Exploring the interplay of epigenetics and individualization

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HIGHLIGHTS

- Recognising inter-individual differences has significantly improved our understanding of eco-evolutionary processes. However, the biological mechanisms underlying individualization are still poorly understood.
- Epigenetic processes allow the same genotype to give rise to different phenotypes, but we still lack an understanding of how epigenetic modifications are regulated and how they produce phenotypic variation.
- We argue that epigenetic modifications could be key mediators of inter-individual differences and that, in turn, individual phenotypic differences can also affect epigenetic patterns on both ecological and evolutionary timescales.
- Simultaneously investigating epigenetic and phenotypic variation within individuals throughout ontogeny and in response to environmental changes will advance the fields of ecology and evolution.

ABSTRACT

Considering individual differences enhances our understanding of eco-evolutionary processes. Epigenetic modifications, which enable the same genotype to produce different phenotypes, may serve as a key proximate mechanism underlying these differences. We propose that epigenetic mechanisms mediate the realization of individualized niches. This process is best understood by distinguishing between environmentally inducible and non-inducible epigenetic modifications, as they play distinct roles in shaping individualization. Furthermore, we suggest that the realization of individualized niches can contribute to the emergence of epigenetic variation. Niche processes can modify the epigenomes of individuals and their offspring, even in the absence of germline transmission. Additionally, these processes may buffer selection, thereby preserving epigenetic variation.

INDIVIDUALIZATION AND EPIGENETICS

Recent studies have shown that considering individual phenotypic differences within and between plant, animal and human populations helps us to better understand ecological and evolutionary phenomena [1-3]. This phenotypic variation arises because individuals have different requirements, leading to differences in how they respond to changes in their environment [4]. The recognition of the importance of integrating individual differences into evolutionary and ecological research led to the conceptualization of the **individualized niche** [5] (Box 1, see Glossary). Individualized niches can be dynamic and are realized through three core processes termed **niche choice**, **niche construction** and **niche conformance** [5, 6] (Box 1). Although these processes have been repeatedly documented [5, 6], the underlying molecular mechanisms remain poorly understood.

Concurrently, interest in **epigenetics** (Box 2) has grown with the advent of new technologies that enable the study of these highly variable and dynamic processes that can alter gene expression and function in many organisms [7]. However, despite ongoing progress in this emerging field, many fundamental questions remain unanswered. For example, it is still unclear why only certain parts of the epigenome are altered by the environment, are transmitted across generations, and have phenotypic, ecological or evolutionary consequences [8]. These questions are difficult to answer as patterns of epigenetic variation are complex and dynamic. For example, epigenotypes differ among individuals, even within genetically unstructured populations [9], different epigenetic modifications can interact functionally, and epigenetic variants can have a reciprocal and functionally interdependent relationship with genetic variants [10].

Building upon the idea that epigenetic variation contributes to phenotypic differences among individuals [11, 12], it may also play an important role in the realization of individualized niches. This is because epigenetic marks can change in response to environmental cues, providing a mechanism that connects the environment, epigenome, gene expression and phenotype, allowing niche realization [13]. Both theoretical and empirical studies (reviewed in [4, 5]) have highlighted how using the concept of the individualized niche can improve our understanding of ecological and evolutionary processes, which in turn may explain the hitherto not fully understood patterns and dynamics of interindividual epigenetic variation.

Thus, we argue that considering both epigenetic and phenotypic variation in the same individuals will provide a deeper understanding of how both epigenetic and phenotypic differences arise, are maintained and connected. Drawing on empirical evidence, we explore the implications of this perspective on ecological and evolutionary timescales. Lastly, we highlight future directions for the emerging field of individualised epigenetics.

BOX 1: INDIVIDUALIZED NICHES AND THE PROCESSES THROUGH WHICH THEY ARE SHAPED

An **individualised niche** is defined as the subset of a species' niche that is realized by an individual and which represents the range of biotic and abiotic conditions under which such an individual can survive and reproduce [5]. It emerges from the interaction between a focal individual and its environment and affects the phenotype-environment match, which is expected to increase the focal individual's fitness. Individualized niches can be dynamic and are realized and (re-)shaped through the three processes of niche choice, niche construction and niche conformance [5], which are triggered by a

phenotype-environment mismatch. These processes can act concurrently and/or consecutively when a single process cannot fully resolve the phenotype-environment mismatch.

