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Genetic variation in niche construction: implications for development and evolutionary genetics

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Abstract

Niche construction occurs when an organism's traits influence the environment that it experiences. Research has focused on niche-constructing traits that are fixed within populations or species. However, evidence increasingly demonstrates that niche-constructing traits vary among genotypes within populations. Here, we consider the potential implications of genetic variation in niche construction for evolutionary genetics. Specifically, genetic variation in niche-constructing traits creates a correlation between genotype and environment. Because the environment influences which genes and genetic interactions underlie trait variation, genetic variation in niche construction can alter inferences about the heritability, pleiotropy and epistasis of traits that are phenotypically plastic. The effects of niche construction on these key evolutionary parameters further suggest novel ways by which niche construction can influence evolution.

Genetic variation in niche construction

Niche construction is the process by which an organism's traits determine the environment that it experiences [1]. Niche construction can influence all types of environments—abiotic, biotic, and social—and can arise from a variety of behaviors or other traits. Most famously, some organisms literally construct the nests, dams, burrows, webs, cities, or other habitats in which they live. More commonly, organisms can choose a particular habitat, ecological partner, or social group. Once they are in a particular environment, organisms can alter it by excreting chemicals or waste products [1]. An individual can also “construct” its social environment by eliciting behaviors in other individuals, and by influencing behavioral interactions in his or her group [2, 3]. These traits need not be adaptive to be considered niche-constructing. The diversity of mechanisms by which niche construction can occur suggests that niche construction is a common feature of organisms.

Investigators interested in niche construction have primarily focused on situations in which niche-constructing traits are fixed within species, and considered the effects of niche construction over many generations. These studies indicate that niche construction is profoundly important to evolution and ecology (reviewed in [4]). Niche construction overlaps diverse ecological and evolutionary processes (Box 1), further underscoring its broad relevance.

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Recently, there has been a surge of empirical studies demonstrating that niche-constructing traits vary among genotypes within populations. Animals commonly show genetic variation in habitat preferences (reviewed in [5]); plant genotypes differ in the environments in which they choose to germinate [6,7]; birds [8] and fruit flies [9] show genetic differences in group size preferences; and fruit flies [3] and mammals [10] show genetic variation in aggressive behaviors that influence the social environment. Because most traits vary to some extent among genotypes, it is likely that many more examples of genetic variation in niche construction await discovery.

Niche construction theory has been criticized on the grounds that the definition of niche construction is so broad that it could plausibly apply to virtually all organismal traits (reviewed in [11]). We suggest that delineating traits that are and are not niche-constructing is not the primary utility of niche construction theory. Rather, considering a trait from the perspective of niche construction is useful when niche construction theory provides novel insights into evolutionary and ecological processes. Here, we describe how the role of niche construction in trait development provides an overlooked case in which the niche construction perspective can provide novel insights into evolutionary genetics. We emphasize that niche construction influences the developmental environment, that is, the environment in which all organismal traits develop and are expressed. When niche construction varies among genotypes, different genotypes will experience different developmental environments, creating a correlation between genotype and environment. This correlation is critically important for the development of phenotypes that are plastic with respect to the environment that is generated by niche construction. We illustrate how genetic variation in niche construction can thereby influence estimates of heritability, and generate pleiotropy and epistasis. The effects of niche construction on these key evolutionary parameters suggest that niche construction might affect evolution in ways that have not yet been recognized; we conclude by describing some of these evolutionary implications.

Genetic variation in niche construction can affect phenotypic differences among genotypes through phenotypic plasticity

The type of niche-constructing trait expressed by an individual determines the environment that it experiences. A major, but underappreciated, implication of this concept is that genotypes with different niche-constructing traits will systematically experience different environments (Box 2). This differs from other theories of heterogeneous environments, in which environmental variation is random with respect to genotype [12]. For example, aphid genotypes differ in habitat preference [13]. In nature, these preferences are reflected in their distribution among host types, with alfalfa-preferring genotypes found on alfalfa and clover-preferring genotypes found on clover [13]. This correlation between genotype and host type is expected whenever both host types are available to aphids (Figure 1, Box 2).

