

1 **Appreciating the multiple processes increasing**
2 **individual or population fitness**

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19 **Abstract**

20 Natural selection results in adaptation for populations, not individuals. Yet,
21 environmental change can reduce individuals' expected fitness. Selection will favour the
22 evolution of traits that allow individuals to proactively compensate for such reduced
23 fitness. Though several well-known processes can achieve this goal, they are still often
24 neglected, and often not clearly distinguished. To facilitate greater attention to the full
25 range of processes by which individuals can increase their fitness, we present a
26 classification scheme that integrates these: phenotypic change, selection of the
27 environment, and adjustment of the environment,. We outline how these individual-
28 level processes relate to natural selection and population level fitness. This framework
29 may help guide research (and teaching) about how individuals and populations may
30 respond to environmental change.

31 **There are (not so?) many ways to increase fitness**

32 Our motive in writing this is to classify the biological processes that are known to
33 contribute to adaptation (i.e., increased fitness), and thereby show how these processes
34 are interrelated. It is often stated that only **natural selection** (see Glossary) can drive
35 adaptive evolution [e.g. 1,2]. Therefore, when biologists observe local adaptation,
36 parallel evolution, or exaggerated genetic divergence at particular loci, they usually
37 attribute these current patterns to the past (perhaps recent) action of natural selection
38 [3,4]. However, it is well established that habitat choice can also lead to adaptive
39 evolution, population divergence, and even genomic divergence along stretches of
40 chromosomes [5-15]. Similarly, researchers typically invoke natural selection to explain
41 parallel phenotypic divergence between replicated populations in contrasting habitats.
42 Yet, this parallelism might instead result in part or in whole from **adaptive phenotypic**
43 **plasticity** [e.g. 16]. Habitat choice and plasticity are familiar phenomena, but
44 nevertheless frequently get overlooked in our collective focus on natural selection. To
45 avoid this, we argue that biologists should routinely keep in mind the entire set of
46 processes that can cause adaptive change in populations. To be fair, some readers no
47 doubt do so already. Others may be tempted to dismiss our suggestions outright as a
48 polemic endorsing of an “Extended Evolutionary Synthesis” [17], which is not our goal.
49 Rather, our goal is to examine the relationships between long-familiar biological
50 phenomena that affect fitness, to encourage readers to keep all these phenomena in
51 mind when considering the process of adaptation, particularly in the context of local and
52 global environmental change.

53 To facilitate this goal, we present a scheme which we think is helpful. It distinguishes
54 four distinct processes that contribute to increases in individual and/or mean population
55 fitness. Three of these processes rely on individual organisms’ ability to increase their
56 fitness, an ability arising from genotypes that must have previously evolved in response
57 to past natural selection. But having evolved, these abilities can subsequently contribute
58 to increases in fitness without continued natural selection. For example, adaptive
59 habitat choice can allow genotypes to sort themselves across a landscape to better
60 match local conditions, resulting in allele frequency changes at the local level whether
61 or not there is realized variation in survival or reproduction. We consider three
62 processes by which individuals might increase their own expected fitness. When many
63 individuals together use these processes, population mean fitness can increase as well
64 (an outcome typically associated with natural selection). Although the processes we
65 discuss are previously known, empirical and theoretical studies rarely consider all four
66 concurrently. For example, there exist almost no examples of papers that have
67 simultaneously quantified or modelled the relative contributions of the four processes
68 in a single unified study ([12,24] considered models of three of the four). By explicitly
69 describing how these four processes are interrelated, amongst other things we hope to
70 facilitate such studies in the future. Hence, we think our systematic dissection of familiar
71 drivers of increased fitness has a heuristic value in providing a framework and context
72 in which to conduct our research.

73 **A systematic overview of how to increase fitness**

74 In Box 1 we first provide a detailed decomposition of the mechanisms that can increase
75 *individual* fitness. We make a crucial distinction for this term. Individuals have an

76 *expected* fitness, a probabilistic statement of their lifetime reproductive success given
77 their genotype, phenotype, and the environment(s) they experience (including
78 conspecifics and other species). As individuals mature they survive or die, reproduce or
79 fail to reproduce, resulting in a *realized* fitness. This distinction between expected and
80 realized fitness is discussed at greater length in [14].