Niche choice is the process during which an individual selects a physical or social environment that matches its phenotype. Niche choice behaviours include habitat choice, whereby an individual moves to a different habitat, as in arboreal anole lizards (*Anolis* spp.) where individuals choose different perching locations to optimize the experienced temperature and their camouflage [14]. Niche choice also occurs when individuals select specific parts of the environment to interact with, for example through the choice of resources or social groups. In Trinidadian guppies (*Poecilia reticulata*), consistent differences in the selection of social interaction partners among individuals affect the size and strength of their social networks [15].

Niche construction is the process through which an individual actively modifies the environment to increase the match with its own phenotype. Examples of niche construction range from dam-building in beavers through nest-building in birds to soil structure alteration in earthworms [16]. Individuals can also alter their social environment. An example of social niche construction is given by foundress associations of the paper wasp *Polistes gallicus*, where subordinate females can challenge dominant queens and, if successful, become dominant queens themselves [17].

Niche conformance is the process through which an individual adjusts its phenotype to optimize its match with the environment. Niche conformance involves phenotypic **plasticity**, but it also emphasizes the importance of inter-individual variation in plastic responses [18], which is expected to lead to the formation of different individualized niches. Niche conformance can involve irreversible phenotypic changes, as in water fleas (*Daphnia cucullata*) where the expression of inducible defences during

development is a response to anticipated predation risk [19], or reversible changes, as in many plants, where drought prompts increases in the concentration of osmolytes [20].

BOX 2: EPIGENETICS

The term **epigenetics** commonly refers to biochemical mechanisms and modifications that induce changes in gene expression and function without altering the DNA sequence [7]. **Epigenetic modifications** can enhance or reduce the transcription and translation of genes [7]. They consist of **epigenetic marks**, which are chemical modifications like DNA methylation – the addition of a methyl group to the DNA [21]. Marks can also emerge on histones, the proteins around which DNA is wrapped, to increase or decrease the accessibility of packed DNA for transcription [22] . Different epigenetic marks can also interact with each other [23]. A second type of epigenetic modifications are **epigenetic regulators**, which establish, interpret or remove these marks, as well as further processes regulating gene expression [24]. Beyond the enzymes that establish epigenetic marks, a well-known epigenetic regulator is RNA interference, where small [25] or long RNA molecules (siRNA or miRNA, respectively) [26] regulate gene expression by targeting mRNA for degradation or translation repression. Epigenetic modifications are classified by their origin as either **genetically inducible**, **non-inducible** or **environmentally inducible** [27, 28]. Genetically inducible modifications arise non-randomly as a consequence of genetic variation. Non-inducible modifications emerge, similar to genetic mutations, spontaneously and independently of the environment. They are expected to be mostly selectively neutral but may also have sometimes beneficial phenotypic consequences analogous to genetic mutations. By contrast, environmentally inducible modifications (subsequently

158 referred to as ‘inducible modifications’) are modifications that are induced by the
159 environment. Here, we focus on non-inducible and inducible modifications, whose
160 effects differ distinctly from genetic mutations due to their transgenerational stability
161 being around three to four orders of magnitude lower [29].

162 Both non-inducible and inducible modifications can be directly inherited through
163 meiotic pathways, also known as **germline inheritance** [30]**.** In vertebrates, this topic
164 is controversial as extensive epigenetic reprogramming during gametogenesis and
165 embryonic development often resets epigenetic modifications [31]. However,
166 mechanisms of germline inheritance vary substantially across taxa (e.g., modifications
167 are maintained over many generations in nematodes [32]). In addition, both non-
168 inducible and inducible modifications can indirectly impact epigenetic variation in
169 subsequent generations by affecting parental phenotypes, even when germline
170 inheritance is absent. For example, epigenetic modifications within offspring may arise
171 from **experience-mediated inheritance** [33]. Alternatively, niche choice or
172 construction alter parental environments, which, if inherited by the offspring, can
173 induce epigenetic modifications in the offspring generation even when parents are
174 absent, a phenomenon known as **ecological inheritance** [33].

