discussions of plasticity's role in diversification and speciation.

Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology and Evolution* 25:459–467.

This pithy review should be the first stop for anyone interested in plasticity's role in diversification. It accessibly provides an overview of plasticity's impacts on novelty, divergence among populations and species, formation of new species, and adaptive radiation.

Pigliucci, M., and C. J. Murren. 2003. Genetic assimilation and a possible evolutionary paradox: Can macroevolution sometimes be so fast as to pass us by? *Evolution* 57:1455–1464.

Perhaps the most useful aspect of this “early” review of genetic assimilation is the concept map presented in Figure 2. This map can help anyone studying phenotypic plasticity to develop connections among topics and design experiments. The review also traces the history of genetic assimilation. Unfortunately, its explicit treatment of macroevolution could be a bit more thorough. Nevertheless, it provides a framework that, at the time, was relatively novel and insightful.

Schneider, R. F., and A. Meyer. 2017. How plasticity, genetic assimilation and cryptic genetic variation may contribute to adaptive radiations. *Molecular Ecology* 26: 330–350.

This review explores the molecular mechanisms that might lead to canalization of an initially plastic trait in the context of adaptive radiations. The authors use the flexible stem framework developed in West-Eberhard 2003. It is important because most other works focus on phenotypic patterns and the underlying mechanisms remain poorly understood.

Susoy, V., E. J. Ragsdale, N. Kanzaki, and R. J. Sommer. 2015. Rapid diversification associated with a macroevolutionary pulse of developmental plasticity. *eLife*.

This study utilized a comparative analysis of morphology in a group of ninety nematode species. They found that the appearance of a resource acquisition polyphenism coincided with increased complexity and evolutionary rates and that these rates were even higher following genetic assimilation (i.e., loss of plasticity) of a single phenotype.

Thibert-Plante, X., and A. P. Hendry. 2011. The consequences of phenotypic plasticity for ecological speciation. *Journal of*

***Evolutionary Biology* 24:326–342.**

Thibert-Plante and Hendry use a simulation study to evaluate plasticity's effects on ecological speciation. A number of relevant outcomes were observed (such as the timing of plasticity relative to dispersal) that suggest plasticity can have an important influence during ecological speciation and should be considered when investigating the evolution of reproductive isolation.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* 20:249–278.

This review established the theme of subsequent works by West-Eberhard. It is particularly useful for those interested in how phenotypic and genetic accommodation (see Books, Genetic Accommodation, and Novelty) can contribute to diversity. It covers a wide variety of topics that fall under the umbrella of “diversity” and may be preferred over West-Eberhard 2003, a nearly 800-page book that covers similar topics.

West-Eberhard, M. J. 2005. Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences* 102:6543–6549.

In this work, which is an extension of West-Eberhard 1989 and an abridged version of key points from West-Eberhard 2003 (cited under Books), West-Eberhard argues that species differences and novel phenotypes arise through reorganization of ancestral phenotypes followed by genetic accommodation. This work hammers in the point that environmentally induced variants might have greater evolutionary potential than mutationally derived novelties, and that genes may often be followers, rather than leaders, in evolution.

Wund, M. A., J. A. Baker, B. Clancy, J. L. Golub, and S. A. Foster. 2008. A test of the “flexible stem” model of evolution: Ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *The American Naturalist* 172:449–462.

This empirical study was the first explicit test of the “flexible stem” model presented by West-Eberhard. Wund and colleagues showed that when individuals from an “ancestral” population were exposed to “derived” conditions, they developed phenotypes in the direction of those possessed by “derived” individuals. Thus, ancestral plasticity may have facilitated the subsequent phenotypic divergence among stickleback ecomorphs.

Novelty

Generating novelty is one of the most important (and controversial) consequences of phenotypic plasticity. Even defining novelty is difficult; a number of reviews have been written on this topic alone. Therefore, the first works that should be read in this section are Hallgrímsson, et al. 2012; Sterelny 2009; and Pigliucci 2006, because they all provide definitions of novelty, but from different perspectives. Hallgrímsson and colleagues focus on overcoming developmental constraints as a condition of novelty; Sterelny discusses how niche construction can limit the variation available to selection; and Pigliucci discusses three frameworks for investigating novelty. One of the frameworks he suggests is Genetic Accommodation. Moczek, et al. 2011 develops this framework further and includes discussion of its mechanistic details. Uncovering of cryptic genetic variation is an important part of the framework developed in Moczek, et al. 2011. Palmer 2012 goes into a bit more detail on this particular aspect and gives an interesting history of “use” and “disuse.” Despite the attention these works pay to genetic accommodation, the creator of the term, West-Eberhard (see Genetic Accommodation), viewed it as a downstream step in the process of adaptive evolution. Prior to genetic accommodation, West-Eberhard 2005 attributed the origins of novel phenotypes to *phenotypic* accommodation. Gilbert and Epel 2015 is an accessible

resource whose content often relates to the evolution of novelty and is useful for identifying diverse examples. Finally, an experiment from Standen, et al. 2014 suggests a possible role for phenotypic plasticity in the transition of tetrapods from aquatic to terrestrial habitat, and Alif, et al. 2016 is among the few works that explicitly tested whether behavioral plasticity may precede the evolution of morphological novelties.

