Received: 2 June 2019 | Accepted: 21 November 2019

DOI: 10.1111/1365-2435.13494

EDITORIAL

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Epigenetics in ecology and evolution

Anthony Herrel[1] | **Dominique Joly**[2] | **Etienne Danchin**[3]

[1]Département Adaptations du Vivant, UMR 7179 CNRS/MNHN, Paris Cedex 5, France

[2]Laboratoire Evolution, Génomes, Comportement, Ecologie, UMR9191 CNRS/IRD/Université Paris-Saclay, Gif-sur-Yvette, France

[3]Laboratoire Évolution & Diversité Biologique (EDB), UMR5174, CNRS, Université Fédérale de Toulouse, IRD, Toulouse Cedex 9, France

Correspondence
Anthony Herrel
Email: anthony.herrel@mnhn.fr

Funding information
CNRS; Laboratoires d'Excellences (LABEX) TULIP, Grant/Award Number: ANR-10-LABX-41; Laboratoires d'Excellences (LABEX) BCDiv, Grant/Award Number: ANR-10-LABX-03

Handling Editor: Charles Fox

Abstract

1. The discovery of the multidimensional nature of the inherited information carried by the epigenome and the characterization of its intra- and intergenerational dynamics have profoundly changed our understanding of the functioning of biological organisms and the origins of phenotypic diversity.
2. This has raised considerable interest in the study of epigenetics which is emerging as a 'missing link' between environmental and phenotypic variation.
3. Recent discoveries have provided important insights into the mechanisms of phenotypic plasticity, inheritance and adaptation; key concepts at the crossroads of individual-centred approaches (that mostly study proximate mechanisms); and supra-individual ones (that mostly study ultimate processes).
4. In this context, epigenetics emerges as a major source of inquiry for the study of ecological and evolutionary dynamics. This special feature provides an overview of the role of epigenetics in ecology and evolution.

KEYWORDS
ecology, epigenetics, evolution

Over the past two decades, the study of epigenetics has emerged as an important discipline for the understanding of biological evolution (for reviews, see, for instance: Bossdorf, Richards, & Pigliucci, 2008; Danchin et al., 2011; Danchin, Pocheville, Rey, Pujol, & Blanchet, 2020; Jablonka & Raz, 2009; Rando & Verstrepen, 2007; Richards, 2006; Skinner, Manikkam, & Guerrero-Bosagna, 2010; Wang, Liu, & Sun, 2017). From the turn of the third millennium onwards, major advances have been generated by exceptional technological advances in high-throughput sequencing that now allow the simultaneous analysis of genomes, epigenomes and transcriptomes in all their complexity. These approaches, initially developed by molecular biologists, are becoming accessible to researchers in other subdisciplines of biology working on both model and non-model species. Consequently, these approaches have provided a new impetus to studies of the relationships between genes, environment and phenotypes in an eco-evolutionary context. A particularly surprising outcome of the use of recent high-throughput molecular technologies was the discovery that the information encoded into the DNA nucleotide sequence by itself is often insufficient to explain biological variation in all its complexity (Maher, 2008). This resulted in the debate about missing heritability and revealed the existence of other forms of information transmission across generations (Danchin, 2013).

The discovery of epigenetics (any modification other than changes in DNA sequences affecting gene expression, whether those modifications have been shown to be stable or not) profoundly changed our understanding of the functioning of biological organisms and generated considerable interest in its role as a 'missing link' between environmental and phenotypic variation. In particular, recent discoveries have fostered a full revision of the mechanisms of phenotypic plasticity (Bonduriansky & Day, 2018; Herman, Spencer, Donohue, & Sultan, 2014; Jablonka, 2013; Pigliucci, Murren, & Schlichting, 2006; Reed, Waples, Schindler, Hard, & Kinnison, 2010; Sentis et al., 2018; Sultan, 2011; Zhang, Fischer, Colot, & Bossdorf, 2012), inheritance (Bonduriansky, 2012; Bonduriansky & Day, 2018; Danchin, 2013; Day & Sweatt, 2011) and adaptation (Danchin et al., 2011, 2018, 2019; Pocheville & Danchin, 2015, 2017). These three major lines of research in evolutionary biology are at the crossroads between individual-centred approaches (that mostly study proximate mechanisms) and supra-individual approaches (that mostly study ultimate processes) and are all impacted by our understanding of epigenetics (Danchin & Pocheville, 2014; Jablonka & Lamb, 2005; Pocheville & Danchin, 2015). Epigenetics has emerged as a key discipline in the study of ecological and evolutionary dynamics, and this special feature contributes to highlighting the importance of this discipline.

