Theoretical Ecology
https://doi.org/10.1007/s12080-024-00576-6

RESEARCH

Adaptation through organism-induced environmental transformations—a systems representation

Hans-Rolf Gregorius[1,2]

Received: 16 April 2023 / Accepted: 21 February 2024

Abstract

Environments affect phenotypes through two elementary functions: modifying (by affecting the development of individuals' phenotypes) and adaptive (by determining the phenotypes' adaptive significance). Adaptation may be perceived to coordinate the two functions, which may even be performed by the same environmental factor. Organismic transformation of the environment can again affect both functions, where the adaptive functions are commonly addressed via notions of "niche/habitat construction" or "extended phenotype" and modifying function are largely ignored. The multi-causal role of these transformations in evolution and adaptation is hard to model and formalize using standard tools. To arrive at a more comprehensive representation, a systems approach is taken that allows classification and generalization of earlier results and the outlining of new insights. These include the following: ∗ Temporary transformation (restricted to one adaptational episode) is structurally equivalent to adaptation without transformation and therefore provide no new insights. ∗ Prolonged transformation (extending over several episodes) in either adaptive or modifying environments promotes adaptational coordination between the two functions but ultimately prevents persistent adaptedness. ∗ The success of transformations of the adaptive environment that do not affect the modifying environment depends on the diversity in the system states rather than on phenogenetic plasticity. ∗ A substantial difference between transformation of the adaptive and of the modifying environment is that adaptation can be reached within a single episode via transformation of the modifying environment, even if the adaptive environment has no modifying effect. The evolutionary consequences await explicit model analysis. ∗ Migration can be interpreted in terms of environmental transformation of either function, modifying or adaptive, by replacing transformation between environments by migration between them. Established results from migration models can help to reassess existing models of adaptation by environmental transformation and to design new models.

Keywords Adaptation · Environmental transformation · Environmental control · Systems representation · Modifying environment · Adaptive environment · Niche/habitat construction · Extended phenotype · Plasticity · Norm of reaction · Migration

Introduction

Organism-induced environmental transformations are frequently conceived in terms of "extended phenotypes", "niche or habitat construction" and as such give rise to an apparently ever growing field of applications. The field is characterized by increasing complexity of topics addressing general adaptational and evolutionary questions, as was already demonstrated in overviews of Odling-Smee et al. (2013, Table 1) or Laland et al. (2016) and more recently by Trappes et al. (2022). The structural richness of the associated modeling efforts is therefore not unexpected (for a few examples, see Laland et al. 2001, Rendell et al. 2011, Bailey 2012, and more recently de Araújo et al. 2021, Scheiner et al. 2022, Dong 2022 or Longcamp and Draghi 2023 as well as the numerous references given therein).

Essentially, the underlying idea is led by the obvious fact that organisms affect (or control) their environments, where the effect can be envisioned as a property of the organism (in the sense of an "extended phenotype") that is probably realized in coaction with other factors external to the organism. The effect can be of many kinds, including the creation of ecological niches ("niche construction") or deterrents that feed

✉ Hans-Rolf Gregorius
hgregor@gwdg.de

[1] Abteilung Forstgenetik und Forstpflanzenzüchtung, Universität Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

[2] Institut für Populations- und ökologische Genetik, Am Pfingstanger 58, 37075 Göttingen, Germany

back on the organism or affect other organisms. The difference usually made between the two terms is a matter of focus, where niche construction studies concentrate on the adaptive (and by this evolutionary) significance of extended phenotypes (see, e.g., the glossaries in Odling-Smee et al. 2013, Bailey 2012, or Laland et al. 2016). A list of examples of phenotypes with extended effects can be found in Bailey (2012, Table 1).

In all of these cases, the addressed environmental alterations are considered to be governed by specific traits or capabilities of the organism. These traits are by themselves developed under the constraints of the organism's genetic information and the environmental conditions to which it is exposed (the "modifying environment"). The traits gain adaptive relevance if their possession affects the integrity of the organism's vital functions (metabolism) under the respective environmental conditions (the "adaptive environment", also see Table 1).

Though these aspects, including the dichotomy of modifying and adaptive environmental effects, are probably overt, they gave rise to the design of quite a number of models, the complexity of which frequently resisted analytical treatment and thus, to a considerable extent, is subject to numerical (simulation) analysis. While such analyses are indispensable for providing specific answers to questions of comprehensive significance, proper generalizability of the answers requires a broader conceptual framework as is available in system theoretical approaches. In the present context, this framework is set by the systems representation of mechanisms of adaptation. Especially the high complexity of the subject suggests consideration of systems representations, since they generalize and by this simplify perception of the problem at hand.

It is shown in the following that this can be achieved by extending established representations of adaptational systems to include environmental transformations commonly referred to as "extended phenotype," "niche or habitat construction," and related phenomena. Special regard is given to the adaptational interplay between modifying and adaptive functions of the transformed environments. Two examples of published models are presented to demonstrate how established approaches fit the conceptual requirements and to point out open questions.

The systems representation of adaptation

Following Gregorius (1997), an adaptational system is characterized by three necessary components that can be represented as input–output subsystems, each of which is of the form

$$\rho\colon Z \times X \longrightarrow Y$$

where $Z :=$ set of system states (such as the parameters of a model), $X :=$ set of system inputs (such as the independent model variables), $Y :=$ set of system outputs (such as the dependent model variables), and ρ assigns to the system state $z \in Z$ under the action of the input $x \in X$ a unique output (response) $y = \rho(z, x) \in Y$. Occasionally, ρ is addressed as the model's mechanism.

Especially in quantitative genetics applications, Z takes the role of genetic types G, X the role of environments E, and Y the role of the phenotypes P. This leads to the familiar

Table 1 Terminology

Adaptation	– (a) the process of adapting, (b) a feature that inhibits/prohibits impairment of vital functions by specific environmental conditions (phenotype A is an adaptation to environment B).
Adaptedness	– the state of being adapted (requires an adaptation in sense (b)).
Modifying environment	– or environmental condition of modifying function, acts on an individual so as to develop specified phenotypic characteristics; at the community level, the term refers to the totality of such conditions acting on community members.
Adaptive environment	– or environmental condition of adaptive function, acts on an individual so as to affect its vital functions supporting survival and reproduction; at the community level, the term refers to the totality of such conditions acting on community members.
Individual plasticity	– variability in vital functions of an *individual* in response to temporally varying environmental conditions; depending on type of function and its realization, various terms can be addressed such as phenotypic (but see below), developmental, physiological, cultural, behavioral etc.
Phenogenetic plasticity	– phenotypic variability *among* the individual carriers of a *genotype* in response to different (modifying) environmental conditions. This includes temporally and spatially variable conditions. Phenogenetic plasticity shows in non-constant norms of reaction (see below).
Phenotypic plasticity	– refers to individual as well as to phenogenetic plasticity.
Norm of reaction	– is defined for any one genetic type and a trait in the expression of which the genetic type is involved. The differential effects of environmental conditions on the expression of the trait can then be described by a mapping of these conditions onto the trait expressions. This mapping is usually referred to as the reaction norm of a genetic type (with respect to a specified trait and set of environmental conditions).
Adaptational episode	– or adaptational cycle, the period extending between two successive instances of system state regulation (adjustment) in an adaptational system (the feedback event in Eq. (1a)). Examples are physiological regulation with the result of acclimation at the individual level, or regulation via reproduction and death at the community level.
Adaptation at the individual level	– reactions of an individual to varying adaptive challenges by modification of its phenotype (requires individual plasticity); in a systems representation: within an adaptational episode, the adaptive environment simultaneously functions as modifying.

$G \times E = P$ notation, where $G \times E$ is referred to as the "genotype-environment interaction" producing the phenotype. Among others, it is this perspective that gave rise to the notion of the norm of reaction (see Table 1). Occasionally, the term is also applied to intrinsically individual processes in the sense of variable phenotypic responses that an individual can show under variable environmental impacts (see, e.g., Brun-Usan et al. 2022, Glossary). This, however, is a form of individual plasticity (see Table 1) and does not conform with the historically established interpretations, as is demonstrated and discussed in some detail in a review by Sarkar (1999). In the present notation, the *norm of reaction* can be generalized in terms of the mapping $\rho(z, \cdot)\colon X \longrightarrow Y$ that, for any system state $z \in Z$, assigns inputs to outputs.