Alif, B. C., P. A. P. Durst, D. W. Pfennig. 2016. Behavioral plasticity and the origins of novelty: The evolution of the rattlesnake rattle. *The American Naturalist* 188:475–483.

This empirical work is among the few that have explicitly tested the hypothesis that behavioral plasticity may precede the evolution of morphological traits. In this case, defensive tail vibration behavior (a widespread type of behavioral plasticity in snakes) appears to have preceded the evolution of the rattlesnake rattle. Other examples of this type of evolution can be found in the Behavioral Plasticity section (see Wyles, et al. 1983 and Wcislo 1989 in particular).

Gilbert, S. F., and D. Epel. 2015. *Ecological developmental biology*. 2d ed. Sunderland, MA: Sinauer.

While indirect, many of the topics in this book are relevant to the role of plasticity in the evolution of novelty. It is especially useful because of its accessibility and extensive use of examples.

Hallgrímsson, B., H. A. Jamniczky, N. M. Young, C. Rolian, U. Schmidt-Ott, and R. S. Marcucio. 2012. The generation of variation and the developmental basis for evolutionary novelty. *Journal of Experimental Zoology B* 318:501–517.

This review takes a developmental approach to defining novelty. Specifically, Hallgrímsson and colleagues propose that for a trait to be novel it must have evolved by a transition between adaptive peaks and that this transition must have overcome a previous developmental constraint. While this paper does not explicitly deal with plasticity, it is a good resource for discussions of novelty and includes a number of other relevant references.

Moczek, A. P., S. Sultan, S. Foster, et al. 2011. The role of developmental plasticity in evolutionary innovation. *Proceedings of the Royal Society B* 278:2705–2713.

This review should be first piece read in this section. It utilizes the phenotypic/genetic accommodation framework developed by West-Eberhard to explore how evolutionary novelties may arise. Importantly, mechanistic details are discussed and empirical evidence of this framework is presented.

Palmer, A. R. 2012. Developmental plasticity and the origin of novel forms: Unveiling cryptic genetic variation via “use and disuse.” *Journal of Experimental Zoology B* 318:466–479.

Palmer describes a simple model that illustrates how cryptic genetic variation may be exposed to selection via developmentally plastic responses that affect performance because of “use” and “disuse.” Learning and performance are discussed throughout. Starting with Lamarck, this work provides an interesting history of “use” and “disuse” and plasticity.

Pigliucci, M. 2006. What, if anything, is an evolutionary novelty? *Philosophy of Science* 75:887–898.

This review is one of many that could have been chosen that highlights the difficulty with defining “novelty.” Pigliucci discusses some of the attempts others have made at doing so, describes why the Modern Synthesis is ill-equipped for studying the origin of novelties, and presents three frameworks (complexity theory, genetic accommodation, and epigenetic inheritance) that potentially allow greater insight on the origin and evolution of novelties than the Modern Synthesis.

Standen, E. M., T. Y. Du, and H. C. E. Larsson. 2014. Developmental plasticity and the origin of tetrapods. *Nature* 513:54–58.

This intriguing study suggests a role for plasticity in a major evolutionary transition. Standen and colleagues suggest that plasticity in type of locomotion (i.e., terrestrial or aquatic) may have contributed to the colonization of land by early tetrapods. While the scope of this study is significant, an important caveat is that it is unknown whether the plasticity they explored is heritable.

Sterelny, K. 2009. Novelty, plasticity, and niche construction: The influence of phenotypic variation on evolution. In *Mapping the future of biology*. Edited by A. Barberousse, M. Morange, and T. Pradeu, 93–109. New York: Springer.

An important aspect of this book review is that it incorporates niche construction with plasticity to give an explanation of how evolutionary novelties arise. Of particular interest, Sterelny discusses how niche construction can effectively limit the extent of environments experienced by a plastic organism and the importance of this limitation on the supply of variation presented to selection.

West-Eberhard, M. J. 2005. Phenotypic accommodation: Adaptive innovation due to developmental plasticity. *Journal of Experimental Zoology B* 304B:610–618.

While many of West-Eberhard's works in this bibliography entry have similar themes, the focus of this review is on developmental reorganization in response to some stimulus (environmental or mutational). This reorganization, termed phenotypic accommodation, is a particularly useful framework for thinking about how novelties arise. Here, this framework is explored as an abridged version compared to that in West-Eberhard 2003 (cited under Books).

