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1 **Epigenetics in ecology and evolution – a primer**

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11 ABSTRACT

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

23

24 KEYWORDS

25 ecology, epigenetics, evolution

26

27 Over the past two decades, the study of epigenetics has emerged as a key stone discipline for the
28 understanding of biological evolution (for reviews, see for instance: Richards, 2006; Rando, 2007;
29 Bossdorf et al., 2008; Jablonka, 2009; Skinner, 2010; Danchin et al., 2011; Wang, 2017; Danchin
30 et al. 2019). From the turn of the 3rd millennium onwards, major advances have been generated by
31 exceptional technological advances in high-throughput sequencing that nowadays allow the
32 simultaneous analysis of genomes, epigenomes, and transcriptomes in all their complexity. These
33 approaches, initially developed by molecular biologists, are becoming more and more accessible
34 to researchers in other sub-disciplines of biology working on both model and non-model species.
35 Consequently, these approaches have provided a new impetus to studies of the intricate
36 relationships between genes, environment and phenotypes in an eco-evolutionary context. A
37 particularly surprising output of the use of recent high throughput molecular technologies was the
38 discovery that the information encoded into the DNA nucleotide sequence by itself is often
39 insufficient to explain biological variation in all its complexity (Maher, 2008). This resulted in the
40 debate about missing heritability and revealed the existence of other forms of information
41 transmission across generations (Danchin, 2013).

42 The discovery of epigenetics (any modification other than changes in DNA sequences affecting
43 gene expression, whether those modifications have been shown to be stable or not) profoundly
44 changed our understanding of the functioning of biological organisms and generated considerable
45 interest in its role as a ‘missing link’ between environmental and phenotypic variation. In
46 particular, recent discoveries have fostered a full revision of the mechanisms of phenotypic
47 plasticity (Bonduriansky & Day, 2018; Herman, Spencer, Donohue, & Sultan, 2014; Jablonka,
48 2013; Pigliucci, Murren, & Schlichting, 2006; Reed, Waples, Schindler, Hard, & Kinnison, 2010;
49 Sentis et al., 2018; Sultan, 2011; Zhang, Fischer, Colot, & Bossdorf, 2012), inheritance
50 (Bonduriansky, 2012; Bonduriansky & Day, 2018; Danchin, 2013; Day & Sweatt, 2011) and
51 adaptation (Danchin et al., 2011, 2018, 2019; Pocheville & Danchin, 2015, 2017). These three
52 major lines of research in evolutionary biology are at the crossroads between individual-centred
53 approaches (that mostly study proximate mechanisms) and supra-individual approaches (that
54 mostly study ultimate processes) and are all impacted by our understanding of epigenetics
55 (Danchin & Pocheville, 2014; Jablonka & Lamb, 2005; Pocheville & Danchin, 2015). Epigenetics
56 has emerged as a key discipline in the study of ecological and evolutionary dynamics, and this

57 special feature contributes to highlighting the importance of this discipline.

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

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

84 The characterization of parental transmission of epigenetic variation to offspring is of major
85 importance to understand how rapid individual phenotypic changes are passed on through

86 generations and stay heritable over generations. A number of studies have been devoted to
87 demonstrating how maternal processes shape the physical and social context of offspring
88 development through behavioral and physiological mechanisms (Adkins-Regan, Banerjee, Correa,
89 & Schweitzer, 2013; Galloway, 2005). Yet, very little is known on how the paternal transmission
90 occurs. Champagne (2020) describes the current state of knowledge regarding paternal epigenetic
91 effects, the interplay between maternal and paternal influences, and the importance of considering
92 the complex nature of reproduction when predicting the transmission of phenotypes across
93 generations. The paper reviews experimental evidence on how sperm can drive the paternal
94 transmission of epigenetic marks by a diversity of environmental effects, such as nutritional or
95 toxicological effects, and may shape offspring characteristics. The review also emphasizes how
96 the environmental exposure history of males may alter female mate preference through sexual
97 selection processes. It hence argues for a better integration of behavior in the transgenerational
98 transmission of epigenetic variation.

99 Biological invasions are a global scourge and a major issue in the current context of globalisation
100 and the world-wide and rapid transport of organisms outside of their native range. However, for
101 an invader to be successful it needs to be able to rapidly respond to and cope with different
102 environmental conditions. Marin and collaborators examine the possible link between stress and
103 epigenetic changes and transposable element activity in generating phenotypic and genetic
104 variation in invasive populations. They argue that these mechanisms can contribute to the
105 success of biological invasions by facilitating plasticity as well as rapid adaptive evolution.
106 Indeed, whereas epigenetic variation and transposable elements are generally well regulated and
107 thus 'hidden' in natural populations, these mechanisms may be released from their regulation in
108 new and stressful environments. As such, Marin and collaborators argue that the epigenome
109 needs to be studied in greater detail if we want to understand the mechanisms by which
110 populations successfully colonize and adapt to new environments.

111 Given the ability of epigenetic mechanisms to allow organisms to respond to rapid changes in their
112 environment, they may also play an important role in conservation. Indeed, the paper by Rey et al
113 (2020) argues strongly that epigenetic variation and more particularly DNA methylation represent
114 important components of biodiversity linking genome to environment. They highlight the
115 importance of DNA methylation in providing biomarkers for past and present environmental

116 stress, the ecological structuring of wild populations, improving translocations and for studying
117 landscape connectivity. As such, epigenetic mechanisms appear as a promising and important tool
118 in conservation biology that may allow conservation biologists to overcome essential challenges.

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

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

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