81 Natural selection occurs when variance in realized fitness covaries with phenotype. But,
82 during their lifetime individuals can take actions that alter their expected (and realized)
83 fitness (note that we focus on absolute, rather than relative, fitness except where
84 noted). To see how, consider a fitness landscape (Box 1), a theoretical (and empirical)
85 representation of how individuals' expected fitness is related to their phenotype, in a
86 particular environment [18]. However, neither an individual's trait value, nor its fitness
87 landscape, are fixed phenomena. Traits can be plastically adjusted to the environment.
88 The environment can be changed locally, in order to adjust it to the characteristics of
89 the individual. Alternatively, the environment that an individual interacts with can be
90 changed by choosing another environment out of the set of available environments. In
91 order to distinguish between these two ways to change the environment in which the
92 individual has to perform, we use the term "**adjustment of the environment**" for the
93 first option, and "**selection of the environment**" for the second one (habitat choice
94 being a special case of selection of the environment; see Box 2 on terminology).

95 Population mean fitness then can be calculated from the fitness landscape that
96 individuals experience, and their phenotype distribution (Box 3). The phenotype
97 distribution can be influenced by natural selection (a population-level process), but can
98 also be influenced by the individuals directly, by changing their phenotypes. The fitness
99 landscape can be changed by altering the environments that individuals experience. For
100 example, if locally maladapted individuals depart towards other populations because
101 their fitness is greater elsewhere, then (at least temporarily) both donor and receiver
102 population mean fitness can increase [matching habitat choice; 7,11-15,18].

103 In Figure 1 we visualize how the three broad individual-level processes identified in Box
104 1 relate to each other, and to (population-level) natural selection. While this might be a
105 subjective way to classify them, it seems like a productive way, and it is supported by
106 the following reasoning. On the one hand, fitness depends on the phenotype-
107 environment match. So we distinguish *what changes* in order to increase fitness: the
108 phenotype, or the environment? On the other hand, *how are these changed?* There are
109 only two ways to change a phenotype distribution or environment: via reducing some
110 variants and/or increasing others, or via alteration of the existing variants. (We note a
111 similarity with the Price Equation [19] here, which also includes only two terms to
112 explain generic trait change: a term that captures who contributes to the next
113 generation and how much (i.e. a selective term), and a term that captures whether the
114 next offspring systematically differ from their parents (i.e. an alteration term); see Fig.
115 1). Combining these two options produces four different combinations (Fig. 1). At the
116 individual level, there is no selection among a set of phenotypes; this process (natural
117 selection) acts only at the population level. Each of the remaining three options is only
118 open to individuals (though such actions by a collection of individuals can change
119 population mean fitness; Box 3). The past action of natural selection has put in place the
120 physiological, developmental, or behavioural systems that make it possible for

121 individuals to increase their own fitness (positive arrows in Fig. 1), i.e. the individual
122 capacity to increase fitness has evolved due to natural selection. Because these three
123 individual-level processes can reduce variation in realized fitness, during present-day
124 environmental change they may reduce the scope for, and thereby undercut the effect
125 of, natural selection (negative arrows in Fig. 1). This is in fact why these processes
126 evolved via natural selection in the first place (evolutionary dependency): they allow
127 individuals to avoid being selected against. Hence, these three individual-level processes
128 should be continuously fine-tuned by natural selection (the dynamic feedback as
129 indicated by the arrows). Importantly however, natural selection in the present day is
130 not required for each process to alter individual and population mean fitness
131 (operational independency).

132 The three individual-level processes could be productively subdivided further. Equation
133 3 in Box 1 distinguishes between constitutive versus responsive phenotype change.
134 These two components are well-known as environment-independent ageing and
135 growth, versus phenotypic plasticity. It is equally well-known that their causes and
136 consequences can be very different, so this extra resolution is necessary and helpful.
137 Along the same lines, the same distinction could and should be made for adjustment
138 and selection of the environment: both can depend on time and genotype only
139 (constitutive change), or on individuals' environment, phenotype, or phenotype-
140 environment match (responsive change) (see eq. 3 in Box 1). Unlike phenotypic change
141 however, this distinction is rather poorly incorporated when the environment is being
142 changed by individuals. For habitat choice (selection of the environment with respect to
143 habitat), different terminology has now been recognized for these different
144 components: genetic habitat choice for the constitutive component, versus
145 (environment-dependent) imprinting and (phenotype-environment match-dependent)
146 matching habitat choice (see [7, 18]). It is also slowly becoming clear that the
147 evolutionary and ecological dynamics of these distinct components can be quite
148 different (e.g. [15]). Therefore, studies on habitat choice (and selection of the
149 environment in general) have to be more specific on which component(s) they are
150 actually studying or modelling. This is probably true even more so for adjustment of the
151 environment, as we are not aware of a systematic distinction and treatment of its
152 constitutive versus responsive components. This additional insight gained from the
153 comparison and equal treatment of the distinct processes of the framework is an
154 example of its heuristic value.