The three subsystems of an adaptational system are (*i*) the *modifying system*, which responds to the impact of an external condition (*modifying environment* X_m as input) acting on the system's state Z_m so as to produce an output Y_m (trait), (*ii*) the *comparator system*, which verifies the response of the first subsystem as to its conformity to another external condition (the *adaptive environment* X_a, which may be identical to the modifying environment) and produces as output a *corrective* Y_c that serves in the (*iii*) *state regulation system* as the determinant for a change in state Y_r of the first subsystem. Whenever traits and their modifying environments are referred to, the pathways along which the traits are developed under the impact of the relevant environmental time series are included.

Note that all differentially indexed quantities Z, X, Y are sets of elements (or variables). Continuing the above systems notation, the three subsystems can be represented by three response mappings (with all components indexed by the respective subsystem),

$$\begin{aligned}
&\rho_m\colon Z_m \times X_m \longrightarrow Y_m, \ \text{modifying system}\\
&\rho_c\colon Z_a \times X_a \longrightarrow Y_c, \ \text{comparator system}\\
&\rho_r\colon Z_r \times X_r \longrightarrow Y_r, \ \text{state regulation system}
\end{aligned}$$

which are coupled sequentially to yield the coherent adaptational feedback system by equating the output of one subsystem with the state of the following subsystem. Thus, $Z_a = Y_m$ and $Z_r = Y_c$. Since the state regulation system changes the state Z_m of the modifying system, both X_r and Y_r are equal to Z_m (X_r referring to the initial and Y_r indicating the changed state):

$$\begin{tikzcd}
\rho_m\colon Z_m \times X_m \longrightarrow Y_m \arrow[d] \\
\rho_c\colon Y_m \times X_a \longrightarrow Y_c \arrow[d] \\
\rho_r\colon Y_c \times Z_m \longrightarrow Z_m \arrow[uu, bend left]
\end{tikzcd} \tag{1a}$$

The feedback event is symbolized here by the upward arrow which also indicates completion of the *adaptational episode*. See Fig. 1 for an illustration.

Adaptational feedback systems of this basic kind can be viewed as connecting the effects of the input variables X_m and X_a via regulation of the system state so as to maintain, restore, or enhance all biological (vital) functions supporting survival and reproduction. Hence, in order for an environment to be classified as adaptive, it ought to act on an organism's trait such that this action affects the integrity of the organism's vital functions. Adaptivity of an environment therefore exists only with respect to a specific trait expression, and, in reverse, adaptivity of a trait expression always relates to a specific environment.[1]

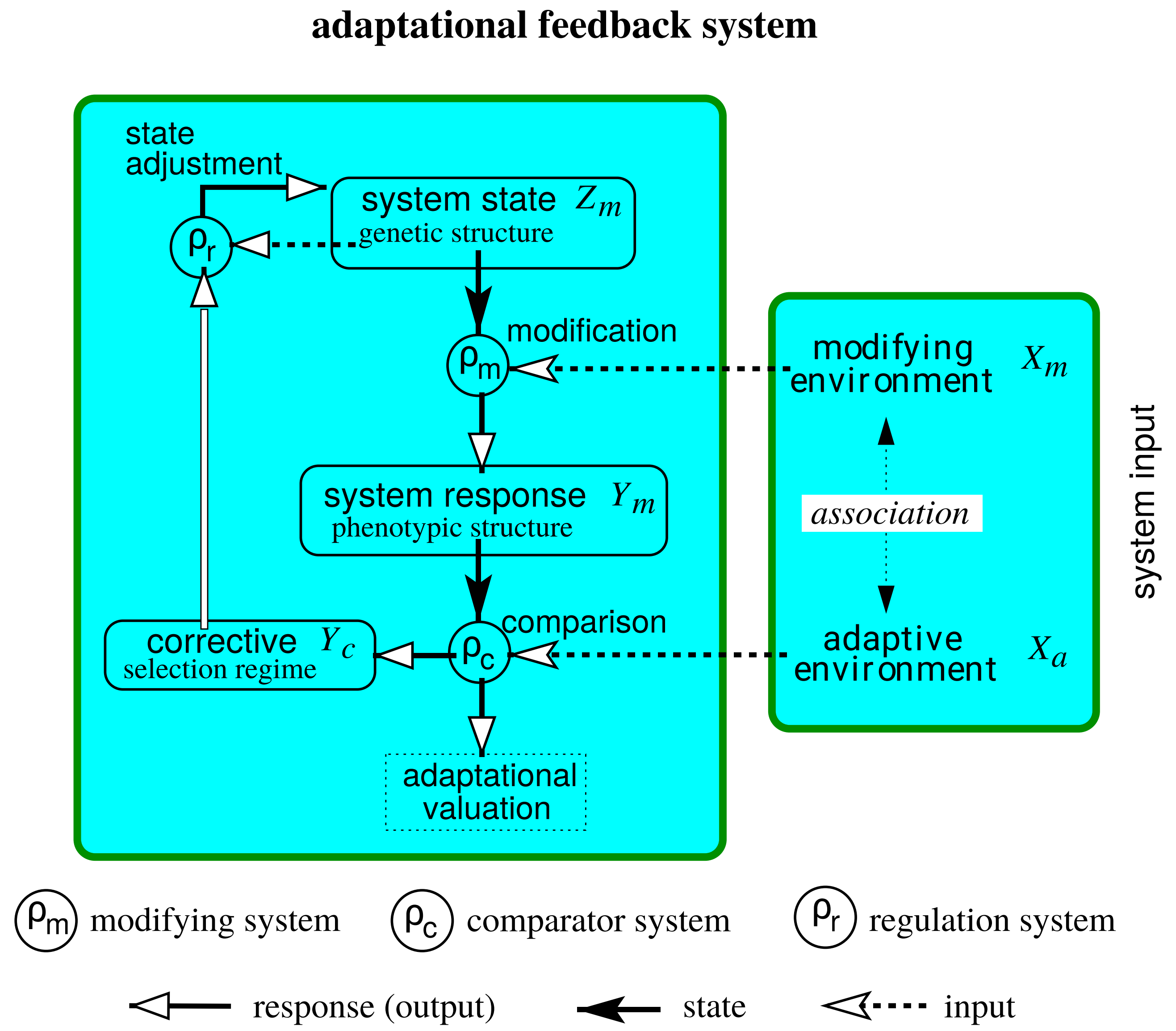
In the above specification of an adaptational system, the environment functions in a *dichotomous* manner via its modifying and its adaptive component. This specification formalizes a number of earlier suggestions to be found, for example, in Levins (1968, p. 12), Mesarović (1968, p. 81), Cavalli-Sforza (1974, p. 46), or Moran (1992). In Levins' diction, the suggestion is that "the environmental factor to which the response is an adaptation (need not also be) the signal that evokes the response." The two environmental functions may therefore be exerted by different factors or by the same factor. The obvious challenge here is to identify possible mechanisms that connect the two environmental functions so that the development of a response to the modifying environment becomes an adaptation to the adaptive environment.

Connections between adaptive and modifying environments

In the above systems representation, adaptational processes work on persistent modifying and adaptive environments, with the result that the adaptational challenge realized in one adaptational episode can only be met by a change in system state. In the following episode, the thus changed system state gives rise to an altered trait expression that could show higher conformity (adaptedness) to the adaptive environment. From an alternative point of view, this process improves the adjustment between the two environmental functions. Disturbance of either of the two environmental functions, however, is likely to delay the reaching of a state of adaptedness or even lower the chances that it will be reached at all.

