

1 **TOWARDS A BETTER UNDERSTANDING OF ADAPTATION:**
2 **PROBLEM DESCRIPTION, PARTIAL SOLUTIONS, AND RECOMMENDATIONS**

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80

81 *This paper is the product of an international workshop aiming to make progress in our*
82 *general understanding of adaptation. We met from 5-7 February 2025 in Hannover*
83 *(Germany), funded by the foundation “Volkswagen Stiftung”. For our group of*
84 *theoretical and empirical biologists, social scientists, and philosophers of science we set*
85 *up a program to facilitate communication and collaboration between people with*
86 *diverse backgrounds and viewpoints. The overall goal that the scientific community*
87 *should strive for, we think, should be to obtain concrete conceptual, analytical, and*
88 *experimental tools for researchers to understand and study all the processes of*
89 *adaptation, and thereby the global phenomenon of adaptation. Our workshop aimed to*
90 *contribute to this overall goal. For this, we discussed the relative strengths and*
91 *weaknesses of different approaches, identified areas of consensus, identified areas of*
92 *disagreement, and resolved (sub)areas of disagreement. Here we briefly report on the*
93 *progress we have made during the workshop. We lay out the problem, discuss*
94 *terminology, present a visual framework to think about adaptation, suggest useful*

95 *approaches for its study, and provide recommendations for practitioners and*
96 *policymakers.*

97 **What is the problem with adaptation?**

98

99 A basic fact of life is that environments are not constant. Instead, abiotic conditions (e.g.,
100 temperature, precipitation, nutrient concentrations) and biotic conditions (e.g.,
101 predation risk, food availability, social and demographic population structure) change
102 over time and space. Another basic observation is that not all combinations between
103 environmental conditions and organisms are equally successful. Survival and
104 reproduction depend on an organism's traits and abilities (or 'phenotypes') being well-
105 matched to the environment it is interacting with (Edelaar & Bolnick 2019). This means
106 that organisms – including humans – need to cope with the environmental variation and
107 changes, and need to change too – they need to adapt. The systematic emergence of
108 more successful phenotype-environment associations is known as adaptation, where
109 greater success is understood to mean greater ecological performance and reproductive
110 success. (Unfortunately, the word 'adaptation' is rather ambiguous: see Box 1 for a brief
111 overview.)
112

Box 1. What is adaptation? Adaptation is an ambiguous term (Lewens 2009; Lewontin 1978; Reeve and Sherman 1993), in the sense that it has several different, albeit related, meanings. An adaptation is a characteristic that enhances the survival or reproduction of organisms that bear it, relative to alternative character states (Futuyma & Kirkpatrick 2017). So here the adaptation is a feature of the individual organism. For some people, adaptation can also be a feature of a population, as in 'this population has adapted', or 'there is maladaptation'. Finally, adaptation can be used to refer to the process of becoming adapted over time, a dynamic change (more similar to a verb) rather than a static state (a noun). To summarize, adaptation can be a state of being adapted, the process of becoming adapted, or refer to particular traits whose values provide increased reproductive success.

But what they have in common is that adaptation is evaluated in the context of increasing ecological performance (e.g., nutrient intake rate, or predation avoidance) and ultimately reproductive success. To avoid misunderstanding among these different meanings when writing 'adaptation', we often use alternative wording, for example by talking about the traits themselves, or by describing the process. In other cases the context hopefully avoids confusion.

Other ambiguities exist. One is about the level of biological organization at which adaptations happen and exist. For some people, adaptation only occurs at the population level, via evolution. For others, individual organisms can also adapt, for example via adaptive plasticity and other forms of development. To enable a broader treatment of the topic of adaptation, we follow this inclusive perspective. Another ambiguity is whether an adaptation might come about because of a shift in function (the distinction between adaptation and exaptation; Gould & Vrba 1982), and whether adaptation might be a side effect of selection for other traits (e.g., when a trait that is not under selection evolves because it is genetically correlated with one that is; Futuyma & Kirkpatrick 2017). These ambiguities are less relevant for our treatment here.