Ecological and Community-Level Effects

While the evolutionary significance of phenotypic plasticity may be a bit contentious, its ecological importance is well-documented. Indeed, at its core, plasticity is a phenomenon dependent on ecological conditions. Most of the literature on ecological and community implications of plasticity focus on plants—likely because they are easier to make into experimental communities than animals. Miner, et al. 2005 should be the first piece read in this section because it takes a relatively broad look at how plasticity can influence ecological processes. Three other reviews focus on a trait-based approach to exploring how plasticity affects species interactions (Callaway, et al. 2003; Werner and Peacor 2003; Berg and Ellers 2010). A major takeaway from these reviews is that essentially all ecological interactions and processes can be significantly affected by phenotypic plasticity. Valladares, et al. 2007 discusses how trait-mediated interactions can have costs (or limits) that restrict further community interactions and which internal and ecological factors might limit the extent of phenotypic plasticity in plants. Agrawal 2001 and Turcotte and Levine 2016 look at species interactions and coexistence more broadly than the aforementioned works, but the general conclusion remains: plasticity can play an important role in shaping the outcome of species interactions. Finally, Hendry 2016 provides a summary of our knowledge of plasticity's role in ecology and evolution. Importantly, this work highlights a number of areas where our understanding is currently insufficient and it is useful for determining future research directions for graduate students and professionals.

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326.

This review primarily deals with reciprocal phenotypic change of interacting organisms. Table 1 is particularly useful as it describes a number of phenotypic responses that diverse organisms exhibit in response to different types of ecological interactions. It also touches on plasticity's role in helping organisms colonize novel environments.

Berg, M. P., and J. Ellers. 2010. Trait plasticity in species interactions: A driving force in community dynamics. *Evolutionary Ecology* 24:617–629.

Berg and Ellers provide two predictions: 1) plasticity in resource requirement induced by availability of resources enlarges the fundamental niche of species and causes reduction of vacant niches for other species, and 2) plasticity in the proportional resource uptake results in expansion of the realized niche, causing a reduction in the possibility for coexistence with other species. They also give a review of other facets related to plasticity's impacts on evolution and community ecology.

Callaway, R. M., S. C. Pennings, and C. L. Richards. 2003. Phenotypic plasticity and interactions among plants. *Ecology* 84:1115–1128.

Similar to the reviews Berg and Ellers 2010 and Werner and Peacor 2003, this article explores a trait-based approach to understanding ecological interactions. Specifically, the authors discuss how plastic responses to variation in abiotic environments, variation in the presence and identity of neighbors, and variation in herbivory can affect plant interactions. In some cases, interactions are affected in ways that one might not predict.

Hendry, A. P. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *Journal of Heredity* 107:25–41.

This review describes eight questions that are central to phenotypic plasticity's role in ecology and evolution and discusses the empirical support—largely from natural populations—for each. Almost invariably, the answer to each question is, “it depends.” Nevertheless, this is a great resource that highlights gaps in knowledge and where further data needs to be collected.

Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* 20:685–692.

This should be the first-read of the papers in this section. As the title suggests, this review article focuses on plasticity's ability to influence ecological interactions and processes and is accessible to advanced undergraduates and above. A strength is that it also explores nutrient cycles in addition to “typical” ecological interactions.

Turcotte, M. M., and J. M. Levine. 2016. Phenotypic plasticity and species coexistence. *Trends in Ecology and Evolution* 31:803–813.

Turcotte and Levine emphasize the importance of measuring fitness and niche differences when two species compete and note that plasticity that reduces interspecific competition should generally promote coexistence.

Valladares, F., E. Gianoli, and J. M. Gómez. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* 176:749–763.

This paper explores the internal and ecological factors that can limit the extent of plant phenotypic plasticity in the wild. Particular attention is paid to the effects of herbivory and how trait-mediated interactions can entail costs that limit further interactions in the community.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.

Werner and Peacor provide a review of trait-mediated indirect interactions (TMIs) that emphasizes the role of plasticity (via phenotypic modifications) in community dynamics. They find that the effects of TMIs are often as strong as or stronger than the effects of density on ecological communities. A variety of simple ecological interactions are explored.