---

[1] Situations of adaptedness (in which case the relevant trait expression is called an "adaptation," see Table 1) can be identified only by changing the adaptive environment or the trait expression and observing an impairment of the vital functions. Changes in the modifying environment are not relevant in this definition.



The adaptational feedback system with its three constituent subsystems: modifying, comparator, and regulation system. Small script in boxes refers to populations as an example of an adaptational system. The outcome of the adaptational valuation need not directly affect state regulation but indicates the system's integrity. The term "association" used in the system input box allows in its extreme both environmental functions (modifying and adaptive) to be exerted by the same environmental factor.

Fig. 1 Adaptational feedback system

In a recent overview, Trappes et al. (2022) implicitly referred to the above idea of the adaptational process by stating that "niche conformance" is acquired in that "individuals adjust their phenotypes in response to the environment." Identifying the niche with the environment to which adjustment is required (i.e., adaptive environment), the actual adjustment is obtained "in response" to that environment (implying that it functions as modifying environment). This situation where the two environmental functions are performed by the same environmental condition turns out to be a special case of the system specification in Eq. (1a) when starting with the second line (ρ_c), proceeding with the third line, and completing the circle with the first line in which X_m has to be replaced by X_a.

Many modeling efforts of adaptational systems seem to reduce the role of phenotypes to their adaptational significance, apparently ignoring the (modifying) conditions that brought about the phenotype. Yet, as just demonstrated, without at least taking account of the modifying implication of the adaptive stimulus, these efforts could not lead to the specification of an adaptational system. Equating the two environmental functions seems to be a natural approach, but there may be other more reasonable approaches to infer modifying forces from adaptational challenges. Many of these rely on information directly obtainable from trait characteristics and the way they are affected by the challenges. A well-known example is the occurrence of frost damage in plants before growth conclusion. Environmental variables controlling the timing of growth conclusion are obvious candidates for modifiers of this trait. The timing of frost events is of adaptive significance in relation to the timing of growth conclusion. Apparently, the timing of frost events might affect the timing of growth conclusion as a consequence of the damage, but it is evidently not the adaptationally relevant modifying force.

Example

The following example is meant to demonstrate a case that might appear ambiguous in its interpretation as an adaptational system.

Consider facultative parthenogenesis, where insufficient pollination or lack of compatible mating partners constitutes a biotic environmental condition that causes a switch from sexual to asexual modes of reproduction. Availability of mating partners presents itself as a modifying (biotic) environment X_m in that the absence of these partners causes a phenotypic reaction by changing an individual's mode of reproduction Y_m from sexual to asexual. Mode of reproduction thus is a trait that is individually plastic. Moreover, availability of mating partners is an environmental factor that affects mode of reproduction and by this is adaptationally relevant, since it concerns the organism's vital functions. Hence, availability of mating partners is both a modifying X_m and an adaptive X_a environmental condition with respect to the trait "mode of reproduction."

Adaptedness is realized for both environmental conditions, i.e., by sexual reproduction in the presence of mating partners and by asexual reproduction otherwise. Adaptational processes are of an individual kind, and they are triggered by a change in environment X_m from presence to absence of mating partners. Assuming that sexual reproduction is the default mode, asexual reproduction presents itself as an adaptation to a special environmental condition X_a, namely the absence of mating partners. From the system perspective, there exists a single system state Z_m that responds to two system inputs X_m (presence, absence of mating partners) by different outputs Y_m (sexual and asexual modes of reproduction). This perspective introduces facultative parthenogenesis in terms of a norm of reaction of a particular system state. The norm represents a situation of adaptedness, and therefore an adaptation, that developed over the course of previous evolutionary processes acting on variable system states.

Adaptational valuation

Returning to the systems representation in Eq. (1a), the adaptationally crucial role is played by the corrective (Y_c) and the way it enters state regulation (ρ_r). In general, adaptational regulation may fail, resulting in maladaptedness of the modified trait expression and thus in endangerment of system integrity. To account for this possibility, the system response must be *valuated* for its conformity with the adaptational demands, so that the higher the conformity, the higher the adaptational valuation. This includes situations of complete adaptedness (maximum valuation) in the sense that the respective association between trait expression and environment does not impair the system's integrity.

The primary variables to be compared for this valuation are therefore Y_m and X_a. Since both variables also determine the corrective variable Y_c, the valuation can just as well be based on this variable or can even be part of it. In population genetics, the adaptive value is frequently referred to as fitness. In any case, valuation serves first of all the assessment of the system's integrity (operability, intactness, functioning).

As the parthenogenesis example demonstrates, adaptation implies reactions of the organism that indicate the demand for regulation of vital processes. Since these reactions (appearing, e.g., as stress symptoms) can again be considered as traits that are modified by the adaptive environment, this adaptive environment equally functions as a modifying environment but for another trait. The significance of these traits (that parallel the corrective Y_c) lies in their indication of adjustment needs, and they may therefore play a central role in adaptational valuation.

The state transition (feedback)

The adaptational state transition resulting from composition of the three subsystems in Eq. (1a) can be represented as a mapping

$$\rho \colon Z_m \times X_m \times X_a \longrightarrow Z_m$$

specified by

$$\rho(z_m, x_m, x_a) := \rho_r(\rho_c(\rho_m(z_m, x_m), x_a), z_m) \tag{1b}$$

where $z_m \in Z_m$, $x_m \in X_m$, and $x_a \in X_a$ denote expressions of the respective variables.

In explicit modeling efforts, the response mappings ρ_m, ρ_c, ρ_r of the subsystems appear as functions that transform the input variables into output variables, where these functions can be specified explicitly or implicitly. The third mapping can, for example, be obtained from solutions of difference, differential, or integral equations. Only after they are composed according to Eq. (1b) can these functions complete the adaptational cycle (episode) and thus define adaptation as a dynamical system in terms of transitions between system states from state space Z_m.

For reasons of simplicity, the units of reference are mostly addressed as organisms in the introduction, so that the adaptational system described there would usually be referred to as individual-level adaptation. Yet, all of the system descriptions apply as well to other levels of biological organization such as organelles, cells, organs, organisms, communities of organisms, or nutritional networks. The system variables must be specified accordingly, so that at the level of communities, for example, the system state Z_m is determined by the species affiliations (or genetic types) of all community members, X_m and X_a summarize (mostly in the form of frequency distributions) their modifying and adaptive environments, respectively, Y_m refers to the totality of their trait expressions, and Y_c specifies the selection regime resulting from the action of X_a on Y_m.

Building on this, the regulation ρ_r of the system state Z_m involves mating systems and modes of inheritance. In combination with Y_c, ρ_r thus governs the change and thus the state transition in species or genetic composition of the community. The adaptational valuation is commonly performed via properties of the selection regime, particularly if it provides information on the community's multiplication rate as indicator of adaptedness. On this level, the adaptational system thus refers to phenomena of evolutionary adaptation.

The environmental extension (system-internal control of the environment)

Via their trait expressions, organisms can create or alter their abiotic or biotic environmental conditions in that the organisms function as modifying or adaptive environments that react on themselves (feedback), or organisms can act as environments in either of the two functions on other organisms. Effects on other organisms may be treated as aspects of intra-, inter-, or trans-specific interactions. The type of interaction may vary widely, including individual feedback that extends from one trait of the organism to another trait of the same organism. In this way, one trait could provide the (modifying) conditions for development of another trait that mitigates the stress acting at the former trait, or it could establish (adaptive) conditions suitable for reducing the stress caused by another trait.

The adaptational aspect, in particular, is restricted to those environmental conditions that are part of the feedback system, where the feedback is realized by the regulation ρ_r. Moreover, since environments are considered only with respect to their modifying and adaptive functions, they can be viewed within the scope of niche construction in the generalized sense stated at the end of the introduction, which largely agrees with the definition to be found in Odling-Smee et al. (2013, Glossary). Indeed, living conditions and thus niches of organisms are addressed by environments that take part in trait modification and adaptation.