113

114 Adaptation as a state can come about in various ways, so adaptation as a process has
115 been classified in various ways. Sometimes adaptation is divided into two types. Quoting
116 Haig (2007, p.424): “Adaptation has historically referred to two processes in biology. The
117 first process is the adaptive response of an individual organism to its particular
118 environment (adaptation 1). (...) Such adaptive responses are often considered to be
119 acquired characters (or characters that are induced by the environment). The second
120 process is the change in the heritable properties of organisms over evolutionary time
121 (i.e. generations) that makes organisms more suited to their environments (adaptation
122 2). Neo-Darwinists believe that phylogenetic adaptation (adaptation 2) occurs by natural
123 selection of random genetic variation and that among the products of natural selection
124 are processes of ontogenetic adaptation (adaptation 1).”

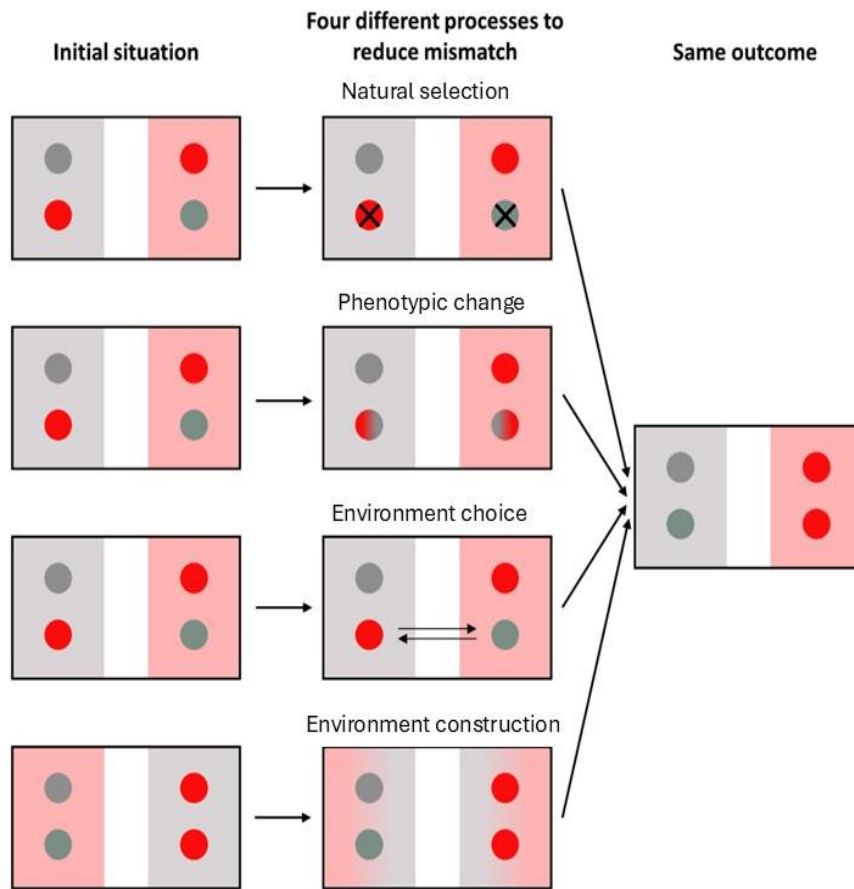
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126 However, adaptation at the individual level does not only happen because of a response
127 of an individual organism to its particular environment (Haig’s adaptation 1), it may also
128 just be the consequence of non-responsive (constitutive) development. For example, as
129 a prey organism grows larger, it may no longer be at risk of predation by smaller
130 predators. In addition, this simple binary classification tends to obfuscate that there are
131 two targets for improvement of the phenotype-environment match (Edelaar & Bolnick
132 2019): the individual organism’s phenotype, and its environment (see Figure 1). There
133 are many examples of organisms adaptively making changes to their environment to
134 improve the phenotype-environment match. These include the making of constructions
135 (a change of the local environment), changing the behaviour of other individuals via
136 communication or control (also a change of the local environment), or choosing to move
137 to another environment (Odling-Smee et al. 2003). Recognising these additional
138 dimensions of change, of the individual organism’s phenotype or of its environment, has
139 resulted in recognising four fundamental ways to achieve successful trait-environment
140 associations (Edelaar & Bolnick 2019; Trappes et al. 2022; Figure 1):

141

- 142 (1) certain individuals survive and/or reproduce better than others in a given
143 environment because of their characteristics (natural selection - a population-level
144 process),
- 145 (2) individuals change their phenotypic traits,
- 146 (3) individuals choose the environment (e.g., habitat, food resources, mate, or social
147 group),
- 148 (4) individuals construct their local environment.