The implications of genetic variation in niche construction for functional and evolutionary genetics stem from the importance of the environment in the development and expression of phenotypes. Namely, phenotypic plasticity is the phenomenon in which a single genotype expresses different types or levels of phenotypes in different environments. It is exceptionally common, across taxa, across traits, and across abiotic, biotic, and social environments (for reviews see [14–17]). Many types of plasticity have been identified [16, 17]; here we consider only the most basic element of plasticity, i.e., that individuals of a given genotype can develop and express different levels or types of a trait in different environments.

One or more traits of a niche-constructing organism might be phenotypically plastic with respect to the environment that is generated by niche construction. In this case, the expression of the plastic traits depends on the environment that is shaped by the organism's niche-constructing traits ([16, 17]; Figures 1–2).

Typically, the amount of phenotypic variation in a (sample of a) population, V_P , represents the sum of the genetic variance, V_G (i.e., phenotypic differences among genotypes) and environmental variance, V_E . V_E can be thought of as the degree of phenotypic plasticity, because V_E describes the effect of the environment on the phenotype. In this case, $V_P = V_G + V_E$ [18]. This equation assumes that V_G and V_E are independent. However, when genotypes vary in niche construction, genetic effects can be correlated with the effects of phenotypic plasticity (i.e., environmental effects), because different genotypes experience different environments (Box 2). When genotypes differ in niche construction, phenotypic variation V_P is described by $V_P = V_G + V_E + 2\text{cov}_{GE}$ [18]. cov_{GE} describes the covariance between genetic variance in the phenotype and the phenotypic effect of the environment on that phenotype, i.e., the effects of phenotypic plasticity.

The idea that genetic variation in niche construction can contribute to phenotypic differences between genotypes makes sense intuitively. Typically, genotypes within a population are assumed to differ only in DNA sequence (including mitochondrial sequence, etc). When genetic variation in niche construction is present, genotypes differ both in DNA sequence *and* in the environments they experience as a consequence of niche construction (Figure 1; note that other processes can also generate gene-environment correlations, see Box 2). Thus, the genotype affects the phenotype not only through the production of proteins and other products in cells and tissues, but also by influencing the niche-constructing traits that determine the environment in which all other traits develop and are expressed (Figures 1–2; [19, 20]). This idea has been widely recognized in the case of parental effects: when parents' traits influence the environment in which offspring develop, individuals can differ phenotypically because of genetic variation they inherit from their parents and because of the developmental environment that their parents partially create [21, 22]. Here, we emphasize that this process can also occur for a single individual within a generation.

For example, Swallow et al [23] studied mice that had been either artificially selected for high levels of voluntary wheel running (HR lines) or not (Control lines). The lines showed a variety of physiological differences, including in ovary size, but only when they had access to running wheels. The authors concluded that the physiological differences were the result of phenotypic plasticity; and therefore, the environment-dependent differences between HR and Control lines were a consequence of genetic differences in their voluntary exposure to the wheel-running “environment” [23]. This example illustrates how genetic variation in niche construction can contribute to phenotypic (e.g., ovary size) differences between genotypes, V_G .

Genetic variation in niche construction can affect heritability

Broad-sense heritability, H^2 , is the proportion of variance in a trait that is attributable to genetic differences: V_G/V_P . As described above, genetic variation in niche construction can contribute to differences between genotypes, V_G , for traits that are phenotypically plastic. These findings suggest that the heritability of a phenotypically-plastic trait can be influenced by genetic variation in niche construction [11]. This same logic applies to narrow-sense heritability (i.e., h^2 , the proportion of variance in a trait that is attributable to *additive* genetic differences), if the niche-constructing trait is inherited additively [18]. Further, the mouse example [23] illustrates that when one environment permits the expression of niche-constructing traits (Figure 1 right), and another environment does not (Figure 1 left), the

heritability of phenotypically plastic traits is expected to differ across those environments if genotypes differ in niche construction.