Transgenerational Plasticity

An oft-cited critique against plasticity playing a role in evolution is the widespread assertion that environmentally induced phenotypic changes cannot be inherited. However, certain forms of environmentally induced phenotypic change (plasticity) *can* be transmitted from one generation to another. Indeed, transgenerational plasticity occurs when the environment experienced by a parent influences the phenotype expressed by its offspring. Often, transgenerational plasticity is discussed within the context of maternal effects. Therefore, a number of works in this section deal with maternal effects explicitly. Mousseau and Fox 1998 thoroughly covers the topic and should be the first work read in this section. Next, Wolf and Wade 2009 provides a useful review that tries to delineate which phenomena are true maternal effects. Uller 2008 discusses the evolutionary outcomes of parental effects when there is parent–offspring conflict. Its major contribution might be Box 4, which provides useful direction for future research in this field. Stepping out of the maternal (or parental) effect language, Agrawal, et al. 1999 provides the first clear example of transgenerational phenotypic induction. The authors of Galloway and Etterson 2007 go a step further than most other researchers and show that that transgenerational plasticity actually confers a fitness advantage—especially in the wild. While maternal effects and transgenerational plasticity are both becoming well-documented, their molecular underpinnings are still being unraveled. Jablonka and Lamb 2005 gives a good overview of transgenerational epigenetic inheritance and its significance in evolutionary biology. The review paper Heard and Martienssen 2014 is perhaps more accessible than Jablonka and Lamb’s book, but it focuses more on the mechanisms of epigenetic inheritance than on their evolutionary implications. Finally, the extensive review Meaney 2001 takes a different direction than other works in this section and explores the transgenerational benefits of parental care.

Agrawal, A. A., C. Laforsch, and R. Tollrian. 1999. Transgenerational induction of defences in animals and plants. *Nature* 401:60–63.

This work documented the well-known example of transgenerational inheritance of inducible helmets in *Daphnia* as well as showing a similar induced transgenerational response to herbivory in *Raphanus raphanistrum*. Subsequently, *Daphnia* have become a common animal model for studying transgenerational plasticity.

Galloway, L. F., and J. R. Etterson. 2007. Transgenerational plasticity is adaptive in the wild. *Science* 318:1134–1136.

Galloway and Etterson determined that the herb *Campanulastrum americanum*—whose life history strategy is influenced by its

maternal light environment—has 3.4 times higher fitness when grown in the same light environment as its mother than when grown otherwise. They suggest that transgenerational plasticity might be particularly important for sedentary organisms in the wild.

Heard, E., and R. A. Martienssen. 2014. Transgenerational epigenetic inheritance: Myths and mechanisms. *Cell* 157:95–109.

This review should be the starting point for anyone interested in the mechanistic bases of transgenerational plasticity. Heard and Martienssen are comprehensive in their coverage of transgenerational epigenetic mechanisms.

Jablonka, E., and M. J. Lamb. 2005. *Epigenetic inheritance and evolution: The Lamarckian dimension*. Oxford: Oxford Univ. Press.

Jablonka and Lamb, champions of transgenerational epigenetic inheritance, explore the evolutionary implications of this hereditary system. While plasticity is not central a theme in this particular work, it does show up in later works by these authors (not cited here) that should definitely be read as well.

Meaney, M. J. 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience* 24:1161–1192.

As the title suggests, this lengthy review explores the significant role maternal care plays in affecting the stress levels, gene expression, and behavior of offspring. This topic is covered at various levels ranging from the hormonal/physiological to behavioral. The review focuses on mammal models, but the concepts could be applied to other systems.

Mousseau, T. A., and C. W. Fox, eds. 1998. *Maternal effects as adaptations*. Oxford: Oxford Univ. Press.

This book should be the first source read in this section. It is the first synthesis of this field and remains relevant for anyone studying maternal effects. A variety of topics ranging from evolutionary implications to detecting maternal effects are covered. In addition, various examples and four detailed case studies are included.

Uller, T. 2008. Developmental plasticity and the evolution of parental effects. *Trends in Ecology and Evolution* 23:432–438.

This review focuses on the evolutionary outcomes of parental effects under cases of weak and strong parent–offspring conflict. Although potentially dated as of the publication of this bibliography, Box 4 should be particularly useful for researchers interested in going forward in this field.

Wolf, J. B., and M. J. Wade. 2009. What are maternal effects (and what are they not)? *Proceedings of the Royal Society B* 364:1107–1115.

These authors define maternal effects as the *causal* influence of the maternal genotype or phenotype on the offspring phenotype. This definition differs from others because it treats maternal effects as a phenomenon, not a statistical construct. The authors argue why maternal cytoplasmic inheritance and genomic imprinting are not true maternal effects.

Behavioral Plasticity

Behavior is sometimes considered independently of other forms of plasticity because it is “hyperplastic” and can change moment to moment in some cases. As an introduction to studying behavior and some of the terminology, Sih, et al. 2004 is a must-read. Similarly Dingemans, et al. 2010 should be read early because it places behavioral plasticity into a reaction norm framework and seeks to unify those studying behavioral plasticity and animal personality. Then, focusing more explicitly on behavioral plasticity, Snell-Rood 2013 provides an excellent overview of how it can affect and be affected by evolution. Of course, understanding the mechanisms that lead to certain behaviors is important for understanding their evolution. Therefore, Duckworth 2009 explores the mechanistic bases of behaviors and how they can impede or promote evolutionary change. Renn and Schumer 2013 also focuses on the evolution of mechanisms underlying behaviors, but pays particular attention to patterns of gene expression undergoing Genetic Accommodation. Relatedly, a concept that has long been relevant for evolutionary biologists is the possibility that behavioral change may precede and facilitate morphological evolution. Wyles, et al. 1983 and Wcislo 1989 both provide compelling arguments for this line of thinking, and Allf, et al. 2016 (cited under Novelty) provides empirical support in the case of the rattlesnake rattle. For a cautionary note, see Huey, et al. 2003. Many of these ideas stem from the Baldwin effect (see Genetic Accommodation) and are related to Plasticity-First Evolution.