155 We emphasize that none of the four processes that we distinguished here are new ideas:
156 they all have a history of relevant research and an extensive literature, and it is well
157 known that they can play a role in ecology and evolution [1,6,9-12,20-26]. (Similar
158 processes have also been distinguished in the social and economic sciences: 27,28).
159 There are also a number of studies considering pair wise action of two such processes,
160 for example, evaluating the relative effects of plasticity or selection [29]. Nonetheless,
161 as far as we know, these disparate processes are typically not placed within a single
162 framework that highlights both their shared and unique features. Sometimes the three
163 individual-level processes discussed here are all lumped under plasticity, or under
164 behaviour, or even under niche construction [30]. Or some (e.g. habitat choice, as part
165 of selection of the environment) may be seen as "just another behaviour". We argue
166 here that these three processes can be seen as conceptually distinct from each other.

167 This means that they operate distinctively, and therefore that they can have
168 consequences for ecological performance and related ecological and evolutionary topics
169 that are *independent* of the others (though not mutually exclusive). This merits
170 considering them as being categorically different from each other, and from natural
171 selection. In turn, this leads us to call for more studies that estimate the concurrent
172 effects of all of these processes that facilitate adaptation. By recognizing the
173 relationships between the four distinct processes as outlined in Fig. 1 we are more likely
174 to interpret our data in the light of all four alternatives, and measure their relative
175 effects.

176 **Considering all four processes can improve our research**

177 There are several reasons why studies of adaptation should consider multiple adaptive
178 processes (and preferably all of them) concurrently.

179 First, when we see (or infer) increased realized fitness in a certain situation, we want to
180 know what caused it, and for this we must consider the contribution of each of these
181 processes. For example, when we identify ‘genomic islands’ of extreme allele frequency
182 divergence between populations we usually attribute this pattern to the past action of
183 selection. But, it might be appropriate to also ask to what extent the same result can
184 arise from genetic variation in habitat preference.

185 Second, some of these processes are well-studied (natural selection, adaptive
186 phenotypic plasticity), whereas the other routes towards increased fitness (adjustment
187 of the environment, selection of the environment) are more often overlooked by
188 researchers. It is possible that these latter processes are relatively infrequent or less
189 consequential in nature, but this conclusion must be empirically established rather than
190 assumed. When not systematically considering all processes in design, measurement
191 and interpretation, we are unknowingly including specific biases into our research, and
192 therefore in our explanations and view of the world. For instance, many reciprocal
193 transplant experiments to test for divergent natural selection involve caging that
194 prevents dispersal or habitat choice, so we cannot evaluate whether habitat choice
195 would otherwise allow individuals to escape maladaptation and avoid divergent natural
196 selection [e.g. 9,31].

197 Third, there might be relevant combinations (correlations and/or interactions) between
198 these processes (within and between individuals, within and between generations,
199 etcetera: see Fig. 1) that we cannot capture if we study them in isolation, or if we don’t
200 recognize them as distinct yet equivalent. For example, the reaction norm framework
201 for adaptive phenotypic plasticity [25] focuses on the selective benefits of having a
202 certain phenotypic intercept and slope (an environment-dependent responsive
203 component of phenotype change), i.e. on the interaction between plasticity and natural
204 selection. Other theoretical studies also investigated the evolution of habitat choice (a
205 form of selection of the environment [7,10,12,32,33]), and of adjustment of the
206 environment [34,35]. However, studies considering the interaction between habitat
207 choice and plasticity are rare [but see 12,24], and as far as we know none consider all
208 four processes.

209 The scheme we present here hopefully will encourage researchers to pose new research
210 questions and to design studies that consider the impacts of these four processes on
211 each other and on fitness, and that this results in new insights. (Some examples follow
212 below, and see Outstanding Questions.)