As most disciplines in molecular biology, the study of epigenetics initially benefited considerably from the use of model organisms. Today, however, the time is ripe to transfer discoveries from model organisms to non-model organisms, rendering these approaches more ecologically relevant. The transfer of knowledge to non-model organisms and more complex naturalistic settings may then allow us to study the molecular basis of the complex interactions among organisms within communities and ecosystems. As such, the study of epigenetic inheritance may provide novel insights into previously unexplained aspects of complex ecological interactions. With this special feature on the impact of epigenetics in the field of ecology, and particularly that of functional ecology, we want to stimulate ecologists to embrace epigenetics as a major source of information allowing the study of the interactions among organisms and their biotic and abiotic environment with the hope of fostering a better understanding of adaptation and evolution.

The potential role of epigenetics in answering important ecological and evolutionary questions is illustrated in this special feature. First, Pimpinelli and Piacentina (2020) discuss how transposons may contribute to translating phenotypic plasticity into genetic variability through their impact on epigenetic mechanisms. Especially in the context of rapid environmental change, it may be important to be able to translate phenotypic plasticity into variation that is encoded in the genome, and thus under direct natural selection. Pimpinelli and Piacentina argue that modifications induced by transposons would not only impact epigenetic mechanisms but also be stably inherited. Indeed, transposable elements are environment-responsive molecular elements that can rapidly produce phenotypic and genotypic variants in response to environmental perturbations by causing regulatory changes in the transcription of the genome. As such, transposons may play an important role on the relevant ecological time-scales within which organisms need to respond to the current and ongoing rapid changes in their environment. At the end of their review, Pimpinelli and Piacentina discuss a few model systems where transposons are likely to have played a role in the rapid phenotypic diversification observed and suggest promising avenues for future research.

The characterization of parental transmission of epigenetic variation to offspring is of major importance to understanding how rapid individual phenotypic changes are passed on through generations and stay heritable over generations. A number of studies have been devoted to demonstrating how maternal processes shape the physical and social context of offspring development through behavioural and physiological mechanisms (Adkins-Regan, Banerjee, Correa, & Schweitzer, 2013; Galloway, 2005). Yet, little is known about how paternal transmission occurs. Champagne (2020) describes the current state of knowledge regarding paternal epigenetic effects, the interplay between maternal and paternal influences, and the importance of considering the complex nature of reproduction when predicting the transmission of phenotypes across generations. The paper reviews experimental evidence on how sperm can drive the paternal transmission of epigenetic marks by a diversity of environmental effects, such as nutritional or toxicological effects, and may shape offspring characteristics. The review also emphasizes how the environmental exposure history of males may alter female mate preference through sexual selection processes. It hence argues for a better integration of behaviour in the transgenerational transmission of epigenetic variation.

Biological invasions are a global scourge and a major issue in the current context of globalization and the world-wide and rapid transport of organisms outside of their native range. However, for an invader to be successful it needs to be able to rapidly respond to and cope with different environmental conditions. Marin et al. (2020) examine the possible link between stress, epigenetic changes and transposable element activity in generating phenotypic and genetic variation in invasive populations. They argue that these mechanisms can contribute to the success of biological invasions by facilitating plasticity as well as rapid adaptive evolution. Indeed, whereas epigenetic variation and transposable elements are generally well regulated and thus not expressed in natural populations, these mechanisms may be released from their regulation in new and stressful environments. As such, Marin and collaborators argue that the epigenome needs to be studied in greater detail if we want to understand the mechanisms by which populations successfully colonize and adapt to new environments.

Given the ability of epigenetic mechanisms to allow organisms to respond to rapid changes in their environment, they may also play an important role in conservation. Indeed, the paper by Rey et al. (2020) argues strongly that epigenetic variation and more particularly DNA methylation represent important components of biodiversity linking genomes to environments. They highlight the importance of DNA methylation in providing biomarkers for past and present environmental stress, the ecological structuring of wild populations, improving translocations and studying landscape connectivity. As such, epigenetic mechanisms appear to be a promising and important tool in conservation biology.

