

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

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

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

96

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

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.

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

123

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

139

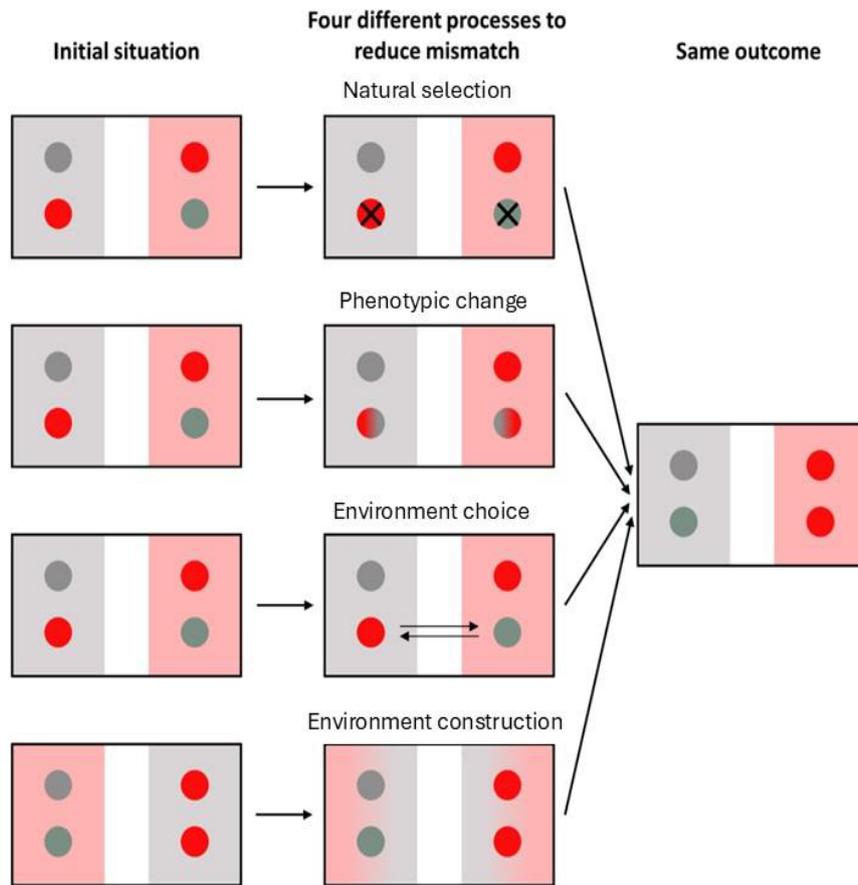
140 (1) certain individuals survive and/or reproduce better than others in a given
141 environment because of their characteristics (natural selection - a population-level
142 process),

143 (2) individuals change their phenotypic traits,

144 (3) individuals choose the environment (e.g., habitat, food resources, mate, or social
145 group),

146 (4) individuals construct their local environment.

147



149

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

164

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

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

172

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

181

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

192

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

215

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

230

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

238

239 **Towards a better understanding of adaptation**

240

241 *Improving terminology and its use*

242

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

263

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

273

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

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

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

298

299 *A framework to understand the processes driving adaptation*

300

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

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

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

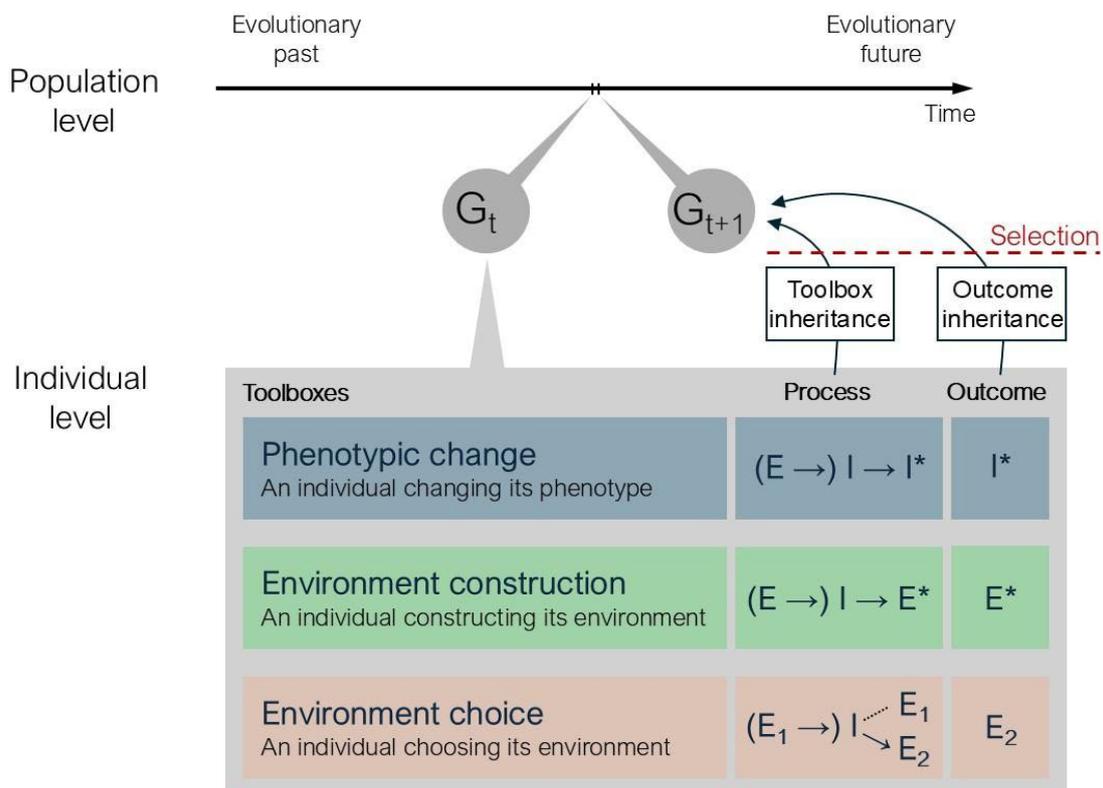
308 ● considers potential interactions between these mechanisms (in their current
309 operation and in their evolution),

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

315

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

321



322

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

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

348 *Integrating mathematical approaches to adaptation*

349

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

366

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

368

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

375

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

378

379

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

380

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

390

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

393

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

397

398 ● Developmental costs. Changing the phenotype takes energy and other resources.
399 Likewise, exploring and choosing another environment, and changing and
400 maintaining the local environment likely takes resources.

400

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

404

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

410

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

412

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

415

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

423

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

431

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

447

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

451

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

463

464 *Generate predictive models*

465

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

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

483
484 Simulation models allow for the modelling of complex scenarios and allow for the
485 execution of virtual experiments. For example, after running the models over many
486 generations, we can modify the environmental conditions and observe changes in the
487 genetic parameters (intercept and slope of the reaction norm) underlying the liability of
488 the three actions. We can also observe how the genetic variances responsible for
489 individual differences in their actions are maintained throughout evolution, and
490 whether any positive or negative genetic correlation emerges from their coevolution
491 (i.e., how the different developmental adaptation processes influence each other
492 evolutionarily).

493

494 **Additional recommendations**

495

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

499

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

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

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

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

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

539

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