213 **Application of the framework across contexts and research fields**

214 The framework of Figure 1 can be broadly applied. For example, the environmental
215 variable with which our organism interacts can be an abiotic characteristic, another
216 species, a competing conspecific, a potential mate, et cetera. To illustrate the latter,
217 consider a focal individual with a certain sexual signal aiming to mate with other
218 individuals who have certain preferences. Our framework proposes that in principle an
219 individual's mating success (a component of fitness) can be increased via three
220 individual-level processes: (i) phenotype change - e.g. the individual may change its
221 signal to match the preferences of potential partners, by growing, learning, or otherwise
222 changing its trait; (ii) selection of the environment - e.g. it may seek out and court
223 individuals who are more favourably predisposed to like its signal (for a spatial setting,
224 see 36,37); or (iii) adjustment of the environment - e.g. it may seek to change the
225 partner's preferences or choosiness. To the extent that such individual actions fail to
226 equalize fitness across individuals (negative arrows in Fig. 1), sexual selection (top-left
227 process of Fig. 1) then occurs and may cause evolutionary change across generations in
228 phenotype change, selection of the environment, or adjustment of the environment
229 (positive arrows in Fig. 1).

230

231 The same exercise can be carried out for any kind of environmental variable, such as
232 those listed above (see Figure 2 for another example). Hence, the framework can be
233 used to distinguish the different processes operating in the context of sexual selection,
234 of social selection [38], of indirect genetic effects [39,40], of coevolution [41], et cetera.
235 Potentially, this can help to uncover research topics that are well-researched in some
236 fields but underexplored in others, or to uncover approaches that can be transferred or
237 aligned between fields studying the same process but in different contexts (Box 4).

238

239 **Relationship to the idea of the extended phenotype**

240 Biologists typically write that organisms adapt to their environment [1,2,6,22,30,42].
241 This bears the connotation that it is the environment that dictates, and the organisms
242 that change [29,43]. Our framework emphasizes this cause-effect relationship, but also
243 its inverse, in which organisms can improve fitness prospects by adjusting or selecting
244 their local environment (right- versus left-hand side of the framework, Fig. 1, 2). The
245 adjustment made to the environment is sometimes called an "**extended phenotype**"
246 [44], in which an organism's genotype influences features of the external environment,
247 which in turn affect its fitness. Typical examples include beaver dams, bird and termite
248 nests, and host manipulation by parasites. If those adjustments to the environment
249 (resp. of water level, microclimate, and host behaviour) increase fitness, then natural
250 selection will favour genotypes capable of executing such adjustments. By extension, if
251 a specific environment is selected (a breeding cavity, a sexual or social partner, a habitat,
252 etc.), and this selected environment can increase fitness, then in principle the selected
253 environment could also be seen as an extended phenotypic trait (as a result of the

254 interaction between the genotype and the environment) [see also 30,43,45]. Hence, the
255 left side of the framework deals with fitness increase via changes in the phenotype, and
256 the right side via changes in the extended phenotype (Fig. 1).

257

258 **Relevance for population adaptation and global change**

259

260 The ability of individuals to make adaptive changes to their phenotypes, as well as to the
261 environments in which these phenotypes have to perform, will generally contribute to
262 adaptation at the population level (Box 3). When the fitness of many individuals is
263 improved, population mean fitness may increase as well (assuming fitness is not a zero-
264 sum game, such as can occur with a strictly regulated carrying capacity). Hence, the
265 individual-level mechanisms (phenotypic change, selection of the environment,
266 adjustment of the environment) can all contribute to the ability of populations to cope
267 with environmental variation. Importantly, this may also include rapid environmental
268 changes caused by humans [26,46] and other causes of global change. What is often
269 unclear is the relative contribution of the individual-level processes to cope with current
270 or future environmental changes. For example, in the case of higher temperatures due
271 to climate change, do individuals cope by changing their thermal physiology (phenotypic
272 plasticity), by being active in cooler places (including shifting to cooler climates) or at
273 cooler times (selection of the environment), or do they make deeper burrows or thinner
274 nests to stay cooler (adjustment of the environment)? Or, are individuals unable to
275 (sufficiently) execute these strategies and therefore subjected to natural selection, at
276 which point the population's fitness may increase via evolutionary change? It is again
277 important to distinguish between constitutive and responsive changes in individual
278 fitness. On the one hand, responsive changes in individuals' phenotype or environment
279 to something like climate change (like the examples above) may allow individuals to
280 rapidly and adaptively adjust within the time span of single generations. On the other
281 hand, their responses might be maladapted to the novel challenges, reducing individual
282 and population fitness. In contrast, the constitutive changes are not expected to be
283 adaptive in novel conditions, so these could only help individuals to cope with global
284 change after they evolved to new states via natural selection, i.e. across generations.
285 Thus, the relative effects of the different processes we discuss here and the time spans
286 over which they may increase fitness will dictate how individuals and populations
287 respond to global change.