Dingemans, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology and Evolution* 25:81–89.

Dingemans and colleagues place commonly studied aspects of animal behavior (i.e., personality and plasticity) into a reaction norm framework, thereby making their study more analogous to studies of phenotypic plasticity on other components of an organism’s phenotype. Importantly, this approach allows personality and plasticity to be studied within the same framework, rather than as separate entities.

Duckworth, R. A. 2009. The role of behavior in evolution: A search for mechanism. *Evolutionary Ecology* 23:513–531.

Duckworth delves into the mechanisms underlying behavioral shifts and links within-individual changes to population-level processes in order to explore whether behavior drives or impedes evolutionary change. As expected, emphasis is placed on understanding the developmental mechanisms of behavior. A framework is provided to facilitate asking how and under what conditions do behaviors affect evolutionary processes.

Huey, R. B., P. E. Hertz, and B. Sinervo. 2003. Behavioral drive versus behavioral inertia in evolution: A null model approach. *The American Naturalist* 161:357–366.

The authors caution that it is inappropriate to ask, “Does behavior drive or inhibit evolutionary change in other traits?” By focusing on thermoregulatory behavior and thermal physiology of lizards, the authors suggest that behavior can buffer evolution for one trait while simultaneously driving the evolution of others.

Renn, S. C. P., and M. E. Schumer. 2013. Genetic accommodation and behavioural evolution: Insights from genomic studies. In *Special Issue: Behavioural plasticity and evolution*. Edited by S. A. Foster and A. Sih. *Animal Behaviour* 85:1012–1022.

This important work by Renn and Schumer links the processes of genetic accommodation and assimilation to patterns of gene expression. This review not only provides examples of how patterns of gene expression can be united with behavioral plasticity, but also outlines ideal characteristics of a study system and describes some of the tools available to implement this approach. Thus, it almost serves as a “how-to” guide to studying behavioral plasticity in a genetic accommodation context.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution* 19:372–378.

Behavioral syndromes occur when the rank-order of a particular behavior among individuals is maintained across environments, and they can limit behavioral plasticity, explain non-optimal behavior, and help to maintain individual variation in behavior. These behavior effects can have dramatic ecological and evolutionary consequences. This review is somewhat broader than others in this section, but certainly relevant and important for anyone interested in behavioral plasticity.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioral plasticity. In *Special Issue: Behavioural plasticity and evolution*. Edited by S. A. Foster and A. Sih. *Animal Behaviour* 85:1004–1011.

This overview, which is part of the same special issue on behavioral plasticity and evolution as Renn and Schumer 2013. It should be the first-read piece for those new to the field because it discusses major types of behavioral plasticity, their consequences in novel environments, and promising avenues of future research. These topics are potentially relevant to all studies of behavior and its evolution.

Wcislo, W. T. 1989. Behavioral environments and evolutionary change. *Annual Review of Ecology and Systematics* 20:137–169.

This seminal review by Wcislo is a must-read that emphasizes how behavioral changes (in the form of plasticity) may often precede morphological change. A historical overview, behavior's role in evolution, explorations at multiple levels of biological organization, and a short suggestion on hypothesis testing are discussed.

Wyles, J. S., J. G. Kunkel, and A. C. Wilson. 1983. Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences* 80:4394–4397.

This work introduces “behavioral drive,” which posits that anatomic evolution relies on behavioral acquirement of a new skill that leads to novel environmental exploitation and subsequent social transmission of the skill throughout the population. This new skill then alters selection pressures such that it can become adaptive via traditional natural selection. This process is essentially the Baldwin effect (see Genetic Accommodation), but more emphatically suggests that the behavior arises before any meaningful environmental change.

Learning as Plasticity

Through learning, an organism can adjust its behavior to better suit future conditions. Such behavioral adjustments certainly count as phenotypic plasticity. Spalding 1873 provides one of the earliest discussions of behaviors being learned (plastic) versus instinctual (canalized). Osborn 1896 highlights the possibility that most adaptations may arise as a result of new behaviors or environments. This entire tradition of learning as plasticity is largely derived from Baldwin and the Baldwin effect (see Genetic Accommodation). Fast-forwarding nearly one hundred years, Hinton and Nowlan 1987 showed that learning organisms are capable of evolving much faster than non-learning equivalents even if the traits are not transmitted to the genome. However, there is a trade-off between costs and benefits of learning (Mayley 1996) that can constrain or limit its utility. A decade later, Paenke, et al. 2007 provided a framework for studying how plasticity and learning affect evolution under directional selection, and found that the rate of evolution depends on the sign

of the fitness gain gradient relative to that of selection. Computational biology has given a lot of attention to learning and the Baldwin effect. This body of literature may often go unnoticed by evolutionary biologists. Some introductory references are included here. French and Messinger 1994 provides evidence that learning-based plasticity can and does produce directed changes at the genotypic level and that over generations populations may transition from genetically based inheritance to learning based. Relatedly, Turney, et al. 1996 gives an overview of a hundred years of studying the Baldwin effect and refers to various other sources in the computational literature that may be useful for studying learning within the context of plasticity. This is definitely a key source for the computationally minded.