Specifically, quantitative genetics theory predicts that, for traits that are phenotypically plastic, genetic variation in niche construction can increase heritability if cov_{GE} is positive (Figure 1). Genetic variation in niche construction can also reduce heritability if cov_{GE} is negative. For example, Roff and Shannon [24] studied cricket lines that were artificially selected for either high rates of macroptery--that is, the development of long, flight-capable wings--or low rates of macroptery. In this species, the likelihood of developing the macropterous morphology depends on genotype and on the temperature the cricket experiences as a nymph [24]. Roff and Shannon found that, when reared at a constant temperature, the two lines showed strong differences in rates of macroptery. However, the lines also showed striking differences in temperature preferences: nymphs from the high-macroptery line preferred temperatures that made them less likely to become macropterous, and nymphs from the low-macroptery line preferred temperatures that made them more likely to become macropterous [24]. Thus, genetic variation in temperature preferences could conceal genetic differences in rates of macroptery. In this sense, a negative cov_{GE} can be considered a form of homeostasis.

The potential effects of genetic variation in niche construction on trait development suggest that heritability studies can benefit from considering genetic variation in niche construction. Studies that explicitly consider genetic variation in niche construction can disentangle V_G , the “typical” genetic variation, from cov_{GE} , the phenotypic effect of genetic variation in niche construction [25]. The expected effects of genetic variation in niche construction on heritability assume that other factors affecting heritability are equal, which is rarely the case in nature [26]. Heritability can be influenced by average environmental quality and by the evolutionary novelty of the environment (reviewed in [27]); by genetic variation segregating in the populations under study [28]; and by selection [29]. Further, these factors might not be independent of niche construction; for example, niche construction can impact environmental quality. Experiments that manipulate the opportunity for niche construction are needed to determine how often genetic variation in niche construction influences the heritability of phenotypically plastic traits, and in which direction.

Genetic variation in niche construction is a form of pleiotropy

Pleiotropy occurs when variation in a single gene underlies variation in more than one phenotypic trait; it is often inferred when genotypes co-vary in two or more traits [18]. Pleiotropy is generally assumed to arise from molecularly-based effects of a given mutation. However, pleiotropy can also result when the expression of one trait depends on the expression of another trait [30]. Because alleles that influence a niche-constructing trait thereby determine the environment in which other traits develop and are expressed, the niche-constructing trait and phenotypically-plastic traits are expected to be genetically correlated (Figure 2; [31]).

By extension, when more than one trait is plastic with respect to the environment shaped by niche construction, all of the phenotypically-plastic traits are expected to co-vary across genotypes, with each other and with the niche-constructing trait. For example, in cliff swallows (*Hirundo pyrrhonota*) choice of colony size is heritable [8]. Swallows in larger colonies spend less time alertly scanning for predators [32] but suffer increased risk of viral infection and ectoparasites [33], relative to swallows nesting in small colonies. A simple prediction is that colony size preference, predator surveillance, and infection status all co-vary, and that this co-variation has a genetic basis. To our knowledge, this idea has not been tested in cliff swallows or in any organism.

The phenotypic effects of genetic variation in niche construction depend on genotype-by-environment interaction

So far we have assumed that all genotypes show parallel reaction norms, i.e., differences in trait values across environments are in the same direction and of the same magnitude for all genotypes. However, genotype-by-environment (G×E) interaction is common. G×E interaction occurs when genotypes differ in phenotypic plasticity. For example, if some cliff swallow genotypes scan for predators more often in large colonies, but others scan less often in large colonies (relative to small colonies), then scanning for predators would show a G×colony size interaction. When genetic variation in niche construction and G×E interaction influence the same phenotype, the total variation in that phenotype is described by $V_P = V_G + V_E + 2\text{cov}_{GE} + G \times E$ [18].