288

289 The individual-level processes can also help buffer populations from demographic
290 declines that can result from selection. Evolution by natural selection entails a
291 demographic load (selective deaths or reduced fecundity) that reduces population size
292 and can increase extinction risk [47]. Individual-level processes such as plasticity or
293 selection of less stressful environments can mitigate this demographic load, buying time
294 for selection to act and thus enabling evolution in lieu of extinction [10,13,26,48].

295

296 The operation or contribution of the three individual-level processes is unlikely to be
297 equal across all populations and species, or conditions. Likewise, there will be variation
298 in the relative importance of population-level natural selection versus individual-level
299 adaptation. At present, we do not have much data or even much theory [12,24] on the
300 relative effects of these alternative processes. How strong are these processes? How do

301 they interact? What historical or contemporary variables influence the relative effects
302 of these processes? And, when and why do some normally adaptive individual responses
303 turn maladaptive in novel environments (e.g. resulting in ecological traps [49]). There
304 are many opportunities for research addressing these and other questions, through
305 observation, experiments, and theory, to better understand the full range of
306 mechanisms that can facilitate individual and population responses to environmental
307 (including global) change (Outstanding Questions).

308

309 Even though natural selection can lead to adaptive evolution of populations, this is not
310 an exclusive feature of natural selection: for example, selection of the environment can
311 also achieve this. When different genotypes choose different habitats across a broad
312 spatial scale, alleles may be sorted non-randomly among geographically distinct
313 populations [5,7,9,11,12-15,19,28]. This genotype-dependent dispersal can lead to local
314 adaptation, genetic divergence between populations, and islands of genomic
315 divergence; patterns that are commonly interpreted as diagnostic signatures of natural
316 selection. Yet, these outcomes can evolve simply as a result of dispersal without
317 requiring realized variation in fitness that is the hallmark of natural selection [e.g.
318 7,14,15,18,33,50]. With natural selection the individual is the selective *target*, while with
319 selection of the environment the individual is the selecting *agent*. Both processes can
320 drive adaptive evolution, and both might generate allele or genotype frequency
321 variation across a landscape.

322

323 **Concluding Remarks**

324 In conclusion, the increase of fitness has a limited number of targets, but can be
325 achieved by many means. We group these means into four distinct processes. We hope
326 this classification framework helps to appreciate similarities and differences among
327 fitness-increasing processes, and thereby helps to structure the planning and
328 interpretation of research. Specifically, we hope the framework draws attention to the
329 need to study all (relevant) processes that may drive adaptation in a given system.

330

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339

340 **Outstanding Questions**

- 341 • Can individuals and populations increase their fitness through any means that is
342 not captured in Figure 1? That is, is the framework (Fig. 1) complete?
- 343 • In natural situations, what determines the relative importance of each of the four
344 processes of the framework? What conditions or biological systems would allow
345 us to sometimes safely ignore some of them?
- 346 • How, and to what extent do the processes in Figure 1 interact with each other?
347 Are there any generalities in these interactions?
- 348 • Can the framework help to transfer or streamline research questions among
349 different fields? Can it help to uncover research topics that have a strong
350 tradition in some fields (e.g. selection of the environment in the context of food
351 resources) but that appear neglected in others (e.g. selection of the environment
352 in the context of sexual selection)?
- 353 • In applied situations, such as conservation biology, agriculture or medicine, how
354 can we manipulate the four processes of the framework to manage problematic
355 or endangered populations? Are some of the processes of the framework
356 unjustifiably neglected, biasing us away from potential solutions?
- 357 • Under current high rates of (global) environmental change, might some
358 processes become more relevant or potent than they used to be? Are flexible
359 responses to the environment more important than the evolution of constitutive
360 change?

361

362

363 **Glossary**

364 **Adaptive phenotypic plasticity:** the ability of a genotype to produce different
365 phenotypes because of exposure to different environmental conditions such that it
366 increases its expected fitness.

367 **Adjustment of the environment:** the ability of a genotype to make changes to its local
368 environment such that it increases its expected fitness. Sometimes called 'niche
369 construction' in the narrow sense.

370 **Extended phenotypic trait:** an element of the environment which is influenced by an
371 individual, and which in turn can affect its fitness.

372 **Natural selection:** systematic differences in reproductive success between individuals
373 with different phenotypes.

374 **Selection of the environment:** the ability of a genotype to bias its usage of different
375 available environments such that it increases its expected fitness.