149



151

152 *Figure 1. A phenomenological visualization of four possible processes leading to the*
 153 *same observed pattern of improved phenotype-environment match (i.e., leading to*
 154 *adaptation as a state). Each box represents individuals in two different separate*
 155 *environments. Individuals are represented by coloured dots and local environments by*
 156 *coloured backgrounds. When colours match, there is a match between their phenotype*
 157 *and their local environment, resulting in adaptation to that environment. All four*
 158 *processes, namely natural selection (a population-level process), and phenotypic change,*
 159 *environment choice, and environment construction (three individual-level processes),*
 160 *can improve initial individual mismatch and ultimately lead to the same outcome of a*
 161 *matching pattern. These may all occur within a single generation, including natural*
 162 *selection (e.g., via selective mortality). This means that without additional information*
 163 *we do not know which processes contributed to any observed organism-environment*
 164 *match. Thus, without additional information observed patterns cannot be interpreted as*
 165 *due to any specific process. (Original figure by Gabriel Munar-Delgado.)*

166

167 This expanded classification is broader than Haig's. The first way is essential to Haig's
 168 adaptation 2 (evolutionary adaptation of the population across generations), but it also
 169 includes within-generation population change via differential survival. The second to
 170 fourth ways cover Haig's adaptation 1 (responsive developmental adaptation of the
 171 individual, within generations), but it also includes non-responsive (constitutive)

172 change, it also includes (flexible/reversible) change in fully-grown adults, and it also
173 includes change in environmental aspects.

174

175 While the concept of adaptation is central to evolutionary biology, the same idea is
176 fundamental in other disciplines. For example, human psychologists try to understand
177 how people developmentally tailor their brains, cognition, and behaviour to harsh and
178 unpredictable environments (Frankenhuis & Gopnik 2023), how the fit between a
179 person's personality and its environment can be improved (Kandler et al. 2024), and
180 economists study the features that allow some companies or organisations to grow
181 where others fail (Child 1997). In all cases we expect to see associations between the
182 traits of organisms (or analogous entities) and the features of their environment.

183

184 Obtaining a good understanding of adaptation is therefore of broad importance. It
185 improves our understanding of the variability, functioning, and fitness of individual
186 organisms. This then also impacts the functioning, persistence, and divergence of
187 populations, species, and ecosystems. (Including captive organisms and agricultural
188 species, even if they may have constraints on their abilities to control their environment
189 because of human intervention). As our world is changing more and more (e.g., climate
190 change, economic globalization, societal changes), a greater understanding of how
191 organisms and analogous entities like companies and organizations cope with and
192 control variability is increasingly relevant to predict responses to these changes and to
193 meet societal challenges.

194

195 However, obtaining a good understanding of adaptation is not an easy task. As shown
196 in Figure 1, adaptation is a rather complex phenomenon. (i) At its most basic, there is
197 not one process of adaptation, but several. These are not strictly comparable: there is
198 developmental adaptation at the individual level (Haig's adaptation 1) and evolutionary
199 adaptation at the population level (Haig's adaptation 2), and this implies different
200 requirements and different dynamics. For example, evolutionary adaptation at the
201 population level requires heredity of the relevant characters, while developmental
202 adaptation at the individual level may require an active organismal response to the
203 environment. (ii) All four processes result in the same outcome (Figure 1). This means
204 that we have four different solutions to what is essentially the same challenge, that of
205 how to increase organism-environment match. (iii) Whenever different solutions can be
206 applied to the same challenge, then the operation of one solution could reduce the
207 scope for the other potential solutions (a negative effect). For example, a change in the
208 phenotype to match the local environment may remove the need for choice of the
209 environment. Alternatively, one solution could facilitate the other (a positive effect). For
210 example, a change in the phenotype facilitates dispersal and therefore choice of the
211 environment. Another option is that a mixture of solutions, within or between
212 individuals, is favoured (frequency-dependent effects; Araya-Ajoy et al. 2025). (iv)
213 Finally, evolutionary adaptation at the population level includes the evolution of the
214 three individual-level processes of developmental adaptation. Therefore, we expect
215 there to be interactions among the different solutions, in their operation, and in their
216 evolution.