Together, these papers not only show the versatility of epigenetic mechanisms in generating phenotypic variability but more importantly show the importance of including epigenetic thinking when addressing questions in ecology and evolution. Especially in our current ever more rapidly changing landscape, understanding how organisms may respond to change appears a crucial biological endeavour for which epigenetic approaches may provide a major contribution. Different aspects would need further theoretical and experimental investigation, including (a) the quantification of epigenetic reversion rate at the individual and transgenerational scales under different environmental scenarios; (b) the characterization of the epimutation pattern (random, directed – as for phenotypic plasticity, or dependent or not on environmental conditions), here again at the different biological levels; (c) the study of the genetic control of epimutations in relation to the possible genetic transmission across generations; and (d) the causal relationship between epigenetics, phenotypes and fitness in order to establish the adaptive value of epigenetics. Among these four points, the latter is probably the most crucial to demonstrate the extent of epigenetics in evolution as well as its impact on the heritability and the stability of the genomic compartment.

We hope that this special feature will stimulate readers to think about the role of epigenetics in ecology and evolution and that it will spark new studies trying to understand variation in nature and its role in allowing populations to respond to variation in biotic and abiotic factors.

ACKNOWLEDGEMENTS

The authors would like to thank the CNRS for funding the RTP and GDR 3E networks that have allowed to stimulate research on epigenetics and evolution in France. We would also like to thank all the members of the scientific committee of the RTP and GDR 3E networks for fruitful discussions. This work was supported by the Laboratoires d'Excellences (LABEX) TULIP (ANR-10-LABX-41) and Laboratoires d'Excellences (LABEX) BCDiv (ANR-10-LABX-03).

ORCID

Anthony Herrel https://orcid.org/0000-0003-0991-4434
Dominique Joly https://orcid.org/0000-0001-8000-4308
Etienne Danchin https://orcid.org/0000-0002-5013-9612

REFERENCES

Adkins-Regan, E., Banerjee, S. B., Correa, S. M., & Schweitzer, C. (2013). Maternal effects in quail and zebra finches: Behavior and hormones. *General and Comparative Endocrinology*, *190*, 34–41. https://doi.org/10.1016/j.ygcen.2013.03.002

Bonduriansky, R. (2012). Rethinking heredity, again. *Trends in Ecology & Evolution*, *27*, 330–336. https://doi.org/10.1016/j.tree.2012.02.003

Bonduriansky, R., & Day, T. (2018). *Extended heredity: A new understanding of inheritance and evolution*. Princeton, NJ: Princeton University Press.

Bossdorf, O., Richards, C. L., & Pigliucci, M. (2008). Epigenetics for ecologists. *Ecology Letters*, *11*, 106–115.

Champagne, A. (2020). Interplay between paternal germline and maternal effects in shaping development: The overlooked importance of behavioural ecology. *Functional Ecology*, *34*(2), 401–413. https://doi.org/10.1111/1365-2435.13411

Danchin, É. (2013). Avatars of information: Towards an inclusive evolutionary synthesis. *Trends in Ecology & Evolution*, *28*, 351–358. https://doi.org/10.1016/j.tree.2013.02.010

Danchin, É., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: Integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, *12*, 475–486. https://doi.org/10.1038/nrg3028

Danchin, É., Nöbel, S., Pocheville, A., Dagaeff, A. C., Demay, L., Alphand, A., … Isabel, G. (2018). Cultural flies: Conformist social learning in fruit flies predicts long-lasting mate-choice traditions. *Science*, *362*, 1025–1030. https://doi.org/10.1126/science.aat1590

Danchin, É., & Pocheville, A. (2014). Inheritance is where physiology meets evolution. *Journal of Physiology*, *592*, 2307–2317. https://doi.org/10.1113/jphysiol.2014.272096

Danchin, É., Pocheville, A., Rey, O., Pujol, B., & Blanchet, S. (2019). Epigenetically-facilitated mutational assimilation: Epigenetics as a hub within the inclusive evolutionary synthesis. *Biological Reviews*, *94*, 259–282. https://doi.org/10.1111/brv.12453

Day, J. J., & Sweatt, D. (2011). Epigenetic mechanisms in cognition. *Neuron*, *70*, 813–829. https://doi.org/10.1016/j.neuron.2011.05.019

Galloway, L. F. (2005). Maternal effects provide phenotypic adaptation to local environmental conditions. *The New Phytologist*, *166*, 93–99. https://doi.org/10.1111/j.1469-8137.2004.01314.x

Herman, J. J., Spencer, H. G., Donohue, K., & Sultan, S. E. (2014). How stable 'should' epigenetic modifications be? Insights from adaptive plasticity and bet hedging. *Evolution*, *68*, 632–643. https://doi.org/10.1111/evo.12324

Jablonka, E. (2013). Epigenetic inheritance and plasticity: The responsive germline. *Progress in Biophysics and Molecular Biology*, *111*, 99–107. https://doi.org/10.1016/j.pbiomolbio.2012.08.014

Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions. Genetic, epigenetic, behavioural, and symbolic variation in the history of life*. Cambridge, MA: MIT Press.