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495

496 **Box 1.**

497 **Zooming in on how to increase fitness.** We present a simple model illustrating the
498 processes that can increase fitness (see Figure I for a graphical representation). We
499 consider a simple non-stochastic Gaussian fitness function, translating an individual i 's
500 trait x in environment j (x_{ij}) into its expected absolute fitness W_{ij} :

501

$$502 \quad W_{ij} = c_j \exp -\left(\frac{(x_{ij}-X_j)^2}{2\omega_j^2}\right) \quad (\text{eq. 1}),$$

503

504 where X_j is the trait optimum for environment j , ω_j is inversely related to the strength of
505 stabilizing selection in that environment, and c_j dictates the maximum achievable fitness
506 for environment j (e.g. environment quality). Note that we are using absolute fitness
507 (expected lifetime reproductive success) here, on the logic that individuals are more
508 likely to adjust their phenotype or their environment based on assessments of their own
509 performance (e.g. stress, nutrition, mating success), rather than on their performance
510 relative to others.

511

512 Using the chain rule (Geber method [51]), we can partition the various ways in which
513 individual fitness can change through time:

514

$$515 \quad \frac{dW_{ij}}{dt} = \frac{\partial W_{ij}}{\partial x_{ij}} \frac{\partial x_{ij}}{\partial t} + \frac{\partial W_{ij}}{\partial X_j} \frac{\partial X_j}{\partial t} + \frac{\partial W_{ij}}{\partial \omega_j} \frac{\partial \omega_j}{\partial t} + \frac{\partial W_{ij}}{\partial c_j} \frac{\partial c_j}{\partial t} \quad (\text{eq. 2}).$$

516

517 This equation summarizes the four different means by which an individuals' expected
518 fitness (eq. 1) can change through time. What do these four terms mean? (See Figure I).

519

520 Term 1, $\frac{\partial W_{ij}}{\partial x_{ij}} \frac{\partial x_{ij}}{\partial t}$, says that individual i 's fitness (given environment j) can increase
521 through time as a result of temporal change in an individual's trait values (see Figure I).

522 The trait can change through time in distinct ways: $\frac{\partial x_{ij}}{\partial t} \sim f(t) + f(x_{ij}, X_j) + \varepsilon$ (eq.
523 3). The first term represents constitutive trait change through time (e.g., age-
524 dependent growth). The second term represents the effects of the individual's current
525 trait value, its environment, and their interaction (which includes its current expected
526 fitness). Note that other individuals within the population are part of its environment,
527 so frequency-dependent interactions and game theory concepts can enter our model
528 through this term. The last term represents developmental noise (ε).

529

530 Term 2, $\frac{\partial W_{ij}}{\partial X_j} \frac{\partial X_j}{\partial t}$, says that individual fitness can increase through time as a function of
531 temporal change in the local environmental optimum (see Figure I). Again, this can be
532 subdivided into different components. For simplicity, we assume the environment
533 optimum X_j changes along a geographic transect ($X_j = a + j$). The intercept a represents a
534 baseline fitness, and j represents the effect of an individual's position j on the transect.

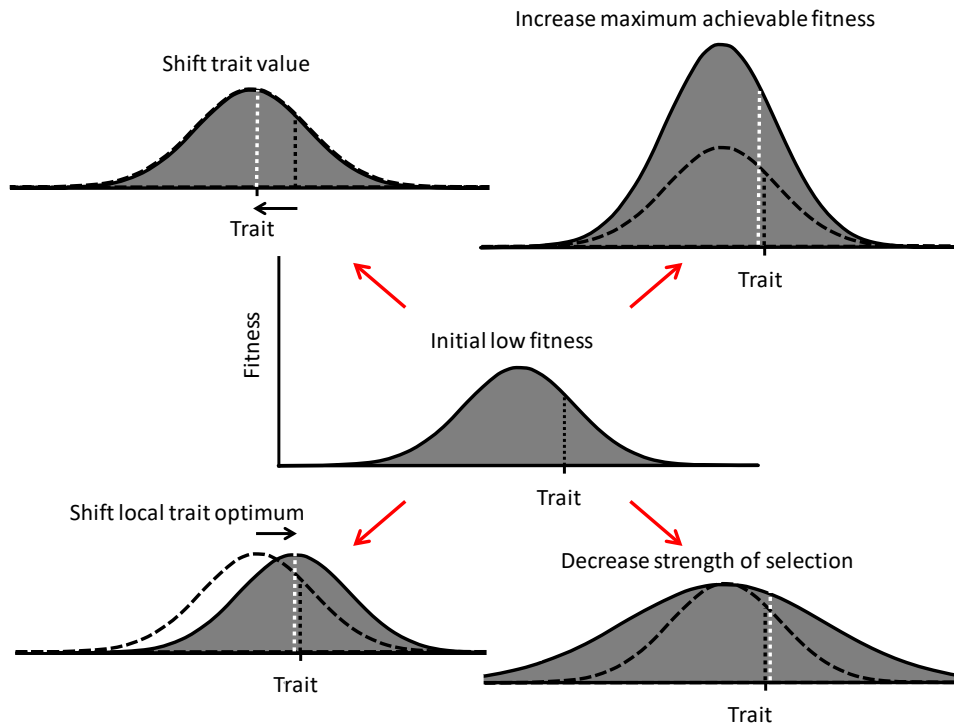
535 We can again apply chain rule decomposition (even when the cline is non-linear): $\frac{\partial X_j}{\partial t} =$
536 $\frac{\partial X_j}{\partial a} \frac{\partial a}{\partial t} + \frac{\partial X_j}{\partial j} \frac{\partial j}{\partial t} + \xi_X$ (eq. 4), to show that the environmental optimum can change either
537 by altering one's local environment (changing a), or by moving to a new environment
538 (changing j). The new environment could entail dispersal to a new location in the