217

218 Unfortunately, these four processes of adaptation are largely studied in isolated
219 research programs, even within biology. We are typically not considering all processes
220 at the same time, we tend to isolate the processes, and we tend to pay more attention
221 to some processes than to others (changes to the environment generally receive less
222 attention). This means that some processes are understudied, and the interactions
223 between processes as mentioned above are understudied. For example, researchers
224 studying habitat choice (a form of choice of the environment) or niche construction (a
225 form of construction of the environment) typically ignore phenotypic plasticity (a form
226 of change of the phenotype), and *vice versa*. This isolation can be problematic, because
227 then we ignore that the different organismal solutions to the same challenge may
228 constrain each other or act synergistically (at the moment, and during their evolution).
229 It also means that without additional information we do not know which processes
230 contributed to any observed phenotype-environment match, and thus that observed
231 patterns cannot be interpreted as due to any specific process (Figure 1).

232

233 Comprehensive studies investigating all of these processes would benefit from a
234 common and general framework, but such a framework is currently insufficiently
235 developed (Botero et al. 2015; Edelaar et al. 2017; Fokkema et al. 2021; Munar-Delgado
236 et al. 2023; Scheiner 2016; Scheiner et al. 2021, 2022; Gonzalez-Forero 2023, 2024).
237 Moreover, research in other disciplines (e.g., psychology, sociology, economy, and
238 philosophy) developed similar ideas and concepts on adaptation (e.g. Childs 1997;
239 Johnson 2007), but crosstalk between the disciplines is rare (Saltz 2019).

240

241 **Towards a better understanding of adaptation**

242

243 *Improving terminology and its use*

244

245 In our workshop we reviewed, compared, and connected existing terminologies. There
246 are, unfortunately, many terms and descriptions that cover at least part of the same
247 biological phenomena, possibly because they have each been developed to describe
248 certain biological phenomena without considering their relation to adaptation as a
249 general phenomenon, and their relation to the many processes that can lead to
250 adaptation. That is, they have been developed in the absence of a common framework.
251 As a result, existing terms in the literature vary in breadth and in specificity. As an example
252 of a narrow term, ‘matching habitat choice’ only relates to habitat choice, not to choice
253 of the environment entirely, because that would also cover the choice of a social or
254 sexual partner, or when to be active (temporal choice) (D’Aguillo et al. 2019; Edelaar et
255 al. 2008; Kaiser et al. 2024; Ravigné et al. 2004). Moreover, it is a specific form of habitat
256 choice, one that is driven by an active assessment of local performance by the organism,
257 and thus different from habitat choice due to a genetic preference or a preference
258 developed via imprinting (Edelaar et al. 2008; Ravigné et al. 2004). As an example of a
259 broad term, niche construction covers the change in the local environment for the
260 individual doing the construction, but also the effects for other conspecifics or even
261 heterospecifics. Some people also see habitat choice as a form of niche construction, so-
262 called ‘relocational niche construction’ (Odling-Smee et al. 2003). And in an even
263 broader interpretation, even phenotypic plasticity has been interpreted as a form of
264 niche construction (Sultan 2015).

265

266 In the workshop we spent a lot of time reviewing and discussing the terminology, in part
267 because different people have different understandings of the same term and have
268 different preferences. In the end, we concluded that there may not be a single
269 terminology that the entire scientific community needs to use, because some
270 subdisciplines have a tradition of terminology that is unlikely to be replaced by another.
271 However, we do advise authors to provide more information about what they mean
272 when they use specific terms, and to be aware of the connections with other
273 terminology. Some considerations for the three processes of developmental adaptation
274 are as follows.

275

276 ● **Environment Choice.** It seems better to use the word ‘choice’ instead of
277 ‘selection’, to avoid confusion with natural selection. We use the term
278 ‘environment’ to be as inclusive as possible with respect to what is chosen (a
279 habitat, a niche, a resource, a location, a mate, a social group, etc.). ‘Habitat use’
280 is a broader term than ours; use is the outcome of choice, but use still occurs
281 even when there is absence of choice due to the lack of options. Note that choice
282 does not necessarily mean change: perhaps the current option is chosen, and no
283 change is observed (Trappes et al. 2022).

284 ● **Environment Construction.** We use the term ‘construction’ instead of
285 ‘modification’ because it has a stronger connotation with adaptation:
286 deterioration is also modification. ‘Adjustment’ suggests only changing
287 something already existing, whereas construction also includes new elements.
288 We again use the term ‘environment’ to be as inclusive as possible with respect
289 to what is constructed (something physical, the habitat, the behaviour of other
290 organisms, etc.).