Furthermore, genetic variation in niche construction and G×E interaction can act synergistically. For example, genetic factors correlate with the likelihood that adolescents will associate with peers who use alcohol and tobacco [34]. The finding that different genotypes experience different social environments suggests genetic variation in social niche construction, although in this study the underlying behavioral mechanisms were not identified. Further, the likelihood that adolescents will use alcohol and tobacco themselves depended on a G×E interaction: some genotypes were more sensitive to peer pressure, i.e., encouragement by their friends to use substances had a greater effect on their likelihood of substance use. Interestingly, the genotypes whose (inferred) social niche-constructing traits generated a social environment with the greatest peer pressure (i.e., friends who use substances) were also the most sensitive to peer pressure [34]. The type of complex gene-environment interplay identified in this study is believed to be a common feature of organismal development [35] and supports the notion that genetic variation in niche construction might serve as a “multiplier” of genetic differences [36]. To date, we are aware of very few studies that comprehensively evaluate genetic variation in niche construction and its developmental effects across natural genotypes (but see [6, 7, 37]).

Genetic variation in niche construction can generate epistasis

The presence of G×E interaction indicates that the phenotypic effects of mutations can vary across environments [38]. When genotypes vary in niche construction, the environment in which mutations exert effects is determined by the alleles underlying the niche-constructing trait. That the phenotypic effect of a mutation depends on alleles at other loci indicates that genetic variants underlying niche-constructing traits act epistatically to alleles underlying variation in phenotypically-plastic traits (Figure 2; [1, 20]).

Recently, the epistatic effects of alleles underlying genetic variation in niche construction were demonstrated in *Arabidopsis thaliana*. Chiang et al [39] studied near-isogenic lines (NILs) containing naturally-varying alleles of genes that are associated with germination time (*DOG1*) and with flowering time (*CRY*, *FLC*, *FRI*) in laboratory conditions. When the NIL plants were grown from seeds in nature, however, *CRY*, *FLC*, and *FRI* were not directly associated with flowering time. This was surprising because *CRY*, *FLC*, and *FRI* are canonical flowering-time genes (e.g., *FLC* stands for “flowering locus C”). Instead, the germination-time gene, *DOG1*, accounted for differences in flowering time among the NILs, and interacted epistatically with *CRY*. The authors inferred that, by controlling germination time, *DOG1* also controlled the seasonal environment that plants experience. Because flowering time is plastic with respect to season, *DOG1* affected the genetic basis of flowering time through its role in niche construction [39]. This example illustrates that genetic variation in niche construction can have dramatic epistatic effects that impact the genetic basis of phenotypically-plastic traits in nature.

Implications for evolution

Rates of evolutionary change

Heritability, epistasis and pleiotropy are important parameters governing the rates at which populations respond to selection [18, 40]. As outlined above, genetic variation in niche construction can contribute to all three. Thus, genetic variation in niche construction might facilitate accelerated evolution, by contributing to heritability, or retard evolution, by generating low heritability, pleiotropy and/or epistasis ([7, 41]; see also Box 3). Current niche construction models typically assume that the strength or direction of selection might vary across environments but the genetic basis of ecologically-relevant traits does not vary across environments [42, 43]. Models considering the pleiotropic, epistatic, and environment-dependent features of genetic variation in niche construction, are needed to generate specific hypothesis about the role of genetic variation in niche construction in evolution (Box 3).

Maintenance of intrapopulation genetic variation

Niche construction research at the species level has emphasized that selection pressures can differ across environments. Applying this same idea to intrapopulation genetic variation in niche construction suggests that genetic variation in niche construction can facilitate the action of spatially-varying selection—which adaptively maintains genetic variation in populations—by ensuring that individuals experience a variety of environments in every generation [44, 45, 46]. This process might be particularly potent for social niche construction: because the social environment is composed of individuals in the population, populations harboring genetic variation in social behaviors might generate spatially-varying social selection that adaptively maintains itself [3, 47–49].