539 landscape, or it could be changes in one's social group, partner, microhabitat, et cetera.
 540 These include changes in the trait distribution of other individuals, which can generate
 541 frequency-dependent interactions and game-theory-like behaviour. The last term is
 542 environmental noise.

543

544 Term 3, $\frac{\partial W_{ij}}{\partial \omega_j} \frac{\partial \omega_j}{\partial t}$, says that individual fitness can increase through time when stabilizing
 545 selection relaxes (see Figure I). This is particularly favourable for maladapted individuals,
 546 whose fitness gets to approach that of the fittest individuals (whose fitness changes
 547 little; see Fig. I). Term 4, $\frac{\partial W_{ij}}{\partial c_j} \frac{\partial c_j}{\partial t}$, says that individual fitness can increase through time
 548 by increasing the environment-specific constant (i.e. overall environment quality), which
 549 affects everyone proportionally (see Figure I). Term 3 and 4 both correspond to
 550 environmental change, just as term 2. Hence, terms 3 and 4 can also be decomposed
 551 further as we did for term 2, into changes in local environmental conditions or
 552 movement to a different environment.

553



554

555

556 **Figure I. Visual representation of the four components of the fitness function that can**
 557 **be changed when fitness is initially low for a certain individual (central panel).** Top-
 558 left: the trait value x_{ij} can be shifted towards the optimum value. Top-right: the maximum
 559 achievable fitness c_j can be increased. Bottom-left: the optimum trait value X_j can be
 560 shifted. Bottom-right: the strength of selection ω_j can be decreased. These components
 561 can be all changed either constitutively (as a matter of time, e.g. ageing of the
 562 individual), or as flexible responses to environmental and phenotypic conditions (see
 563 main text). In outer panels we depict the original central fitness curve and achieved
 564 fitness (black dotted lines) and the new and increased expected fitness (white dotted
 565 line).

566 We then substitute the decompositions of these four terms in equation 2, to get:

567

568 $\frac{dW_{ij}}{dt} = \frac{\partial W_{ij}}{\partial x_{ij}} [f(t) + f(x_{ij}, X_j) + \varepsilon] +$

569 $\frac{\partial W_{ij}}{\partial X_j} \left[\frac{\partial X_j}{\partial a} \frac{\partial a}{\partial t} + \frac{\partial X_j}{\partial j} \frac{\partial J}{\partial t} + \xi_X \right] +$

570 $\frac{\partial W_{ij}}{\partial \omega_j} \left[\frac{\partial \omega_j}{\partial d} \frac{\partial d}{\partial t} + \frac{\partial \omega_j}{\partial j} \frac{\partial J}{\partial t} + \xi_\omega \right] +$

571 $\frac{\partial W_{ij}}{\partial c_j} \left[\frac{\partial c_j}{\partial f} \frac{\partial f}{\partial t} + \frac{\partial c_j}{\partial j} \frac{\partial J}{\partial t} + \xi_c \right] \quad (\text{eq. 5}),$

572

573 which we colour coded to represent different biological processes. The terms in yellow
574 correspond to phenotype change (e.g., growth, plasticity) that alters fitness. The
575 remaining elements represent changes to the environment. The blue terms represent
576 changes made to the local environment, which we therefore call “adjustment of the
577 environment”. The green terms represent individuals choosing between different
578 environments, which we call “selection of the environment” (see Box 2 on terminology,
579 and Figure 1). (The remaining stochastic elements do not deterministically increase
580 fitness, so are not further discussed). Note that for this illustration an individual adjusts
581 or selects only a single environment; one can readily elaborate this framework to
582 account for an individual adjusting or selecting multiple environments.