As recalled above, although these explications are framed for organisms, they apply analogously to levels of biological organization below and above that of organisms. In particular, when organisms alter environments in ways that affect other organisms, the unit of adaptation extends to the community that encompasses these organisms. Since this generalizability holds equally in the following deliberations, the concentration on organisms as units of demonstration will be continued.

Focusing on adaptation, there are two basic modes according to which organisms can affect their dichotomous environment, (1) by alteration (or transformation) of the modifying (X_m) environment with the option that the modified trait expression realizes a better fit to the extant adaptive environment and (2) by alteration (or transformation) of the adaptive (X_a) environment with the option that the extant trait expression gains in adaptedness. Since environmental conditions are altered in both cases by the (internal) system activities, they may now appear as system outputs which can occasionally be fed back into the system. In the case of feedback, the transformation is part of the internal system mechanisms to the degree that the transformation is not affected by system external conditions.

According to the definition of individual-level adaptation (see Table 1), transformation of the modifying environment is relevant only if the adaptive environment does not simultaneously function as modifying environment. It is essential to keep this in mind in the following analysis of mode (1) of environmental transformation.

Mode (1)—transformation of the modifying environment

For mode (1) of environment alteration, two additional subsystems are needed. The first establishes a transformation ρ_{tm}

of the modifying environment that is brought about by the effect of the adaptive environment on the trait expression, i.e.,

$$\rho_{tm}\colon Y_m \times X_a \longrightarrow X_{tm}.$$

The second specifies the effect of the altered modifying condition X_{tm} on the trait expression, i.e.,

$$\rho_{me}\colon Z_m \times X_{tm} \longrightarrow Y_{me}$$

Its integration into the above basic adaptational feedback system then yields the extended adaptational system (transformation of the modifying environment)

$$\begin{tikzcd}
\rho_m\colon Z_m \times X_m \longrightarrow Y_m \arrow[d] \\
\rho_{tm}\colon Y_m \times X_a \longrightarrow X_{tm} \text{ (``extended phenotype'')} \arrow[d] \\
\rho_{me}\colon Z_m \times X_{tm} \longrightarrow Y_{me} \arrow[d] \\
\rho_c\colon Y_{me} \times X_a \longrightarrow Y_c \arrow[d] \\
\rho_r\colon Y_c \times Z_m \longrightarrow Z_m \arrow[uuuu, bend left]
\end{tikzcd} \tag{2}$$

In essence, ρ_{tm} and ρ_{me} realize the alteration of the initial trait expression by means of transforming the modifying environment in response to an adaptational demand. In this way, a “transformed phenotype” (from Y_m to Y_{me}) is created with the potential result that *the phenotype is adjusted to the adaptive environment without state regulation*. Successful adjustment implies that the corrective Y_c does not effect a change in system state, i.e., when $\rho_r(y_c, z_m) = z_m$ (or $\rho_r(\rho_c(y_{me}, x_a), z_m) = z_m$).

Of course, adjustment of the phenotype can also be achieved in the absence of environmental transformation by state regulation without alteration of the modifying environment. Equation (2) would then reduce to Eq. (1a) (compare Figs. 1 and 2). The difference between the two consists in the fact that with transformation, the adjustment could take place within a single adaptational episode, while without transformation, the adjustment occurs only in the subsequent episode.

Generally, the traits that transform the environment need not be the traits that are affected by the transformation. Day et al. (2003, p. 91) relate to this fact by stating that “For any clade of organisms, it should be possible to establish those phenotypic characters (recipient traits) that might have been selected as a consequence of feedback from prior niche-constructing traits.” In this case, the variable Y_m is considered to be composed of two components, *one representing the trait that effects the environmental transformation and the other representing the trait that is being affected by the transformation*. Both traits may or may not be correlated or may even be the same. The two components are then represented in both Y_m and Y_{me}.

Though the transformation of the modifying environment into X_{tm} is realized by system-internal mechanisms, it remains an external force whose effect on the system response must be specified. Herewith, *the effect of the environmental transformation can be considered to be either temporary or prolonged*. When temporary, the initial (un-transformed) modifying condition (X_m) again becomes effective after feedback and elicits a response determined by the contingently adjusted system state. Otherwise, if the transformation is prolonged, it replaces the modifying environment of the preceding adaptational episode, and this condition persists unless changed by either external events or by further environmental transformation in subsequent adaptational episodes. The “ecological inheritance” mentioned in the overview of Odling-Smee et al. (2013), for example, belongs to the prolonged transformations.

The major components of the adaptational system as stated in Eq. (1a) thus remain the same, with the extension that the modifying environment possibly undergoes a transformation that affects the system response. Hence, the subsystems ρ_{tm} and ρ_{me} can be conceived to simply mark a two-step “detour” between ρ_m and ρ_c.

Though rarely addressed, there are many cases of temporary transformation of modifying environments. As just one example, consider traits that modify light spectra for other traits, such as sun-leaves in trees or other plants do for shade-leaves. Here, light is the transformed environmental factor, where the transformation induced by sun-exposed leaves affects the development of subordinate leaves as the second trait via light diffusion.

Mode (2)—transformation of the adaptive environment

To arrive at a systems representation of mode (2) of environment alteration, one requires a transformation ρ_{ta} of the adaptive environment (X_a) that acts on the trait expression (Y_m) into another adaptive environment (X_{ta}) that replaces X_a in its action on Y_m, i.e.,

$$\rho_{ta}\colon Y_m \times X_a \longrightarrow X_{ta}$$

In contrast to mode (1), the relevant adaptive environment (X_{ta}) is now under partial control of the organism itself. Even though the transformation again yields an extended phenotype in the present sense, its adaptive connotation is frequently expressed with reference to the term “niche construction” (see, e.g., the glossary in Odling-Smee et al.