Speciation

It has long been recognized that genetic variation in host choice (a niche-constructing trait) can facilitate sympatric speciation by generating assortative mating among individuals with similar, genetically-influenced host preferences; assortative mating can generate reproductive isolation between host types [50,51]. Now, high-throughput genetic tools enable the identification of genes underlying species-specific niche construction [52]. Genetic variation in niche construction can also provide novel insights into speciation because of the intimate relationship between niche construction and phenotypic plasticity. Phenotypic plasticity and, in particular, the expression of alternative morphs, is considered important to the formation of incipient species [53, 54].

Conclusion

The concept of niche construction had long been a part of the evolutionary lexicon, but its implications were primarily considered from the perspective of species differences. New empirical results highlighting the ubiquity of intrapopulation genetic variation in niche-constructing traits provide an exciting challenge to evolutionary genetics theory and experimentation. Because the environment—shaped by niche construction—is central to trait development and expression and to selection, genetic variation in niche construction illuminates novel processes by which individuals, genotypes and populations can differ phenotypically. Understanding the many implications of genetic variation in niche construction will require us to consider the interplay between the ecological and genetic bases of trait expression and the consequences of niche construction for natural and sexual selection.

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Box 1: Processes related to niche construction

Extended phenotype—describes the effects of an organism's genotype on its external environment [55, 56]. The extended phenotype concept differs from niche construction because the extended phenotype must be attributable to the organism's genotype, and because traits are extended phenotypes only if they are adaptations [4]. By contrast, any trait that influences the environment that individuals experience can be considered niche-constructing, regardless of its influence on fitness. Niche construction research has typically focused on the effects of niche construction on the organism engaging in niche construction, while research on extended phenotypes had generally considered the effects of niche construction on interacting individuals and species.

Ecosystem engineer—describes modifications of the abiotic environment by one species that create habitats for other species [57]. Ecosystem engineering can be an outcome of niche construction in some cases. As with the extended phenotype concept, the ecosystem engineering framework emphasizes the effect of environmental modification on other species, without necessarily considering the effects of environmental modification on the “engineering” species. The latter topic is the focus of niche construction research.

Indirect genetic effects (IGEs)—describe how traits of an individual are influenced by genetic variation in the traits of other individuals [58]. IGEs represent one mechanism of genetic variation in social niche construction, because traits that differ among genotypes influence the social environment, i.e., the behaviors of interacting conspecifics.

Box 2: The relationship between gene-environment correlation and cov_{GE}

Gene-environment correlation describes the situation in which genotype frequencies are correlated with environment types, i.e., particular genotypes are more likely to experience particular types of environments than expected by chance. Gene-environment correlation is the expected outcome of genetic variation in niche construction, because genotypes with different niche-constructing traits will systematically experience different environments. However, selection can also cause gene-environment correlation. In this case, individuals experience environments at random but some genotypes are removed from the local environment by selection because their traits are maladaptive. Niche construction can facilitate this process by altering the selective environment [42, 43].

cov_{GE} describes the covariance between the genetic effect on the phenotype, V_G , and the environmental effect on the phenotype, V_E . The distinction between gene-environment correlation and cov_{GE} is particularly confusing because gene-environment correlation refers to the correlation between genotype frequencies and environment types, but says nothing about the effects of genotypes or environments on phenotypes. By contrast, cov_{GE} refers to the covariance between the *phenotypic effect* of the genotype and the *phenotypic effect* of the environment.

If gene-environment correlation is absent, genotypes and environments are independent of each other, and cov_{GE} must be zero. If gene-environment correlation is present, then cov_{GE} can be non-zero, as long as there is genetic variation in the phenotype of interest, V_G and the environment influences the phenotype of interest (i.e., phenotypic plasticity), V_E . Thus, gene-environment correlation “sets the stage” for cov_{GE} .