175

176 **EPIGENETIC MECHANISMS AS MEDIATORS OF NICHE PROCESSES**

177 Individualized niches emerge through interactions between an individual and its
178 environment (Fig. 1). Niche realization may occur when epigenetic modifications affect
179 genes underlying phenotypic traits involved in niche choice, construction or
180 conformance. We suggest that inducible and non-inducible epigenetic modifications
181 (Box 2) play different roles in this process. That is because inducible modifications,
182 which are under environmental control, are likely to be functionally significant due to

past selection on environmental induction, and thus should be more often relevant for the realization of individualized niches. In contrast, non-inducible modifications, which are independent of the environment, are often selectively neutral. However, when non-neutral, they may likewise encode information about past selection regimes [29].

Individual responses to future phenotype-environment mismatches can be affected by non-neutral, non-inducible modifications and by inducible modifications, particularly those established during early-life. That is because these epigenetic modifications may predetermine phenotypes relevant for both niche choice and niche construction. Hence, we expect that non-inducible and/or inducible epigenetic modifications that are present prior to a phenotype-environment mismatch can affect individual decision-making in relation to these two niche processes. Alternatively, a phenotype-environment mismatch may directly trigger changes in inducible epigenetic patterns, with potential phenotypic consequences. Niche conformance occurs when an individual changes its phenotype to alter and ideally optimize the match between its phenotype and the environment. Hence, we expect that epigenetic modifications induced directly by a phenotype-environment mismatch facilitate niche conformance.

Given the framework described above, one possible prediction is that individuals with similar epigenotypes will occupy similar individualised niches. However, such a pattern may be confounded in a number of situations. First, similar phenotypic responses may arise from different sets of epigenetic modifications. This is especially true for highly polygenic traits, as epigenetic modifications at different genes affecting the same phenotype may converge towards similar phenotypic outcomes. Moreover, individuals with different genotypes may rely on different epigenetic modifications to achieve the same phenotypic outcomes due to the interdependence between genetic and epigenetic variation. Second, multiple niche processes can act concurrently or sequentially when a single niche process is not sufficient to resolve a

phenotype-environment mismatch, and different niche processes will likely be mediated by epigenetic modifications at different genes. Third, both non-inducible and inducible **epigenetic allele** frequencies could potentially change as a consequence of niche processes. For example, if individuals differ in niche conformance due to pre-existing non-inducible epigenetic differences, an environmental change that triggers niche conformance may non-randomly select individuals and thereby alter the frequencies of non-inducible modifications in populations. Likewise, we might also observe inducible epigenetic modifications after niche choice or construction because the chosen or constructed niche has induced those changes. Although it remains empirically challenging to establish causal links between epigenetic variation and individualised niches, we stress that both non-inducible and inducible epigenetic modifications should be considered as potential mechanisms that mediate the realization of individualised niches.

EPIGENETIC PATHWAYS THAT ALLOW NICHE PROCESSES TO ACT ACROSS GENERATIONS

Non-inducible and inducible epigenetic modifications underlying individualised adjustments to niches could provide an alternative route to evolutionary adaptation if they can be transferred across generations (i.e. inter- or trans-generational inheritance). While this idea has been debated at length, experimental support is still limited and remains controversial [34]. Nonetheless, documented examples exist for at least three different pathways through which epigenetic modifications can be transferred inter- and/or trans-generationally (Box 2), namely germline inheritance, experience-mediated inheritance and ecological inheritance [33].

Germline inheritance, as described for *Caenorhabditis elegans* (Box 3), can involve both non-inducible and inducible epigenetic modifications. It is important to recognise that most but not all epigenetic modifications are 'erased' during gametogenesis and embryonic development in many organisms, including mammals and birds [35, 36], and that the extent of this process may differ between paternal and maternal gametes [37].

Experience-mediated inheritance involves inducible epigenetic modifications in the offspring generation whose status is determined by specific events, such as the type of parental care. Unlike germline transmission, an epigenetically determined phenotype in the parental generation induces the same epigenetic modifications in the offspring generation [33, 38]. If such epigenetic alleles are also associated with phenotypes relevant for any of the three niche processes, experience-mediated inheritance would represent an alternative mechanism through which phenotypes important for the realization of individualized niches can be inherited. One instance of this may be social niche construction as described for rhesus macaques *Macaca mulatta* (Box 3), where a mother's social rank is linked to epigenetic modifications in her offspring.