291 ● **Phenotype Change.** This term explicitly refers to a change in the phenotype of
292 the individual, providing a clear contrast to change in the environment via choice
293 or construction. Change of the individual could involve a response (to the
294 environment (Schlichting & Pigliucci 1998), to other individuals as with indirect
295 genetic effects (Baud et al. 2022; Wolf et al. 1998), or to other phenotypic traits
296 as with causally covarying traits (Morrissey 2014)). But it also involves the
297 constitutive, unresponsive ontogeny of traits, since this may still increase
298 adaptation. This means that alternative terms like plasticity, flexibility,
299 conformance, or adjustment are not inclusive enough.

300

301 *A framework to understand the processes driving adaptation*

302

303 This discussion of terminology naturally led to a discussion on how the different
304 processes of adaptation operate, how they relate to each other, and how they evolve
305 and influence evolution. This gave rise to the development of a visually intuitive
306 framework to understand the processes driving adaptation (Figure 2). This framework:

307 ● addresses the individual- and population-level mechanisms behind any observed
308 trait-environment association (i.e., identifies the causes of adaptation),

309 ● distinguishes between constitutive (fixed) and responsive (plastic) development,

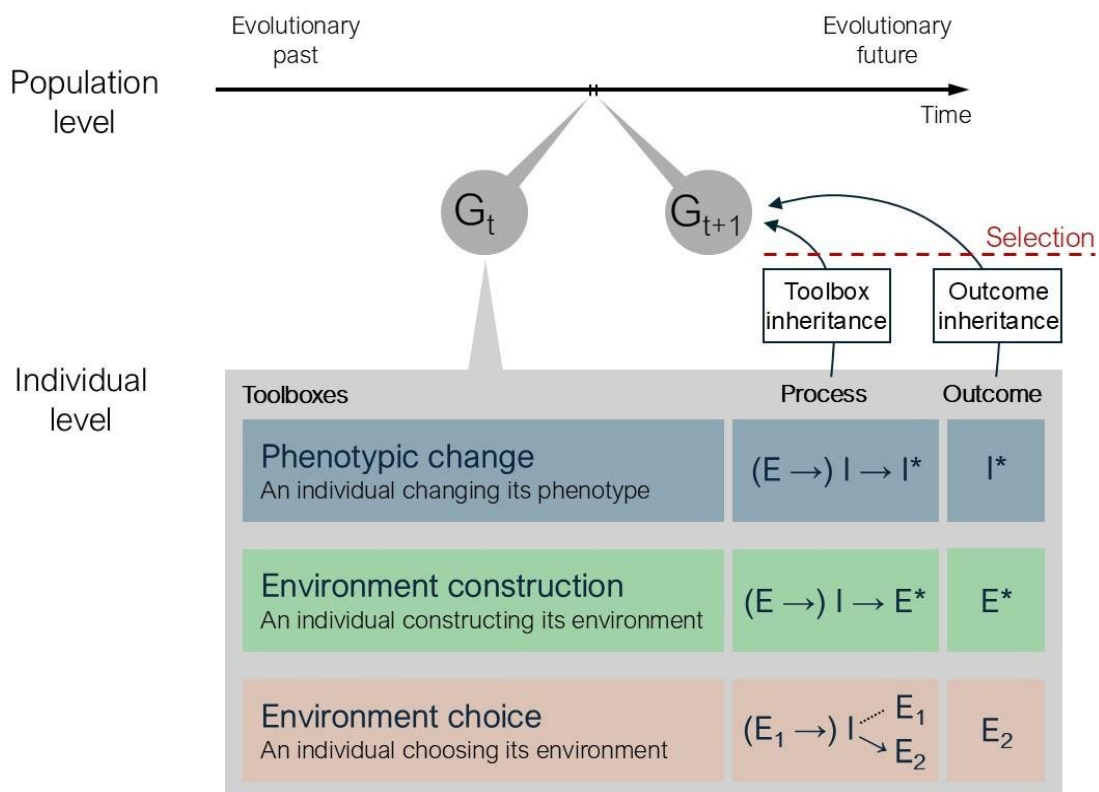
310 ● considers potential interactions between these mechanisms (in their current
311 operation and in their evolution),

- 312 • recognises that organisms are not just passive receivers of environmental effects,
313 but can also be active agents of change,
- 314 • acknowledges the complexity of reality – organisms and environments may both
315 evolve over generations, and the different solutions for trait-environment match
316 may interact.