French, R., and A. Messinger. 1994. Genes, phenes, and the Baldwin effect: Learning and evolution in a simulated population. In *Artificial life IV: Proceedings of the Fourth International Workshop on the Synthesis and Simulation of Living Systems*. Edited by R. A. Brooks and P. Maes, 227–282. Cambridge, MA: MIT.

Although from a potentially obscure source, this work demonstrates that learning-based plasticity at the phenotypic level can and does produce directed changes at the genotypic level. In addition, the degree of plasticity is crucial for the size of the Baldwin effect. Finally, over generations, learning should become easier for the population as a whole and the population may transition from being genetically driven to learning driven.

Hinton, G. E., and S. J. Nowlan. 1987. How learning can guide evolution. *Complex Systems* 1:495–502.

This groundbreaking paper demonstrated that learning provides a good evolutionary path toward sets of coadapted alleles and that this effect allows learning organisms to evolve much faster than non-learning equivalents—even though traits acquired by the phenotype are not communicated to the genotype.

Mayley, G. 1996. Landscapes, learning costs, and genetic assimilation. *Evolutionary Computation* 4:213–234.

This work describes the costs and benefits of learning and how there are trade-offs between the two. It also describes and demonstrates the importance of the correlation between phenotypic distances and genotypic distances between individuals. The relationship between costs and the degree of this correlation is explored.

Osborn, H. F. 1896. Ontogenic and phylogenetic variation. *Science* 4:786–789.

Osborn describes a process similar to the Baldwin effect (see Genetic Accommodation) in which most adaptations arise as a result of new behaviors or environments. Osborn highlights the importance of developmental plasticity (ontogenic variation/evolution) in allowing organisms to adapt to their environment.

Paenke, I., B. Sendhoff, and T. J. Kawecki. 2007. Influence of plasticity and learning on evolution under directional selection. *The American Naturalist* 170:E47–E58.

Paenke and colleagues provide a framework that utilizes a fitness gain gradient for studying the effects of plasticity on the rate of evolution under directional selection. They find that if the gain gradient has the same sign as the direction of selection, then increased plasticity will magnify the selective response. However, if the sign is opposite, the response to selection will be slower.

Spalding, D. A. 1873. Instinct, with original observations on young animals. *MacMillan's Magazine* 27: 282–293.

This is one of the earliest works that discusses some aspects of animal of behavior as learned and others as instinctual. It illustrates that just as some morphological features can become canalized (see Genetic Assimilation and Canalization), apparently some behaviors can be canalized as well. However, other behaviors may be more analogous to plastic responses and need to be learned. Note that the doi does not lead to the original publication but instead references the same article published in 1954 in *The British Journal of Animal Behaviour* 2: 2–11.

Turney, P., D. Whitley, and R. W. Anderson. 1996. Evolution, learning, and instinct: 100 years of the Baldwin effect. In *Special issue: The Baldwin effect*. Edited by P. Turney, D. Whitley, and R. W. Anderson. *Evolutionary Computation* 4:iv–viii.

This article is an introduction to a special issue of *Evolutionary Computation*. In addition to providing a historical perspective on the Baldwin effect, this article references other sources in that issue that could be useful. Furthermore, it highlights work using computational approaches to study learning, the Baldwin effect, and genetic assimilation that should appeal to biologists.

Bet-Hedging

Bet-hedging is sometimes viewed as an alternative strategy to phenotypic plasticity. Like plasticity, bet-hedging involves the production of multiple phenotypes from a single genotype. Unlike plasticity, however, the alternative phenotypes are produced stochastically rather than in direct response to an environmental cue. Despite this important distinction in how phenotypes are produced, the two concepts have similar evolutionary implications, and researchers interested in the consequences of plasticity would benefit from consulting the bet-hedging literature. Cooper and Kaplan 1982 and Kaplan and Cooper 1984 develop a framework for understanding and exploring the existence of random, adaptive phenotypic variation. While this framework itself has not really persisted, its general effort to explain random adaptive variation has continued. Philippi and Seger 1989 provides a straightforward introduction of the concept of bet-hedging with reference to various common examples, but the review Childs, et al. 2010 should be read first because it has twenty more years of material to build upon. Kussell and Leibler 2005 and Starrfelt and Kokko 2012 develop models that show when stochastic switching (bet-hedging) should be favored over environmental sensing (plasticity), and that two commonly described types of bet-hedging—conservative and diversified—represent a continuum rather than a dichotomy, respectively. The authors of Acar, et al. 2008 empirically tested ideas found in Kussell and Leibler 2005 and showed that stochastic switching is favored when it matches the rate of environmental change. Further empirical work by the authors of Beaumont, et al. 2009 found that only one mutation was necessary and sufficient for phenotype switching, but prior mutations were needed in order to adjust the fitness landscape so that the final mutation could be effective. More recently, Scheiner 2014 has provided a different type of model to complement and, potentially contrast with, models in the other works mentioned in this section.