Lastly, ecological inheritance might occur when parents choose or construct the offspring environment. It is independent of the direct transmission of epigenetic modifications and likely involves only modifications that are induced by the environment and which are passed down from parents to their offspring (see Box 3). The offspring would then need to match their phenotypes to the parentally determined environment, which can be achieved by niche conformance. We speculate that ecological inheritance might also prime the offspring, once matured, to perform niche construction or niche choice processes similar to those implemented by their parents, leading to further transmission of the environment to consecutive generations.

BOX 3: EMPIRICAL EXAMPLES OF HOW EPIGENETIC MECHANISMS CAN MEDIATE THE REALIZATION OF INDIVIDUALIZED NICHES

Niche choice has been observed in capelins (*Mallotus villosus*), where one ecomorph chooses to spawn near the bottom of the ocean, while the other adopts a beach-spawning tactic. The different ecomorphs show epigenetic differences [39]. Given that temperature can affect methylation patterns during embryonic development in fishes [40] and that the two breeding habitats differ substantially in temperature, the epigenetic alleles potentially underlying breeding habitat choice are likely induced during embryonic development through ecological inheritance [39]. Additionally, methylation patterns can be stably inherited across generations through the germline in fishes [41]. It thus appears likely that methylation-driven differences in niche choice are also passed on to the next generation through germline inheritance.

Female rhesus macaques (*M. mulatta*) engage in niche construction by shaping their social environment. They do so by intervening in the grooming of other group members. The ability to perform this type of social niche construction depends on an individual's dominance rank [42], which is associated with differences in the DNA methylation of their placental tissue, which likely contributes to foetal programming [43]. Dominance rank is also transmissible to the next generation [44]. The observation that placental DNA methylation patterns predict maternal rank [43], despite maternal rank being flexible, suggests that experience-mediated inheritance can play an important role in this process.

The ground-dwelling nematode *C. elegans* has evolved the ability to conform to more stressful conditions, not only within a single generation but also transgenerationally. Exposure to starvation stress can induce adaptive developmental

arrest through changes in small interfering RNA expression [45]. These small RNAs can also interact with certain histone modifications [46]. They are passed on transgenerationally through germline inheritance and target genes related to nutrition in consecutive generations [32], thus increasing starvation resistance [47].

EPIGENETICS, INDIVIDUALIZATION AND EVOLUTION

Evolution is driven either by **natural selection** or by **genetic drift**. Epigenetic modifications, which can be selected for when they have beneficial phenotypic consequences, may represent an alternative evolutionary pathway, particularly if they are stably transmitted across multiple generations, as they would then act like genetic alleles. Additionally, epigenetic modifications may affect local mutation rates [48], which can result in **genetic assimilation** [49]. Generally, a consequence of genetic assimilation is lower plasticity [49], i.e., a subsequent reduction in the amount of underlying inducible epigenetic modifications.

Niche processes may explain differences in epigenetic variation among individuals and populations. First, because niche choice and construction result in exposure to a novel environment, they may facilitate the emergence of inducible epigenetic modifications. Second, niche processes may buffer selection and facilitate the coexistence of individuals that differ in (epi-)genotypes, thereby maintaining epigenetic variation in populations. Epigenetic modifications can be shared across manifestations of single niche processes (e.g. niche conformance of different traits) or across different niche processes that together optimize the phenotype-environment match, enabling the rapid co-evolution of affected traits. However, individual niche processes are likely mediated by different epigenetic modifications, which evolve independently. In these circumstances, we expect non-inducible and inducible

309 epigenetic modifications to be differentially favoured under different conditions, and
310 also to have distinct evolutionary consequences.

311 A small proportion of non-inducible epigenetic modifications are expected to
312 have phenotypic effects and to be stable enough across generations to serve as
313 targets of natural selection [27, 50]. These modifications should be favoured when
314 environmental conditions are predictably stable over long time periods [51], as plastic
315 responses to changing environments may incur costs [39]. If inducible modifications
316 can be converted to non-inducible modifications in such stable environments, costs
317 could decrease, firstly by non-inducible epigenetic modifications becoming favoured
318 over inducible ones, and secondly through the genetic assimilation of non-inducible
319 modifications. Similar to inducible epigenetic modifications, we also expect the amount
320 of non-inducible epigenetic modifications to decrease following genetic assimilation.