317

318 We further present and discuss this framework in a forthcoming separate publication.
319 We hope this framework helps researchers to avoid making implicit (or unrecognised)
320 assumptions about the absence of certain phenomena by simply ignoring them. For
321 example, when faced with an observation as in Figure 1, to only discuss or test for
322 natural selection and phenotypic change.

323



324

325 **Figure 2.** A schematic framework to understand adaptation and its evolution. Greater
326 adaptation refers here to an improved match between the individual (I) and its
327 environment (E), whose consequence is improved ecological performance and
328 reproductive success. Mechanistically, adaptation occurs at two levels: at the population
329 level and at the individual level. The ability of individuals to adapt (their adaptation
330 'toolbox') evolves at the population level over time, as captured by the horizontal arrow
331 at the top. From one generation (G_t) to the next (G_{t+1}), individuals can employ different
332 adaptation toolboxes. We recognise three distinct ones (the three differently coloured
333 rows): individuals can engage in phenotype change (giving as outcome I^*), individuals
334 can engage in environment construction (giving as outcome E^*), and/or individuals can
335 engage in environment choice (here, E_1 versus E_2 , and giving as outcome E_2). These three

336 *different toolboxes might be employed in a constitutive manner (i.e. fixed expression).*
337 *For example, a plant always develops spines against potential herbivory. Alternatively,*
338 *the toolbox is employed in a facultative manner (i.e., responsively expressed), here*
339 *represented by environmental effects on the individuals within parentheses ($E \rightarrow$). For*
340 *example, a plant only develops spines against herbivory if it detects that herbivores are*
341 *present. When the elements of the toolbox are heritable, and when variation in these*
342 *elements is associated with variation in reproductive success (indicated as ‘Selection’),*
343 *constitutive and facultative toolboxes can evolve at the population level (indicated as*
344 *‘toolbox inheritance’). Additionally, in some cases the adaptation outcome is directly*
345 *(non-genetically) heritable, and can be transmitted to the next generation as a function*
346 *of its effect on reproductive success (‘Selection’). Examples could be epigenetic molecular*
347 *marks passed on via gametes, behaviours that are copied by offspring, or environments*
348 *that are inherited by offspring (Agrawal et al. 1999; Anastasiadi et al. 2021;*
349 *Bonduriansky & Day 2018; Edelaar in press).*

350 *Integrating mathematical approaches to adaptation*

351

352 Addressing a complex topic like adaptation tends to benefit from a mathematical
353 approach, which can provide a precision that language is otherwise lacking, allowing
354 clearer understanding of if, how, and when concepts overlap and diverge. A diverse
355 group of mathematical biologists sat down to discuss different approaches, where the
356 diverse backgrounds and preferences of each became clear. In a forthcoming paper they
357 will present a joint framework, which incorporates all four processes within a single
358 mathematical model, they discuss the correspondence between their approach and
359 existing eco-evolutionary models, and they suggest how this framework might be used
360 to distinguish the effects of each of the four processes of adaptation. There may not be
361 a single best mathematical approach to adaptation, but the group ultimately developed
362 an approach that, interestingly, none of them would have developed individually.
363 Furthermore, they all agreed this approach was better than what they likely would have
364 developed individually. So one lesson is that also in mathematical modelling,
365 collaboration among people with diverse backgrounds pays off. A next step might
366 therefore be greater interaction among theoreticians from different disciplines (e.g.,
367 biology, sociology, economics).

368

369 *Clarifying which features explain and predict the diversity of adaptation*

370

371 There may be organismal or environmental features that favour the evolution of some
372 processes of adaptation over others. If we can identify these, we are able to give better
373 explanations for how adaptation has evolved in the past, and it may also be relevant to
374 predict how adaptation may play out in the future. This turned out to be a big task, or
375 perhaps one that does not have a single solution because too many contingencies are
376 involved. But a few general observations could be made.

377

378 Individual adaptation as a state is often described by the fitness effects of the match
379 between the phenotypical value z and environmental value ϑ :

380

381

$$w_{i,x,t} = \alpha \cdot \exp\left(-\frac{(z_{i,t} - \theta_{i,x,t})^2}{\sigma_{x,t}^2}\right)$$

382

383 where α is a constant, $z_{i,t}$ is the trait value of individual i at time t , $\theta_{i,x,t}$ represents the
384 individual's value of its environment at location X at time t , and $\sigma_{x,t}^2$ is the width of the
385 fitness function (a larger value describes weaker selection on mismatch). As can also be
386 seen from this mathematical description, in confirmation of what was said earlier, an
387 individual can achieve a change in its fitness via a change in the phenotype (z) or a
388 change in the environment (θ). Next, the subscripts capture the three different targets
389 identified in Figure 2: a change of its phenotype in time (z_t) (phenotype change), a
390 change of its environment in space (θ_x) (environment choice), or a change of its
391 environment in time (θ_t) (environment construction).