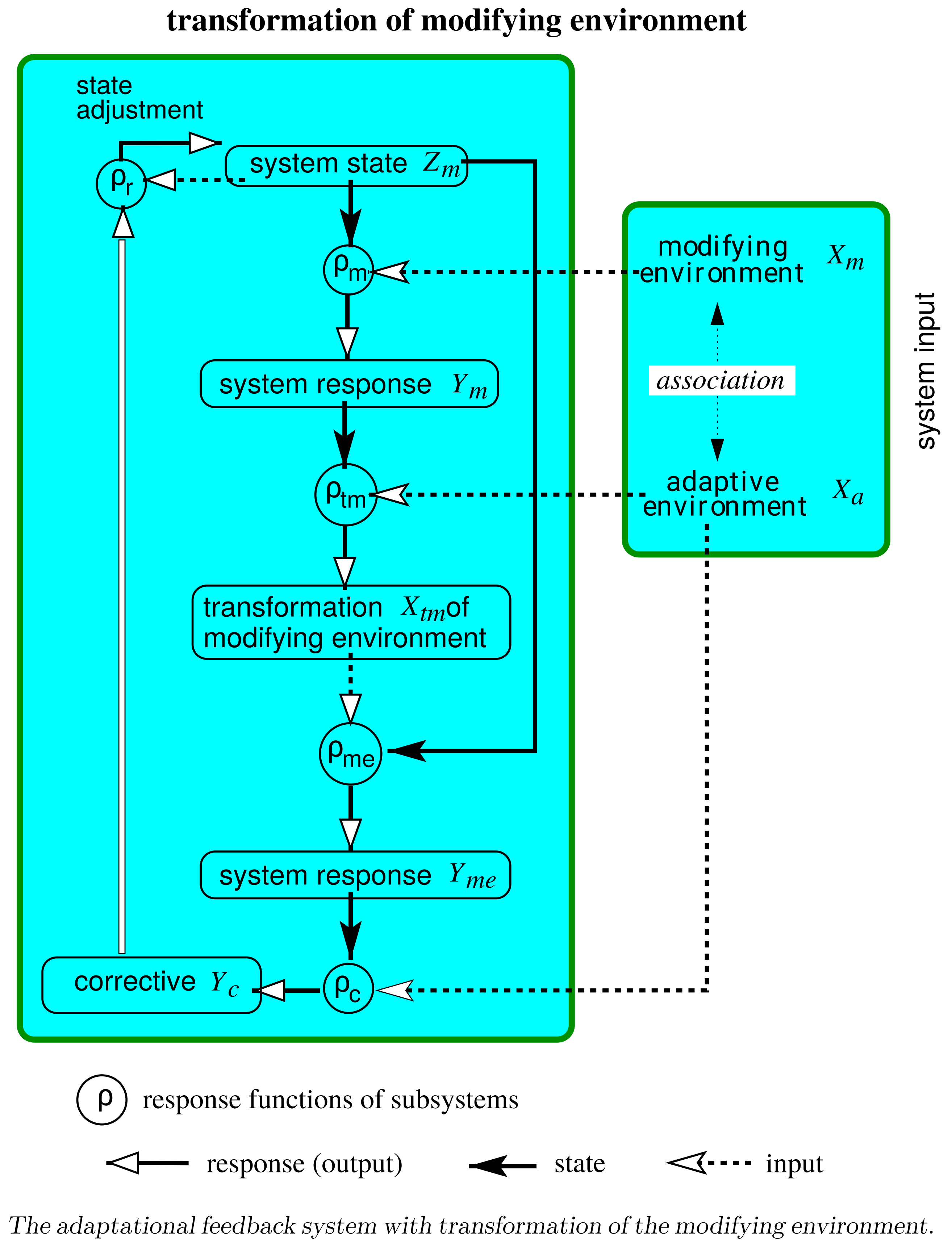


Fig. 2 Transformation of modifying environment

2013). The overall systems representation can then be stated as follows (transformation of the adaptive environment, for illustration, see Fig. 3):

$$\begin{tikzcd}
\rho_m\colon Z_m \times X_m \longrightarrow Y_m \arrow[d] \\
\rho_{ta}\colon Y_m \times X_a \longrightarrow X_{ta} \ (\text{“niche construction”}) \arrow[d] \\
\rho_c\colon Y_m \times X_{ta} \longrightarrow Y_c \arrow[d] \\
\rho_r\colon Y_c \times Z_m \longrightarrow Z_m \arrow[uuu, bend left]
\end{tikzcd} \tag{3}$$

Since Y_m operates in different subsystems (ρ_{ta} and ρ_c) and performs different functions there, it may again be appropriate to consider Y_m to be composed of two components (traits), each corresponding to the respective function, i.e., the component that affects the environmental transformation (ρ_{ta}) and the adaptationally relevant component to which the transformation is compared in the correction (ρ_c). This simply repeats the fact already addressed in connection with mode (1), namely that traits that transform the environment need not be the traits that are affected by the transformation.

Analogous to mode (1) and for the same reasoning, the transformation of the adaptive environment can be either of temporary or of prolonged effect, thus enabling a number of adaptational reactions. If niche construction is temporary, so that X_a remains constant over all feedback loops, adaptation can take place only by changes in Y_m and therefore by the preceding adjustment of the system state (given that adaptation via changes in the modifying environment are excluded). For prolonged niche construction, X_a is replaced by X_{ta} in the second step after each feedback loop.

Again, the major components of the adaptational system remain the same, with the adaptive environment undergoing a system controlled transformation. Modulating the phrasing used in mode (1), mode (2) can be associated with the perception that *the environment is adjusted to the phenotype*. The structural difference from mode (1) consists in the subsystem ρ_{ta} that now marks a one-step “detour” between ρ_m and ρ_c.

The duality of adjusting phenotype to environment and adjusting environment to phenotype is implicit in the claim of Scheiner et al. (2021) that “Still unknown is whether and under what conditions, if both habitat construction and phenotypic plasticity are potential outcomes, each alone would be favored, or when a mix of responses might evolve.” Ernst (2021) cast this issue into the more focused question: “What strategy should an individual follow when faced with a suboptimal environment: change the environment, adapt to the environment, or both?”.

Application to two model examples

To demonstrate the unifying capacity of the above systems representation of adaptation under internal environmental control, two models are considered that cover a longer time span and distinctly different perspectives. One treats cultural niche construction (Laland et al. 2001) and the other adaptive habitat construction (Scheiner et al. 2022). Modeling details including parameterization will be omitted with the intent to capture the adaptationally relevant structure.

The model of Laland et al. (2001)

1. Each individual is characterized by its genotype and a (culturally annotated) phenotype. Since genotype and phenotype are qualified independently, the system state Z_m is defined by their *joint* distribution.
2. Modifying environments that participate in the development of the phenotype are not specified (i.e., how system state and environment jointly produce the phenotype is not specified). Therefore, in ρ_m, Y_m includes the phenotype distribution component of Z_m. Moreover, since the genetic component of Z_m does not participate in the development of the phenotype, it is equally part of the output Y_m with the consequence that $Y_m = Z_m$. The adaptational system is thus limited to mode (2) (transformation of the adaptive environment), as given in Eq. (3) or Fig. 3.
3. Extended phenotypes (X_{ta}) are realized by positive or negative contributions of each phenotype to a (cultural) resource that affects the fitness of the individuals and therefore is a component of the adaptive environment X_a.
4. The resource component X_{ta} of the adaptive environment X_a acts differentially on the genotypes (with the result that genetic selection takes place differentially between phenotypes). Another component of the adaptive environment X_a (the genetic component) acts on the phenotypes differentially for the genotypes (with the result that phenotypic selection takes place differentially between genotypes, see Table 1 in Laland et al. 2001). These twofold selection regimes establish the corrective Y_c as the result of comparing (via ρ_c) both components of Y_m with the two components (cultural and genetic) of the adaptive environment. Genotypes and (the involved) phenotypes are connected by this selection regime, and it yields a joint distribution of genotypes and phenotypes.