321 The accumulation of non-inducible epigenetic modifications should be linked
322 with the evolution of niche choice and construction. In predictably stable environments,
323 non-inducible epigenetic alleles determining the most successful niche choice
324 phenotypes may have been favoured by selection. Similarly, non-inducible
325 modifications underlying niche construction may also have been selected for when the
326 possibility to modify the environment in a given way can be predicted. Consequently,
327 niche choice and construction could promote the partitioning of individuals across
328 different environments, which may lead to the evolution of **ecotypes** and ultimately to
329 speciation. Consistent with this, epigenetic differences between different ecotypes [62]
330 and closely related species [52] have been reported, although the causal links have
331 yet to be determined.

332 On the other hand, inducible epigenetic modifications do not include information
333 on past selection regimes and are instead determined by the current environment [29].
334 Although they are not directly targeted by natural selection at first appearance, they

can mediate rapid intra- and transgenerational plasticity, which increases environmental tolerance and lowers extinction risk under environmental change [53]. The evolution of plasticity, and hence the accumulation of adaptive inducible modifications, should be favoured particularly in heterogeneous environments with different fitness optima and with at least short-term predictability via reliable cues [54]. That is because, despite the low heritability of plastic traits, genetic alleles promoting epigenetic inducibility as a trait itself might be selected for in fluctuating environments (in line with the Baldwin effect, see [55]).

Challenging environmental conditions can increase epigenetic variation, a phenomenon known as **epigenetic buffering** [56]. This may then increase phenotypic variation, leading in turn to a greater level of individualization and an increased probability of population persistence in fluctuating or novel environments. That is because the increased level of epigenetic variation in the population means that there is more epigenetic variation among individuals. Accordingly, epigenetic diversity is often higher among individuals facing challenging environmental conditions, such as in invasive species [57], among individuals at the leading edge of the species distribution during range expansion [58] and in urban versus rural populations [59], although other confounding factors, such as changes in reproductive modes, might also contribute to observed changes in epigenetic diversity.

THE CHALLENGE OF STUDYING EPIGENETIC MODIFICATIONS CONTRIBUTING TO INDIVIDUALIZED NICHES

Identifying adaptive epigenetic modifications associated with niche processes remains difficult. The first challenge is that the majority of epigenetic modifications appear to be neutral and non-adaptive [60]. Additionally, the role of epigenetic variation may be

confounded by population history (e.g., genetic drift), or environmental variation. A practical solution to these challenges are experimental evolution paradigms [61], which enable the quantification of epigenetic changes, their heritability, their contributions towards niche processes and their impacts on individual fitness.

A second relevant challenge is to determine whether epigenetic modifications of interest are non-inducible or inducible. This can be achieved through multi-generational common-garden studies [28] or by comparing within-population and among-population differences [62]. However, epigenetic modifications in the soma can vary among cell types [63], genotypes [64] and sexes [65], and inducible somatic modifications can additionally be influenced by seasonal variation [66], ageing [67] and developmental status [68]. Controlling for these sources of variation requires well-designed experiments with sufficient sample sizes for each potential confounding factor (e.g., for each age class).

As genetic and epigenetic variation are interdependent, a third challenge is that the relative importance of epigenetic processes in individualization can be only assessed by establishing baselines for mutation rates and the mode(s) of inheritance of epigenetic modifications. This can be achieved with controlled experiments in stable environments where selection pressures are minimized and the long-term dynamics of epigenetic processes can be investigated [69]. Additionally, study systems where genetic variation can be controlled or minimized, such as isogenic or inbred lines, may be particularly suitable to experimentally determine the role of epigenetic mechanisms while controlling for genetic variation. Performing such studies across diverse taxa is essential to assess the generality of their outcomes.

Given the challenges described above, the use of clonal species [70] or even epigenetic manipulation [71] may be necessary to validate the functional roles of epigenetic variation in individualization. Furthermore, due to the diversity of epigenetic

mechanisms (Box 1), focusing on only one mechanism becomes a limiting factor. Hence, multi-omics integration is essential. This will facilitate the simultaneous investigation of multiple layers of epigenetic regulation, and shed light on how these layers interact with one another [72] and collectively contribute to phenotypic variation and the realization of individualized niches.