392

393 Which of these processes (the toolboxes of Figure 2) will evolve (via evolutionary
394 adaptation at the population level) will be influenced by a number of factors.

395

396 ● Predictability of the future. Changes of the phenotype or the environment are only
397 adaptive if they increase fitness in the future. This means that such changes are
398 more likely to be adaptive if the future phenotype and/or environment can be
399 predicted with greater reliability.

400

401 ● Developmental costs. Changing the phenotype takes energy and other resources.
402 Likewise, exploring and choosing another environment, and changing and
403 maintaining the local environment likely takes resources.

402

403 ● Risk. Change of phenotype or environment may entail risks. Perhaps the future is
404 not as expected, and mismatch is actually increased due to the organismal change.
405 Or the development of a new phenotype or environment includes a transition phase
406 of greater risk of e.g. starvation or predation.

406

407 ● Time. Information acquisition/processing and subsequent organismal change
408 generally takes time, and during that time it is possible that organismal performance
409 is temporarily reduced. To the extent that all of this takes time, the scale of external
410 temporal variation (e.g. temporal change in the environment) also becomes
411 relevant – change may be so rapid that the organism cannot track it (or tracking it
412 becomes too costly given the short-lived benefit it gives) (Dupont et al. 2024).

412

413 ● Lost opportunity costs. Activating one process of adaptation now might imply that
414 the benefit of using another process of adaptation in the future is diminished.

414

415 ● Benefits. These are in principle specified by the fitness function, but some
416 stochasticity is expected, and for environment construction benefits may be taken
417 by or received from other conspecifics.

417

418 These insights allow for some further inductions. The evolution of adaptive phenotypic
419 change is more likely if the information received from the environment (the cue) is
420 predictive of the expected environmental state within the proper temporal reaction
421 scale of the organism. Hence, we expect phenotypic change to evolve under positive
422 autocorrelation (red noise) of the environmental temporal variation within a lifetime (or
423 across generations in case of transgenerational transmission). Faster temporal variation
424 within a lifetime is more likely to result in the evolution of reversible phenotypic change.

425

426 Adaptive environment choice (either in space or in time) requires local availability of
427 suitable environments within the activity range of the individual organism, and
428 therefore is more likely to evolve when the environments are negatively autocorrelated
429 (blue noise) or uncorrelated (white noise). If within-environment temporal
430 heterogeneity is strong (making any chosen environment unpredictable), then non-
431 informed choice (including diversified bet hedging) is expected to evolve. The same
432 seems true when among-environment variation is positively autocorrelated.

433

434 It is not clear under which conditions construction of the environment is expected to
435 evolve. Perhaps it evolves when the other two individual-level processes of adaptation
436 are somehow limited. This might be when environments vary at such a large scale that
437 it is outside the activity range of the individual organism and does not allow for
438 environment choice. Or when environments vary at such a small respectively large
439 temporal scale that it is too fast respectively too slow for the individual organism to track
440 via phenotype change. Or when the range of environmental variation is so large that it
441 extends beyond the range of the phenotypic variation that could match it – in that case,
442 construction of the environment might reduce the environmental variation enough such
443 that match can be achieved again. Construction of the environment may also be more
444 likely to evolve if the costs are shared between different individuals (especially
445 relatives), or when the benefits of a given investment in construction are larger (e.g.,
446 when more conspecifics are present that can be influenced by the social phenotype of
447 an individual), or when the constructed environments and their benefits are transmitted
448 to relatives.

449

450 Finally, genetic adaptation via natural selection (with outcomes ranging from clines and
451 locally adapted populations to ecological speciation) is more likely for slow
452 environmental change at large spatial scales.

453

454 It is clear that the evolution and operation of the different processes of adaptation are
455 not too predictable as they are dependent on the cost-benefit ratio of each process,
456 within the parameter space delimited by constraints. All of these costs, benefits, and
457 limitations depend on characteristics of the environment, but also on characteristics of
458 the organism. This means that past evolutionary trajectories influence future
459 evolutionary trajectories. For example, environment construction favours residency,
460 which may favour phenotype change but disfavour environment choice. Nonetheless, it
461 does seem that to some extent we might be able to understand and predict the relative
462 contributions of the different processes of adaptation by decomposing the
463 spatiotemporal environmental variation into its different wave signals and contrasting
464 these with the organism's life history and spatial neighbourhood.