The difference between gene-environment correlation and cov_{GE} highlights the different implications of gene-environment correlation generated by selection and gene-environment correlation generated by phenotypic plasticity. When gene-environment correlation is generated solely by selection, the environment influences the adaptive value of an ecologically-relevant trait, but not its expression; and the genetic basis of the trait is expected to be the same across environments, and in situations in which the opportunity for niche construction is limited. In other words, $\text{cov}_{\text{GE}} = 0$. By contrast, when gene-environment correlation is generated solely by genetic variation in niche construction, niche construction will influence any trait that is phenotypically plastic with respect to the environment generated by niche construction. In this case, cov_{GE} will not be 0, and the genetic basis of phenotypically plastic traits will differ when niche construction is permitted compared to when it is limited (see main text and Figures 1–2).

Box 3: Contrasting predictions about the evolutionary implications of genetic variation in niche construction

A major open question in niche construction research is whether pleiotropy, epistasis, and/or low heritability that can be generated by genetic variation in niche construction will act as evolutionary constraints in the manner predicted by classical genetic theory. On one hand, the effects of genetic variation in niche construction can be highly variable across environments. In traditional evolutionary models, pleiotropic and/or epistatic constraints on evolutionary change are consistent across environments (or environments are assumed to be static), and therefore unalterable until new mutations arrive in the population [59]. If evolutionary constraints imposed by genetic variation in niche construction are variable across environments, they might be overcome more rapidly than expected by these traditional models. For example, in the *A. thaliana* example [39], the correlation between germination time and flowering time differed across growing seasons, suggesting that pleiotropy would not constrain evolution in every generation.

By contrast, constraints on evolutionary change might be more difficult to overcome if they are generated by genetic variation in niche construction, relative to traditional mechanisms, because of the functional relationship between traits inherent in niche construction. For instance, in the mouse example [23], it might be physiologically impossible to change the relationship between mouse wheel running and ovary size, regardless of which mutations segregate in the population. In the latter case, genetic constraints imposed by niche construction might act in a manner akin to tradeoffs.

- Niche construction varies among genotypes within populations.
- Such genetic variation creates a correlation between genotypes and environments
- Niche construction can alter the genetic basis of phenotypically plastic traits
- Niche construction may play a wider role in evolution than currently recognized

Figure 1.

Conceptual illustration of the effects of genetic variation in niche construction when $\text{cov}_{GE} > 0$ and there is no $G \times E$ interaction. Top panels illustrate phenotypic distributions in the population; bottom panels represent the phenotypes of individual genotypes. Left: no opportunity for niche construction; all individuals experience Environment 1 (E1) or Environment 2 (E2). Bottom panel shows reaction norms for individual genotypes. The non-zero slopes indicate phenotypic plasticity across environments; parallel slopes indicate no $G \times E$ interaction. Right: opportunity for niche construction. When there is no genetic variation in niche construction (a), genotypes experience E1 and E2 at random. When there is genetic variation in niche construction (b), some genotypes experience E1 and some experience E2, depending on their niche-constructing trait. Bottom panel in (b) illustrates that each genotype expresses one of its possible phenotypes, depending on which environment it constructs.

Figure 2.

Flow chart illustrating the mechanisms by which genetic variation in niche construction can influence evolutionary genetics parameters. Open arrows represent canonical processes by which genetic variation influences traits (i.e., by producing different types or amounts of protein products); filled arrows represent processes by which genetic variation in niche construction can influence the genetic basis of phenotypically plastic traits. A. The level or type of niche-constructing trait that an organism expresses, which can differ across genotypes, influences the environment in which all other traits develop and are expressed. B. A trait is phenotypically plastic (right box) if its expression or development depends on the environment. Since the environment is due in part to genetic variation in the niche-constructing trait, alleles influencing the niche-constructing trait (bottom left) indirectly influence the development of the phenotypically plastic trait, generating pleiotropy. C. The environment can influence the expression or function of gene products. Since the environment is due in part to genetic variation in the niche-constructing trait, alleles influencing the niche-constructing trait (bottom left) indirectly influence the expression or function of alleles underlying the phenotypically plastic trait, generating epistasis.