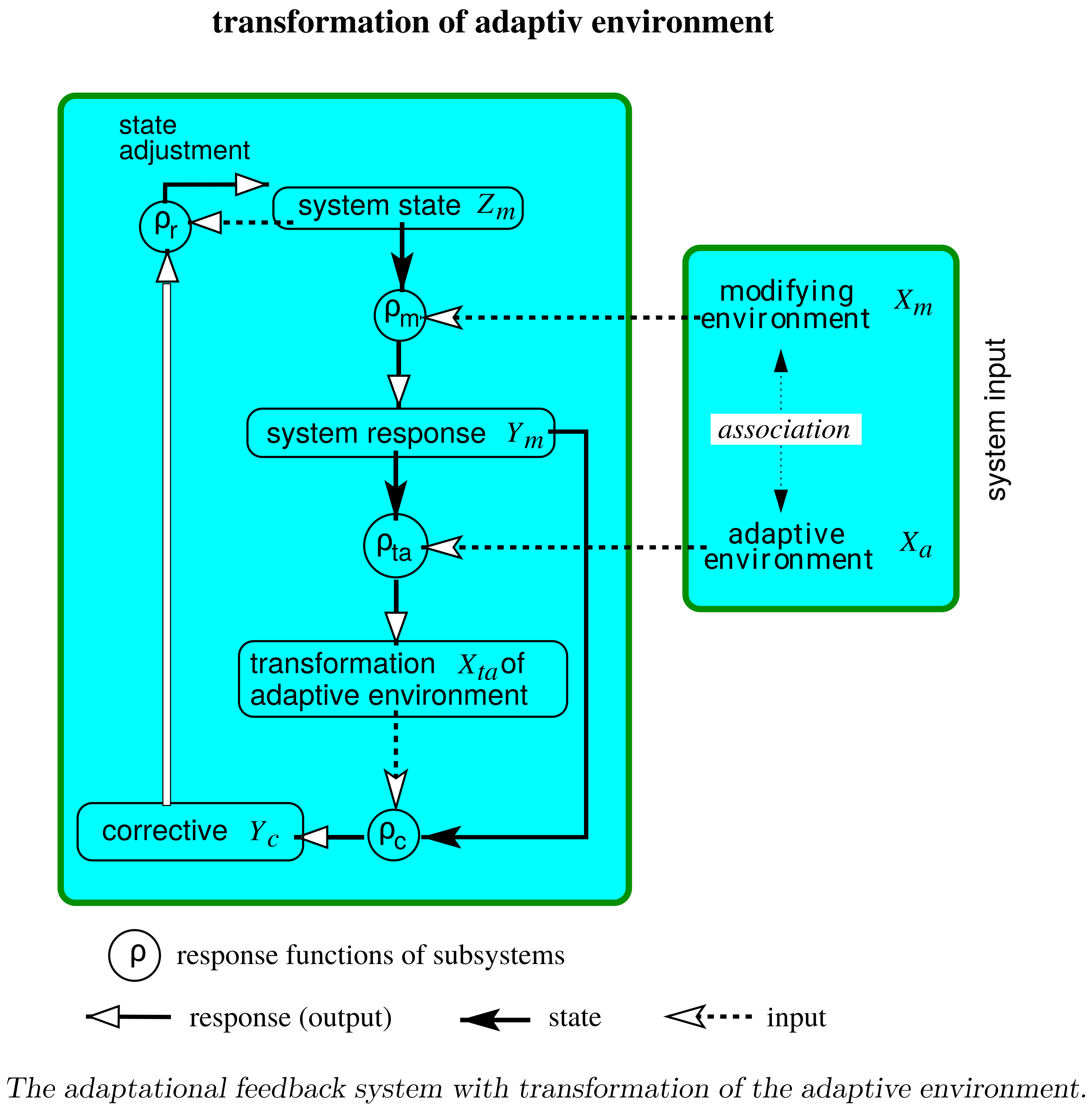


Fig. 3 Transformation of adaptive environment

5. State regulation takes place by random mating and by genetic and phenotypic modes of inheritance that are independent of each other and are based on parent-offspring relations. State regulation thus comprises both components, genetic and phenotypic. Since the phenotype distribution determines the resource and the resource is a component of the adaptive environment, the latter is included in the feedback, which implies that the effect of the transformation of the adaptive environment is prolonged.

Specifications 1 to 5 imply a reduction of the adaptational system represented by Eq. (3) to the form

$$\left\uparrow \begin{array}{l} \rho_{ta}\colon Z_m \times X_a \longrightarrow X_{ta} \ (\text{“niche construction”}) \\ \quad\downarrow \\ \rho_c\colon Z_m \times X_{ta} \longrightarrow Y_c \\ \quad\downarrow \\ \rho_r\colon Y_c \times Z_m \longrightarrow Z_m \end{array}\right.$$

This reveals that the cultural niche construction model is essentially characterized by regulation of the system state, in that the adaptive environment is transformed and the state is subsequently corrected in response to the transformed environment.

6. Adaptational valuation at the population level is not considered but could be routinely done, as will be demonstrated in the subsection after the next.

The model of Scheiner et al. (2022)

1. Metapopulations are considered for which the constituent demes take on the role of environmental conditions that may vary between demes and between generations. Two kinds of traits referred to as "construction propensity" (the "construction trait", for short) and as "adaptive", respectively (corresponding to two components Y_{m1} and Y_{m2} of Y_m) are considered. Both traits are under genetic control, with controlling loci differing between the traits. Expressions of the traits may vary (for the same genotype) among demes, suggesting that demes function like modifying environments X_m at the individual level.
2. Selection acts on the adaptive trait, with the selective forces determined by the deme and by the construction contributions of the construction trait to the environments within the demes. The construction contributions function as an "extended phenotype" that transforms the original adaptive environment within demes (X_a) into the altered adaptive environment X_{ta}. Individual fitnesses are reduced by an amount proportional to their construction contributions (cost of construction). The implied selection regime establishes a connection between the otherwise independent specification of the construction and the adaptive trait. Selection is soft in the sense that deme sizes remain constant.
3. Migration alters the distribution of the phenotypes over demes. The corrective Y_c therefore comprises the selection and migration regime in the appropriate order.
4. Modifying environments are not transformed by phenotypes, so that mode (2) of transformation of the adaptive environment as summarized in Eq. (3) or in Fig. 3 applies. With respect to the two traits, one obtains $Y_m = Y_{m1}$ in ρ_{ta}, and $Y_m = Y_{m2}$ in ρ_c.
5. The system state Z_m of the metapopulation is defined by the genotype distributions within demes (populations).
6. Regulation ρ_r is restricted to random fusion of gametes within communities after application of the corrective, and this yields the system state in the next generation. Moreover, since the construction contributions are included in the feedback, the effect of the transformation of the adaptive environment is prolonged.
7. Adaptational valuation at the metacommunity or deme level is not relevant, since the assumption of soft selection (selection by replacement) implies no dynamics in the deme sizes.

This model is structurally similar to that of Scheiner et al. (2021) and to the corresponding description by Ernst (2021).

In contrast to the model of Laland et al. (2001), all subsystems of the adaptational system for mode (2) are represented in the Scheiner model. Moreover, the Scheiner model makes a distinction between the trait that affects the environmental transformation (Y_{m1} or construction trait) and the trait that is affected by the transformation (Y_{m2} or adaptive trait). The remark following Eq. (3) relates this distinction to the two subsystems ρ_{ta} and ρ_c. In fact, the distinction seems realistic in most situations and is reasonable for both environmental functions, adaptive and modifying.

The role of adaptation in the two models

Generally speaking, adaptation could refer to all processes which serve the stability or stabilization of a system's integrity under the impact of external forces. As far as vital functions of organisms are concerned, this is common sense in that the system is the individual organism, its integrity is specified by the condition of its basic vital functions (survival, reproduction: if either of the two is impaired the organism's integrity is at risk), and external forces are identified with the relevant "environment." The same principles apply to communities of organisms that interact to form systems of survival and reproduction serving persistence of the functions that define the community. System dynamics that are not triggered by external forces cannot be classified as adaptation, since adaptation *ipso facto* requires a unit (a system) that is capable of fitting its actions to an environmental demand or transforming the demand accordingly.

From this perspective, assessing selection processes in populations as adaptational reactions would require that these processes determine population persistence. The central parameter in this context is the average population fitness that is usually expressed in terms of the average selection coefficients. Yet this average is inappropriate for purposes of adaptational valuation as long as it does not determine the population's multiplication rate (with values ≥ 1 signifying population persistence). In fact, in the vast majority of selection studies, the focus is not set on population persistence but rather on the evolution of particular characteristics of population members. This in turn implies analyses of the reproductive performance of types in relation to each other, so that population persistence during the selection process is not at issue. The frequently encountered tacit assumption that selection improves (average) population fitness (known as the "fundamental theorem of natural selection") and by this population persistence through favoring the most fit types has, however, been shown to not apply in many realistic situations (population fitness decreases during the replacement of one type by another, see Gregorius 1984). Hence, *selection might be necessary for population adaptation, but it is not sufficient*.

Returning to the units of selection (the types or trait expressions), it has to be taken into consideration that they are integral parts of a community and, as opposed to individual organisms, therefore cannot be treated as separate units of adaptation. On the other hand, a type with a larger selection coefficient than other types can be considered to be better adapted to the prevailing environmental conditions in the sense that its relevant vital functions are less impaired and thus better fit the environmental demands. Yet, such *relative* assessments entail no statements on the actual adaptedness of a type *per se* in terms of the system integrity of the organisms representing the type. Consequently, no direct conclusions can be drawn as to the effect of selection on community persistence, unless the selection regime supplies information on community sizes. Obviously, if all community members equally increase their individual adaptedness to an environmental challenge, then this entails increased adaptedness at the community level even without selection. Thus, relativizing the above suggestion, selection need not even be necessary for population adaptation.

Indeed, the two models presented above are explicitly designed to find conditions for the evolution of phenotypes that transform environmental conditions of adaptive significance for possibly other phenotypes. The models thus do not explicitly address problems of adaptation on the population level. This becomes particularly apparent in the Scheiner model, where the assumption of soft selection by definition implies that population (deme) sizes do not change. Population or metapopulation persistence thus is not an issue of this model.