CONCLUSIONS

We discuss how the realization of individualized niches can be mediated by epigenetic mechanisms, a process that we believe is best understood by focusing on the distinction between non-inducible and inducible epigenetic modifications and their different roles in determining niche processes. Even though relevant epigenetic modifications may not always be inherited directly through the germline, transgenerational effects of the epigenome may still be possible via experience-mediated and ecological inheritance, and might therefore affect niche realization over several generations. In turn, niche processes can alter patterns of selection and thereby influence the emergence and maintenance of epigenetic variation. Lastly, we outline methodological challenges and provide future perspectives on how to link epigenetic variation to the processes leading to individualized niches (see also Outstanding questions).

In summary, our understanding of eco-evolutionary processes will benefit from the concurrent analysis of genetic, epigenetic and phenotypic variation at the individual level. This approach promises to uncover the mechanisms driving the realization of individualized niches and to elucidate the origin, function and dynamics of epigenetic changes.

OUTSTANDING QUESTIONS

What is the relative contribution of epigenetic versus genetic variation to the realisation of individualized niches?

What fractions of non-inducible and inducible epigenetic modifications contribute towards the realisation of individualized niches, and what fractions are adaptive and/or heritable?

What is the relative importance of non-neutral, non-inducible versus inducible epigenetic modifications to individualization?

Are epigenetic modifications shared within manifestations of each niche process or among different niche processes, causing joint evolution or evolutionary constraints?

Are the epigenetic mechanism(s) driving niche processes ubiquitous across taxa and can they be generalized?

Do epigenetic modifications that are stably passed down through the germline and underlie niche processes represent an alternative evolutionary pathway, and to what extent is this independent of DNA sequence changes?

How does epigenetic variation change over evolutionary timeframes, and does the amount of variance that can be accounted for by individualization change as a result of these long-term dynamics?

GLOSSARY

ecological inheritance: inheritance of the parental environment and its inherent processes and effects on individuals, potentially including epigenetic modifications induced by the environment in the offspring generation.

ecotype: a population of a species that survives as a distinct group under local environmental conditions, potentially because of specific genetic and/or epigenetic adaptations.

epigenetics: biochemical mechanisms and modifications that induce changes in gene expression and function without altering the DNA sequence.

epi(genetic) allele: different variants of a gene that are only distinguished by their epigenetic modifications.

epigenetic buffering: when a population endures challenging conditions and persists through high levels of epigenetic variation, which makes the production of successful phenotypes more likely.

epigenetic mark: chemical modifications made to DNA or histone proteins that influence gene expression without altering the DNA sequence itself.

epigenetic regulator: protein, enzyme or molecular complex that writes, reads or erases epigenetic marks and orchestrates changes in chromatin structure.

epigenetic modification: reversible and heritable biochemical changes that modify gene expression in the absence of changes to the DNA sequence. Includes both epigenetic marks and regulators.

evolution: the change in frequency of genetic sequence variants (i.e., alleles) over time

experience-mediated inheritance: when an induced change in the parental phenotype induces epigenetic modification in the offspring, for example through altered parental care.

genetic assimilation: the process whereby a phenotype initially induced by the environment becomes genetically encoded.

genetic drift: random changes in allele frequencies from one generation to the next.

genetically inducible epigenetic modification: an epigenetic modification that arises non-randomly as a consequence of genetic variation.

germline inheritance: genetic and epigenetic modifications that are passed from one generation to the next through germline cells, its extent varies strongly between the type of epigenetic modification and across taxa.

individualised niche: the range of environmental conditions under which an individual lives and reproduces more successfully than an average conspecific. It is a subset of the species' niche, and it affects the individual's fitness function.

environmentally inducible epigenetic modification: an epigenetic modification at a defined genomic location whose allelic status is controlled by the environment.

natural selection: the increased survival and reproduction of individuals with well-adapted phenotypes.

niche choice: the process through which an individual selects an environment to increase its phenotype-environment match and fitness.

niche conformance: the process through which an individual adjusts its phenotype to increase its phenotype-environment match and fitness.

niche construction: the process through which an individual modifies the environment to increase its phenotype-environment match and fitness.

non-inducible epigenetic modification: an epigenetic modification that arises as a spontaneous epimutation independent of the environment and is a potential target of natural selection.

phenotype-environment mismatch: a situation in which the environmental conditions encountered by an individual do not fit its phenotype, triggering an individual response (niche choice, niche construction or niche conformance) aimed at resolving the mismatch.

plasticity: the ability of a given genotype to generate multiple different phenotypes. Plasticity can occur within a single generation or inter-/transgenerationally when offspring phenotypes are altered by the environment experienced by the parents or previous generations.