Acar, M., J. T. Mettetal, and A. van Oudenaarden. 2008. Stochastic switching as a survival strategy in fluctuating environments. *Nature Genetics* 40:471–475.

Acar and colleagues verified experimentally that production of alternate phenotypes is advantageous when the switching is matched with the rate of environmental change. Although this was shown in individual yeast cells, the general pattern is applicable in other, more complex, organisms. An important caveat is that their yeast strains switched stochastically rather than in direct response to an environmental cue.

Beaumont, H. J. E., J. Gallie, C. Kost, G. C. Ferguson, and P. B. Rainey. 2009. Experimental evolution of bet hedging. *Nature* 462:90–93.

Beaumont and colleagues report *de novo* evolution of bet-hedging in experimental bacterial populations. One mutation was necessary and sufficient for rapid phenotype switching, but its evolution was contingent upon earlier mutations that altered the relative fitness effect of the final mutation. The authors suggest that risk-spreading strategies may have been among the earliest solutions to fluctuating environments.

Childs, D. Z., C. J. Metcalf, and M. Rees. 2010. Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B* 22:3055–3064.

This review is a useful starting point for those new to bet-hedging. It describes the essential theory, delves into the quintessential example of bet-hedging (plant seeds), covers more complicated cases of bet-hedging, and describes a framework that accommodates these complicated examples. The focus is on plants, but the concepts are widely applicable.

Cooper, W. S., and R. H. Kaplan. 1982. Adaptive “coin-flipping”: A decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology* 94:135–151.

This is the foundational work for adaptive coin-flipping and bet-hedging that seeks to explain the existence of random, yet adaptive, phenotypic variation. Cooper and Kaplan argue that individuals are programmed to flip “coins” to decide on phenotypic outcomes and that it is the nature of the coin-flipping, rather than the traits themselves, that is inherited.

Kaplan, R. H., and W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: An application of the “adaptive coin-flipping” principle. *The American Naturalist* 123:393–410.

Building on their earlier work (Cooper and Kaplan 1982), the authors apply their adaptive coin-flipping principle as a mechanism of maintaining intrapopulation variation to amphibian egg size. They go on to discuss the potential significance of a developmental coin-flip for ecological processes in general.

Kussell, E., and S. Leibler. 2005. Phenotypic diversity, population growth, and information in fluctuating environments. *Science* 309:2075–2078.

Using a modeling approach, this article demonstrates that stochastic phenotype switching (e.g., bet-hedging) can be favored over environmental sensing (e.g., plasticity) in clonal species when the environment changes infrequently. The optimal switching rates then mimic the statistics of environmental change. The authors also derive a relation between long-term growth rate and the information available about the fluctuating environment.

Philippi, T., and J. Seger. 1989. Hedging one’s evolutionary bets, revisited. *Trends in Ecology and Evolution* 4:41–44.

This is a relatively straightforward review of bet-hedging that describes the general phenomenon and discusses a few common examples. It is another useful introduction to the topic.

Scheiner, S. M. 2014. The genetics of phenotypic plasticity. XIII. Interactions with developmental instability. *Ecology and Evolution* 4:1347–1360.

Unlike many of the other works that treat plasticity and bet-hedging as alternative strategies, the model provided by Scheiner explores the interaction between plasticity and bet-hedging through developmental instability. He demonstrates that the magnitude and pattern of environmental heterogeneity, the spatial and temporal distribution of individuals, and genetic architecture are important determinants of phenotypic plasticity and developmental instability.

Starrfelt, J., and H. Kokko. 2012. Bet-hedging—a triple trade-off between means, variances, and correlations. *Biological Reviews* 87:742–755.

Starrfelt and Kokko use a general model to demonstrate that conservative and diversified bet-hedging strategies are not necessarily a dichotomy, but instead function as extremes along a continuum. Similarly, they conclude that within- and between-generation bet-hedging are not mutually exclusive.