In the Laland model, the phenotypic (cultural) trait transforms environmental conditions that provide adaptive demands on the trait itself as well as on a genetic trait. The two traits are jointly subjected to selection with selection regimes defined in relative terms. The model is thus bound to analyses of conditions for the joint evolution of the phenotypic and genetic trait expressions. In order to enable an adaptational valuation on the population level, the selection regime would require an extension that supplements the included survival probabilities with mating fecundities, so that population multiplication rates can be obtained via the average fitness of the two-dimensional trait expressions. To obtain results on population persistence under the evolution of cultural niche construction, it would then be required to identify fecundities that do not vary among mating types and that would guarantee population persistence.

Effects of the environmental transformations on adaptedness

Returning to the general systems representation and asking for the differences in adaptational characteristics between the environmental transformations, one of the most basic aspects relates to their capacities to realize and maintain states of adaptedness. By definition, a state of adaptedness is reached if Y_c signals no correction so that $\rho_r(y_c, z_m) = z_m$. As before, y_c and z_m denote special expressions of the variables Y_c and Z_m (cf. Eq. (1b)).

In the simplest case, maintenance of a state of adaptedness can be expected if the system inputs (the environmental conditions) essentially remain the same as those realized at the moment of reaching adaptedness. This holds true in the absence of environmental transformation given in Eq. (1a). Apparently, once the environments x_m and x_a imply no correction for a particular system state z_m, then $\rho_r(y_c, z_m) = z_m$ holds over all feedback loops as long as the modifying and adaptive environments x_m and x_a remain undisturbed.

As is easily verified from Eqs. (2) and (3), the same situation applies to modes (1) and (2) of environmental transformation (modifying and adaptive), if the transformations are temporary. Indeed, without feedback of the transformations and constancy of the initial environmental conditions, the adaptationally relevant system response is Y_{me} in mode (1), where the response is a function of the constant initial environments X_m and X_a. This makes the Eq. (2) functionally equivalent to Eq. (1a) for all system states. *Temporary transformation of the modifying environment therefore introduces no structural changes that deviate from the adaptational system without environmental transformations*.

For mode (2), the situation is analogous for constant initial modifying and adaptive environments with the difference that the adaptational rather than the modifying environment is temporarily transformed. Equation (3) is thus functionally equivalent to Eq. (1a) for all system states. Again, *no structural differences from the absence of environmental transformations exist, if the transformation of the adaptive environment is temporary*.

While these conclusions confirm intuitive expectations, prolonged environmental transformations may appear more involved. Yet, as becomes immediately clear from inspection of Eq. (2), for persistent adaptedness in mode (1), it is required that the modifying environment remains undisturbed and undergoes no transformation. Similarly for mode (2), Eq. (3) reveals that persistent adaptedness requires an adaptive environment that is undisturbed and undergoes no transformation. *Prolonged environmental transformations therefore need to cease ultimately in order to allow for persistent adaptedness*. The environmental transformations are thus turned into lasting conditions.

At this point, a major difference between prolonged and temporary environmental transformations becomes apparent. While the transformation efforts in the former situation reduce to zero when the state of adaptedness is reached, they continue for temporary transformation. This holds true for both modes of environmental transformation.

Prolonged transformations may include external effects that alter the initial transformation in the course of its passage to the next adaptational episode. To reach a state of adaptedness, it is therefore required that internal and external effects on the transformation cancel each other out. In the Scheiner-model, this fact is reflected in the statement that “a steady state is reached” if “construction... balances decay” (p.7).

Process characteristics of adaptation

There is probably general agreement that adaptedness is a state that can be realized under constant environmental conditions but can hardly be reached under continually varying conditions. Under varying conditions, adaptation is a continuing process during which sufficient conformity between system responses and adaptational demands is at stake. Quantification of this conformity is the task of adaptational valuation. Valuation provides a (possibly multidimensional) threshold below which the system’s integrity is considered to be endangered or impaired, and adaptability could be denied if the valuation is likely to consistently fall below the threshold (Gregorius 1997). Since for temporary environmental transformations, the adaptational system is structurally equivalent to the absence of environmental transformations, the pertaining results on adaptational dynamics obtained by Gregorius (1997) apply identically. It thus remains to demonstrate the difference of systems with temporary environmental transformation from systems with prolonged transformations.

This difference becomes most obvious when considering the transition between adaptational episodes (feedback events in the adaptational system) and focusing on the variables that are changed in one episode and passed on to the next episode. In the absence of or with temporary environmental transformations, the system state is the only variable that is passed on, as becomes explicit in transition Eq. (1b). With prolonged transformations, the modifying (mode (1)) and adaptive (mode (2)) environments are passed on in addition to the system state. It is this particular feature that determines the primary characteristic of adaptational systems, namely the coordination between the two environmental functions via the adaptational process. More specifically, the coordination works by enabling the realization of *mechanisms of adjusting modifying to adaptive and adaptive to modifying environments through prolonged environmental transformations*. This answers the initially posed question of mechanisms that connect the two environmental functions in ways that enable adaptation to the adaptive component.

At first sight, this wording seems inconsistent, since adaptation is commonly conceived as a process of adjusting phenotypes to environmental demands rather than of adjusting different kinds of environmental conditions to each other. Yet, as was emphasized earlier, the common concept does not explicitly consider the fact that the development of appropriate phenotypes depends on the availability of appropriate modifying environments. If not available, the system’s capacity to adapt is restricted to state changes that could adjust phenotypes under the action of the original modifying environment. Hence, whatever adaptational mechanism (environmental transformation or state change) is involved, it links the two environmental functions.

Concluding remarks

Without the capacity of a system to control its modifying or adaptive environment, these environments would independently affect the system’s integrity and by this would impose high demands on the adaptational mechanisms (Gregorius 1997; Moran 1992). Obviously, prolonged environmental transformations can help to lower these demands by introducing environmental control via environmental transformation in addition to state regulation. In particular, it aids in discerning the details addressed by the above-referenced central question phrased in the words of Ernst (2021): “What strategy should an individual follow when faced with a suboptimal environment: change the environment, adapt to the environment, or both?”

From the above explanations, the two strategies of adaptation can be distinguished into (a) adjusting phenotypes to (adaptive) environments (mode 1) and into (b) adjusting (adaptive) environments to phenotypes (mode 2). Strategy (a) involves modifying environments in two possible ways: adjusting the system state (without affecting the modifying environment) or adjusting the modifying environment by transformation. The adaptive environment persists in this case. Strategy (b) in turn can be realized for persisting modifying environment (and thus without transformation of this environment) in that the adaptive environment is transformed and the system state is adjusted (when still in adaptational demand).

Phenotype adjusted to environment

While state regulation (or adjustment) is the probably most obvious mechanism of adaptation, possibilities for adaptation without state regulation via environmental transformations may be less apparent. A closer inspection of mode (1) of environmental transformation reveals that adaptation without state regulation actually takes place within an adaptational episode, and it combines two familiar phenomena, (phenotypic) plasticity and individual-level adaptation.

In essence, plasticity is a property of a system state that allows for variable expressions of a trait that is exposed to variable modifying environments (as in the norm of reaction of the state). In Eq. (2), plasticity is addressed in the subsystems ρ_m and ρ_{me}, since there the same system state is exposed to two different modifying environments, resulting in two different trait expressions. The change in trait expression is mediated by an adaptive environment that leads to a transformation of the modifying environment. This change in trait expression can be viewed as the result of individual-level adaptation (see Table 1), and it comprises the subsystems ρ_{tm} to ρ_c, where ρ_c indicates the success of individual-level adaptation.

By definition, individual-level adaptation is limited to a single adaptational episode. Individual-level adaptation therefore either leads to adaptedness within one episode of adaptation or necessitates changes in system state to potentially realize higher degrees of adaptedness in the next episode of individual-level adaptation. Thus, two phases of adjustment or adaptation are realized within one episode, individual-level as the first step and state regulation as the second. This observation conforms with the widely held view that, when adjusting phenotype to environment, individual-level adaptation takes precedence over adaptation by state adjustment. Interestingly, this view can be substantiated via transformation of the modifying environment.