Jablonka, E., & Raz, G. (2009). Transgenerational epigenetic inheritance: Prevalence, mechanisms, and implications for the study of heredity and evolution. *Quarterly Review of Biology*, *84*, 131–176. https://doi.org/10.1086/598822

Maher, B. (2008). Personal genomes: The case of the missing heritability. *Nature*, *456*, 18–21. https://doi.org/10.1038/456018a

Marin, P., Genitoni, J., Barloy, D., Maury, S., Gibert, P., Ghalambor, C. K., & Vieira, C. (2020). Biological invasion: The influence of the hidden side of the (epi) genome. *Functional Ecology*, *34*(2), 385–400. https://doi.org/10.1111/1365-2435.13317

Pigliucci, M., Murren, C. J., & Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, *209*, 2362–2367. https://doi.org/10.1242/jeb.02070

Pimpinelli, S., & Piacentini, L. (2020). Environmental changes and evolution of genomes: Transposons as translators of the phenotypic plasticity into genotypic variability. *Functional Ecology*, *34*(2), 428–441. https://doi.org/10.1111/1365-2435.13497

Pocheville, A., & Danchin, É. (2015). Physiology and evolution at the crossroads of genetics and epigenetics. *Journal of Physiology*, *9*, 2243–2243.

Pocheville, A., & Danchin, É. (2017). Genetic assimilation and the paradox of blind variation. In P. Humeman & D. Walsh (Eds.), *Challenging the modern synthesis. Adaptation, development, and inheritance* (pp. 111–136). Oxford, UK: Oxford University Press.

Rando, O. J., & Verstrepen, K. J. (2007). Timescales of genetic and epigenetic inheritance. *Cell*, *128*, 655–668. https://doi.org/10.1016/j.cell.2007.01.023

Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J., & Kinnison, M. T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. *Proceedings of the Royal Society B-Biological Sciences*, *277*, 3391–3400. https://doi.org/10.1098/rspb.2010.0771

Rey, O., Eizaguirre, C., Angers, B., Baltazar-Soares, M., Sagonas, K., Prunier, J., & Blanchet, S. (2020). Linking epigenetics and biological conservation: Toward a *conservation epigenetics* perspective. *Functional Ecology*, *34*(2), 414–427. https://doi.org/10.1111/1365-2435.13429

Richards, E. J. (2006). Inherited epigenetic variation – Revisiting soft inheritance. *Nature Reviews Genetics*, *7*, 395–401. https://doi.org/10.1038/nrg1834

Sentis, A., Bertram, R., Dardenne, N., Ramon-Portugal, F., Espinasse, G., Louit, I., … Danchin, E. (2018). Evolution without standing genetic variation: Change in transgenerational plastic response under persistent predation pressure. *Heredity*, *121*, 266–281. https://doi.org/10.1038/s41437-018-0108-8

Skinner, M. K., Manikkam, M., & Guerrero-Bosagna, C. (2010). Epigenetic transgenerational actions of environmental factors in disease etiology. *Trends in Endocrinology & Metabolism*, *21*, 214–222. https://doi.org/10.1016/j.tem.2009.12.007

Sultan, S. E. (2011). Evolutionary implications of individual plasticity. In S. B. Gissis & E. Jablonka (Eds.), *Transformations of Lamarckism: From subtle fluids to molecular biology*. Cambridge, MA: MIT Press.

Wang, Y., Liu, H., & Sun, Z. (2017). Lamarck rises from his grave: Parental environment-induced epigenetic inheritance in model organisms and humans. *Biological Reviews*, *92*, 2084–2111. https://doi.org/10.1111/brv.12322

Zhang, Y.-Y., Fischer, M., Colot, V., & Bossdorf, O. (2012). Epigenetic variation creates potential for evolution of plant phenotypic plasticity. *New Phytologist*, *197*, 314–322. https://doi.org/10.1111/nph.12010

How to cite this article: Herrel A, Joly D, Danchin E. Epigenetics in ecology and evolution. *Funct Ecol*. 2020;34:381–384. https://doi.org/10.1111/1365-2435.13494