465

466 *Generate predictive models*

467

468 The topic of coaction, coexistence, and coevolution of the different processes of
469 adaptation, and how they might lead to potential correlations at different hierarchical
470 levels, was also explored via simulation modelling, and, more specifically, a discussion
471 on the elements that a quantitative genetic individual-based simulation model might
472 profitably contain. One interesting consideration was that an organism may need to

473 make many changes during its lifetime, and cycles of decision-making could be modelled
474 for this. In every cycle only a single adaptation process is applied, based on the greatest
475 'liability' for this process. This liability depends on genetic inputs in the form of
476 intercepts of a reaction norm, but also on inputs described by the (equally genetic) slope
477 of the reaction norm. These reaction norms allow the organism to respond to the
478 environmental state (including population density), and its own phenotypic state, and
479 to the phenotype-environment mismatch. Having multiple decision cycles before
480 reproduction allows individuals to dynamically respond to the fast environmental and
481 phenotypic changes, to respond to each other's actions (including transgenerationally
482 transmitted ones), and to display mixtures of processes. The modelling of individuals
483 also allows for differences among individuals to evolve (e.g., different frequencies of
484 distinct strategies).

485
486 Simulation models allow for the modelling of complex scenarios and allow for the
487 execution of virtual experiments. For example, after running the models over many
488 generations, we can modify the environmental conditions and observe changes in the
489 genetic parameters (intercept and slope of the reaction norm) underlying the liability of
490 the three actions. We can also observe how the genetic variances responsible for
491 individual differences in their actions are maintained throughout evolution, and
492 whether any positive or negative genetic correlation emerges from their coevolution
493 (i.e., how the different developmental adaptation processes influence each other
494 evolutionarily).

495

496 **Additional recommendations**

497

498 Our knowledge of adaptation is already quite considerable. However, as outlined in the
499 introduction, there is also a considerable need for future research, and the facilitation
500 of such research. We end with some recommendations that address these goals.

501

502 • We need further development and classification of methods to examine and test
503 the importance of each process of adaptation as an explanation for any observed
504 trait-environment associations. There is likely not a single method that works for
505 all cases, but the exploration for more general methods should be promoted.
506 Descriptive statistical models that still allow for causal inferences would be
507 especially valuable.

508 • We need more empirical studies that investigate multiple processes of adaptation
509 at the same time. Explanatory power of these studies is likely enhanced when
510 combined with experimental approaches, allowing for causal inferences.

511 • In studies that investigate adaptation, authors should address explicitly what
512 processes of adaptation they did consider, and which were not considered (or can
513 be ignored), and what this implies. Ideally, they would also mention what
514 limitations exist and what would be needed to study all processes, as a service to
515 readers and potential funders.

516 • Which processes of adaptation operate likely depends on the spatial scale of
517 environmental variation, and on the temporal scale of environmental and
518 phenotypic variation, all relative to organismal mobility and generation time.
519 These scales therefore need to be quantified or discussed.

- 520 • As we obtain more information on which processes of adaptation operate, we
521 should investigate the costs and constraints of the processes.
- 522 • Regarding the evolution of the individual processes of adaptation, we need more
523 studies on the heritable variation of these processes, on the strength of natural
524 selection on these, and on the ecological causes behind any natural selection on
525 them.
- 526 • We should also investigate the interactions, feedbacks, and trade-offs among the
527 four processes. Can we predict negative or positive interactions among the
528 processes of adaptation with any generality, and how this influences their
529 operation and evolution?
- 530 • A more integral approach to adaptation should feature in our teaching, such that
531 a new generation of researchers becomes familiar with the interrelatedness of the
532 different processes of adaptation.
- 533 • Adaptation is a transversal topic that is relevant in many fields and disciplines, and
534 more interaction and collaboration between people from these diverse
535 backgrounds is advisable. This may require reflection on different scientific
536 cultures and for sure requires getting familiar with different (usage of)
537 terminology. Such collaboration might be easier if it is focussed on a specific
538 problem, for example a societal need. Collaborative research can benefit from
539 seed money for networking or a discovery phase, not unlike our sponsored
540 workshop.

541

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