In an evolutionary context, this corresponds to the apparent fact that individual-level adaptation may proceed faster than evolutionary adaptation. Selection would then operate on the modes of individual-level adaptation coded by the system states.

Environment adjusted to phenotype

Conversely, when environment is adjusted to phenotype as in mode (2) of environmental transformation, adaptation can take place as a first step within a single adaptational episode. If not sufficient, a second step follows after state adjustment, with the potential result of an improved transformation of the adaptive environment in the following episode. Hence, contrasting with mode (1), adaptation is limited to one phase within an adaptational episode, namely state regulation. Even though individual-level adaptation is not at issue here, phenotypic plasticity may still play a role in this mode of environmental control. The reason is that the term "phenotypic plasticity" summarizes two types of plasticity, individual and phenogenetic.[2] Individual plasticity is required in mode (1) of environmental transformation in order to enable individual-level adaptation.

The role of phenogenetic plasticity in the adjustment of environment to phenotype is more involved. The reason is that its analysis requires consideration of different modifying environments that act on the same system state. This, however, is not realized in mode (2), since variation in the modifying environment is not relevant in adaptation by transformation of the adaptive environment (niche construction). Hence, phenogenetic plasticity and thus norms of reaction do not enter the adaptational process in mode (2). Instead, the process depends on the set of phenotypes that emerge as the effect of a particular modifying environment on a collection of system states. *Diversity in system states rather than phenogenetic plasticity is thus essential in the adaptational process of adjusting environment to phenotype*.

As was recalled earlier (following Eq. (1b)), when applied to the community level, the above variables are to be replaced by their distributions in the community, so that the modifying environment of the community becomes the distribution of modifying conditions to which the community members are exposed and so forth. In this case, individuals of the same (geno-)type may be exposed to locally differing modifying conditions, so that phenogenetic plasticity at the individual level is indeed relevant. Yet, at the community level, phenogenetic plasticity would imply that the same distribution of genotypes is exposed to different distributions of modifying environments, which does not happen in mode (2) of community adaptation within one adaptational episode. For communities, diversity in genotype distributions is therefore essential for adjusting environment to phenotype. Diversity (actually differentiation) in genotype distributions in turn requires diversity in genotypes, and this demonstrates the conceptual correspondence between the levels of community and individual.

---

[2] Even though not always expressed clearly (compare Table 1), individual plasticity commonly refers to phenotypic variability of an individual in response to temporally varying (modifying) environmental conditions, while phenogenetic plasticity refers to phenotypic variability among individuals of the same genotype in response to different (modifying) environmental conditions (usually addressed as norm of reaction). This includes temporally and spatially variable conditions. In the general systems representation, when replacing individuals by communities, individual plasticity would show up as changes in trait distributions while species or genetic compositions remain the same.

Migration

As a final aspect of environmental "transformation," migration might be an interesting subject of contemplation, as it potentially entails a change in environment that the organism accomplishes without actively altering its external conditions. Such a change can improve the chances to develop an adaptationally more suitable phenotype, by which the environment has modifying function, or it can improve the adaptedness of the current trait, by which the environment would be adaptive. In the former case, the organism varies its modifying environment without escaping from its adaptive environment, and in the latter case, it escapes from its present adaptive environment. The corresponding adjustments are "phenotype to environment" and "environment to phenotype." In a sense, this relates to the idea of "selection of the environment" put forward by Edelaar and Bolnick (2019).

Indeed, according to mode (1), the transformation ρ_{tm} in Eq. (2) mirrors the migrational move from X_m to X_{tm} in response to the adaptive pressure exerted by X_a on the trait expression Y_m. The subsequent steps correspond directly to the previous explanations. Temporary transformation now relates, e.g., to a return to the places of origin after completion of an adaptational episode, while prolonged transformation implies staying at the destination of migration until the next episode. Hence, the system specification of mode (1) of environmental transformation fully applies to migration.

The same also holds true for mode (2), where the transformation ρ_{ta} replaces ρ_{tm} and the migrational move goes from X_a to X_{ta} in response to the adaptive pressure exerted by X_a on the trait expression Y_m. One thus arrives at the interesting observation that migration can effectively realize all specifications of adaptive systems involving environmental transformation. This presents opportunities for reinterpretation of results from studies of migration models of the type treated by Edelaar et al. (2008) in terms of environmental transformations as well as for the design of new models of adaptation by environmental transformation.

Acknowledgements The author is grateful to two reviewers and the editor for constructive questions that greatly helped to focus the presentation of the topic. He thanks Elizabeth M. Gillet for carefully reading and commenting on the manuscript.

Author contributions H.-R.G. conceived and wrote the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. The author declares that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability Not applicable.

Declarations

Competing interests The author declares no competing interests.

References

Bailey NW (2012) Evolutionary models of extended phenotypes. Trends Ecol Evol 27(10):561–569

Brun-Usan M, Zimm R, Uller T (2022) Beyond genotype-phenotype maps: toward a phenotype-centered perspective on evolution. BioEssays 44:2100225

Cavalli-Sforza LL (1974) The role of plasticity in biological and cultural evolution. Ann. New York Acad. Sci. 231:43–59

Day RL, Laland KN, Odling-Smee J (2003) Rethinking adaptation - the niche-construction perspective. Perspect Biol Med 46(1):80–95

de Araújo GF, Moioli RC, de Souza SJ (2021) The shared use of extended phenotypes increases the fitness of simulated populations. Front Genet 12:617915

Dong X (2022) Evolution of plant niche construction traits in biogeomorphic landscapes. Am Nat 199(6):758–775

Ernst UR (2021) Digest: changing environment often easier than changing phenotype. Evolution 75(7):1898–1899

Gregorius H-R (1984) Selection with two alleles and complete dominance. Biol J Lin Soc 23:157–165

Gregorius H-R (1997) The adaptational system as a dynamical feedback system. J Theor Biol 189:97–105

Edelaar P, Bolnick DI (2019) Appreciating the multiple processes increasing individual or population fitness. Trends in Ecology & Evolution 34(5):435–446

Edelaar P, Siepilski AM, Clobert J (2008) Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. Evolution 62(10):2462–2472

Laland K, Matthews B, Feldman MW (2016) An introduction to niche construction theory. Evol Ecol 30(2):191–202

Laland KN, Odling-Smee J, Feldman MW (2001) Cultural niche construction and human evolution. J Evol Biol 14:22–33

Levins R (1968) Evolution in Changing Environments. Princeton University Press, Princeton

Longcamp A, Draghi J (2023) Evolutionary rescue via niche construction: infrequent construction can prevent post-invasion extinction. Theor Popul Biol 153:37–49

Mesarović MD (1968) Systems theory and biology - view of a theoretician. In: Mesarović MD (ed) Systems Theory and Biology. Springer-Verlag, Berlin etc, pp 59–87

Moran NA (1992) The evolutionary maintenance of alternative phenotypes. Am Nat 139:971–989

Odling-Smee J, Erwin DH, Palkovacs EP, Feldman MW, Laland KN (2013) Niche construction theory: a practical guide for ecologists. Q Rev Biol 88(1):3–28

Rendell L, Fogarty L, Laland KN (2011) Runaway cultural niche construction. Phil. Trans. R. Soc. B 366:823–835

Sarkar S (1999) From the Reaktionsnorm to the Adaptive Norm: The Norm of Reaction, 1909–1960. Biol Philos 14:235–252

Scheiner SM, Barfield M, Holt RD (2021) The evolution of habitat construction with and without phenotypic plasticity. Evolution 75(7):1650–1664

Scheiner SM, Barfield M, Holt RD (2022) The factors that favor adaptive habitat construction versus non-adaptive environmental conditioning. Ecol Evol 12:e8763

Trappes R, Nematipour B, Kaiser MI et al (2022) How individualized niches arise: defining mechanisms of niche construction, niche choice, and niche conformance. Bioscience 72(6):538–548