FIGURES

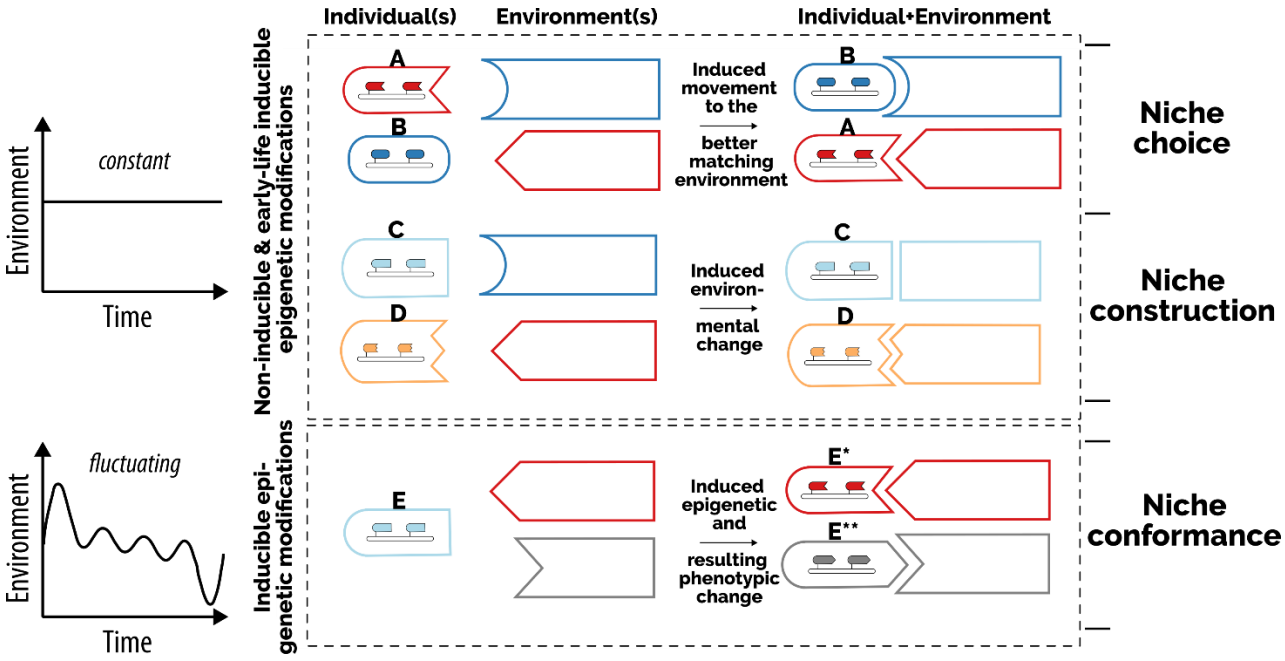

Fig. 1: Schematic depiction of how the three processes involved in realizing individualized niches relate to epigenetic variation. Individuals encounter environmental conditions and resources that either match or mismatch their phenotype. Through the three processes niche choice, niche construction and niche conformance, individuals (denoted with the letters A–E) achieve a suitable match with their environment, leading to the realization of their individualized niche. We argue that niche choice and niche construction are mainly driven by non-inducible epigenetic modifications (whose evolution is favoured by constant environments over ecological timescales, leftmost diagrams) or by epigenetic modifications induced in early life, whereas niche conformance is driven by inducible epigenetic modifications (whose evolution is favoured by variable environments over ecological timescales, e.g., E* or E**). Within individuals, chromosomes are denoted by DNA strands, with the shapes above them representing epigenetic marks. The shapes and colours of epigenetic marks and individuals denote their epigenotypes and resulting phenotypes, and matching shapes and colours on the environmental level suggest an improved phenotype-environment match. Letters above shapes denoting individuals represent how the phenotypes, genotypes and epigenotypes sort or change through the different niche realization processes; asterisks next to letters indicate a change in the epigenotype.

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