Applied Aspects of Plasticity

There are at least three major areas where an understanding of plasticity could have a significant applied impact: conservation biology, human health, and agriculture. The majority of works in this section are related to the first, but the second is also represented. Agriculture is not explicitly discussed. However, since agriculture might primarily focus on *reducing* environmentally induced differences among individuals, the sections on Genetic Assimilation and Canalization should be referenced for this topic. In addition, those interested in agriculture should read Perkins and Jinks 1971 (cited under Experimental Evolution). Returning to conservation biology, Hofmann and Todgham 2010; Reed, et al. 2010; and Merilä and Hendry 2014 all address the issue of climate change and how plastic responses can potentially mitigate the negative outcomes species are predicted to experience and/or highlight current gaps in knowledge. Charmantier, et al. 2008 demonstrates empirically that behavioral plasticity can indeed allow a species to rapidly adapt to a changing environment. Richards, et al. 2006 and Davidson, et al. 2011 look at a different aspect of conservation biology: invasive species. Both works focus on invasive plants, and they come to the same general conclusion: invaders have greater plasticity than natives. However, the greater plasticity of invasive species is not always associated with a fitness advantage. By considering the effects of plasticity, land managers may be better able to conserve and restore native flora and fauna faced with climate change or invasive species. Another major application where knowledge of plasticity can play an important role is human health. Bateson, et al. 2004 argues for the importance of considering developmental conditions when studying disease. The authors explore a few examples that highlight how early development can have major implications for adult health. Gluckman and Hanson 2004 further develops the case for gene-by-environment interactions in disease and should definitely be consulted by the medically minded. Together, these works emphasize that plasticity is not only an interesting phenomenon for evolutionary biologists and ecologists, but has important “real-world” implications as well.

Bateson, P., D. Barker, T. Clutton-Brock, et al. 2004. Developmental plasticity and human health. *Nature* 430:419–421.

This article argues for the importance of considering developmental conditions when discussing public health. Figure 1 is useful because it presents a hypothetical relationship between nutritional level during development and adult health that highlights how environmental inputs early in life can have dramatic outcomes later in life. Although the article primarily focuses on early nutrition and related diseases, it is not difficult to extend the principle to pretty much any disease.

Charmantier, A., R. H. McCleery, L. R. Cole, et al. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320:800–803.

Using a population study of great tits (*Parus major*) in the United Kingdom over forty-seven years, Charmantier and colleagues demonstrated that behavioral plasticity in timing of breeding has allowed the population to rapidly adjust to a changing environment. Interestingly, there was little to no variation among individuals in their response to environmental variation.

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14:419–431.

The short answers to the titular questions are yes, and (sometimes) yes. After performing a meta-analysis on seventy-five invasive/noninvasive species pairs, Davidson and colleagues conclude that invasive species were nearly always more plastic, but only sometimes associated with a fitness benefit. In contrast, noninvasive species were better at maintaining growth when facing low and average resource availability.

Gluckman, P. D., and M. A. Hanson. 2004. *The fetal matrix: Evolution, development and disease*. Cambridge, UK: Cambridge Univ. Press.

In this book, Gluckman and Hanson note that often a genotype itself does not cause a disease, but instead changes the sensitivity to environmental interactions. More broadly, this work highlights the importance of considering the genotype–environment interaction in development and treatment of disease.

Hofmann, G. E., and A. E. Todgham. 2010. Living in the now: Physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology* 72:127–145.

As with many of the other papers in this section, this review primarily deals with climate change—especially temperature and ocean acidification. However, it utilizes a comparative physiology framework to explore the ways in which organisms can cope with some of the changes they will likely face. It is most useful for understanding some of the underlying mechanisms that lead to “higher-order” phenotypic outcomes and where some limits to adaptation may lie.

Merilä, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. In *Special issue: Climate change, adaptation, and phenotypic plasticity*. Edited by J. Merilä and A. P. Hendry. *Evolutionary Applications* 7:1–14.

This paper serves as an introduction to a special issue of this journal and highlights the need for better understanding of how plasticity can contribute to the ability of organisms to adapt to climate change. It does so by performing a methodological assessment of how studies on climate change adaptation have been performed. Readers are encouraged to view the other works in this special issue as well.

Reed, T. S., D. E. Schindler, and R. S. Waples. 2010. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology* 25:56–63.

This synthesis discusses ecological and evolutionary theory in the context of organisms adapting to climate change. In doing so, it highlights the importance of ecological and evolutionary interactions potentially producing an adaptive response. A major conclusion is

that genetic adaptation and phenotypic plasticity need to be considered in models of population persistence. It also—perhaps inadvertently—provides a framework for leveraging climate change to study phenotypic plasticity.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9:981–993.

By pulling from earlier work, Richards and colleagues provide a framework for understanding how an invader might succeed in a new habitat. Table 1 provides qualitative evidence for the different scenarios their framework describes, and they provide recommendations for testing the role of plasticity in invasions. Gaining a fitness increase in favorable conditions through phenotypic plasticity (with or without preventing a decline in fitness in unfavorable conditions) seems to be the most common mode by which invasives outperform noninvasives.

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