583

584 Hence, the increase in absolute individual fitness can be systematically subdivided into
585 distinct components, depending on which aspects of individual fitness they affect, and
586 how this is achieved mechanistically. The equations above can then be used to derive
587 changes in population mean fitness, by integrating the changes above across the joint
588 distribution of environments and phenotypes (Box 3). (This will also affect the relative
589 fitness of individuals).

590

591 **Box 2. Discussing terminology.** The processes that affect fitness in Box 1 and Figure 1
592 have all been described before, albeit with variable terminology. In this box we justify
593 our choices of terminology. The process of natural selection needs little discussion,
594 although it is important to point out that this term covers selection in all contexts
595 (ecological, sexual and social selection). We recommend avoiding the shorthand term
596 “selection”, which could refer to several distinct processes, including selection of the
597 environment. The process of within-individual phenotypic change is covered by
598 “phenotype change” (which includes classical terms like growth and phenotypic
599 plasticity. We use the term “adjustment of the environment” to describe individuals’
600 capacity to adaptively alter their local environment. This process has often been referred
601 to as “niche construction”, but that term unfortunately has been used inconsistently.
602 Often it also includes (1) the effects that organisms have on other species without
603 affecting their own fitness (e.g., photosynthetic organisms release oxygen enabling
604 aerobic life [52]), (2) movement to other environments [33], and (3) phenotypic
605 plasticity changing the experienced niche [29,53]. Since the process we refer to is much
606 more restricted, we feel that the term adjustment of the environment is more
607 appropriate, also because it directly acknowledges that it targets the environment. The
608 term “habitat construction” has also been used [30], but we see the environment as
609 larger than just habitat (for instance including interactions with conspecifics). Finally,
610 selection of the environment also makes this same acknowledgement and
611 acknowledges that it is a selective process (showing its similarity to natural selection,
612 Fig. 1). While the classical term habitat choice may come to mind as an alternative, this
613 is only a specific case: selection of the environment covers any scale (from choice of diet
614 or micro site to near-isolated populations), and any component of the environment (like
615 time, or other organisms).

616 **Box 3.**

617 **Building up population fitness.** Given a model of changing individual fitness (Box 1), we
618 next consider changes in population mean fitness (\bar{W}_j). Assume the population has a
619 normal trait distribution with a mean \bar{x} and a variance σ . To obtain population mean
620 fitness we need to integrate across individual fitnesses (Box 1) times their relative
621 abundances (the normal trait distribution). To an approximation, application of the
622 chain rule then provides:

623
$$\frac{\partial \bar{W}_j}{\partial t} = \left[\frac{\partial \bar{W}_j}{\partial \bar{x}} \frac{\partial \bar{x}}{\partial t} + \frac{\partial \bar{W}_j}{\partial \sigma} \frac{\partial \sigma}{\partial t} \right] + \frac{\partial \bar{W}_j}{\partial X_j} \frac{\partial X_j}{\partial t} + \frac{\partial \bar{W}_j}{\partial \omega_j} \frac{\partial \omega_j}{\partial t} + \frac{\partial \bar{W}_j}{\partial c_j} \frac{\partial c_j}{\partial t} \quad (\text{eq. 6}).$$

624 Here, the first two terms (between brackets) reflect how population mean fitness can
625 increase in time via changes in the trait distribution (mean and variance). This can reflect
626 the effects of natural selection within a population, but the mean and variance of a
627 population can also change due to changes to the individual phenotypes (constitutive
628 and responsive) within a population. Another way would be due to certain phenotypes
629 disproportionately choosing to leave for another environment, or enter the focal
630 environment (selection of the environment). The last three terms in equation 6 are the
631 same as in equation 2 of Box 1: they reflect how changes in the environment (trait
632 optimum, strength of stabilizing selection, and maximum possible fitness) can increase
633 population mean fitness, whether through adjustment or selection of the environment
634 (Box 1).

635 Combining these insights from Box 1 and 3, the increase in population fitness is a
636 combination of a population-level process (natural selection) and several individual-
637 level processes, where each acts on one or several different aspects that determine
638 fitness (trait mean and variance, environment optimum trait value, environment
639 strength of selection, and average environment quality).

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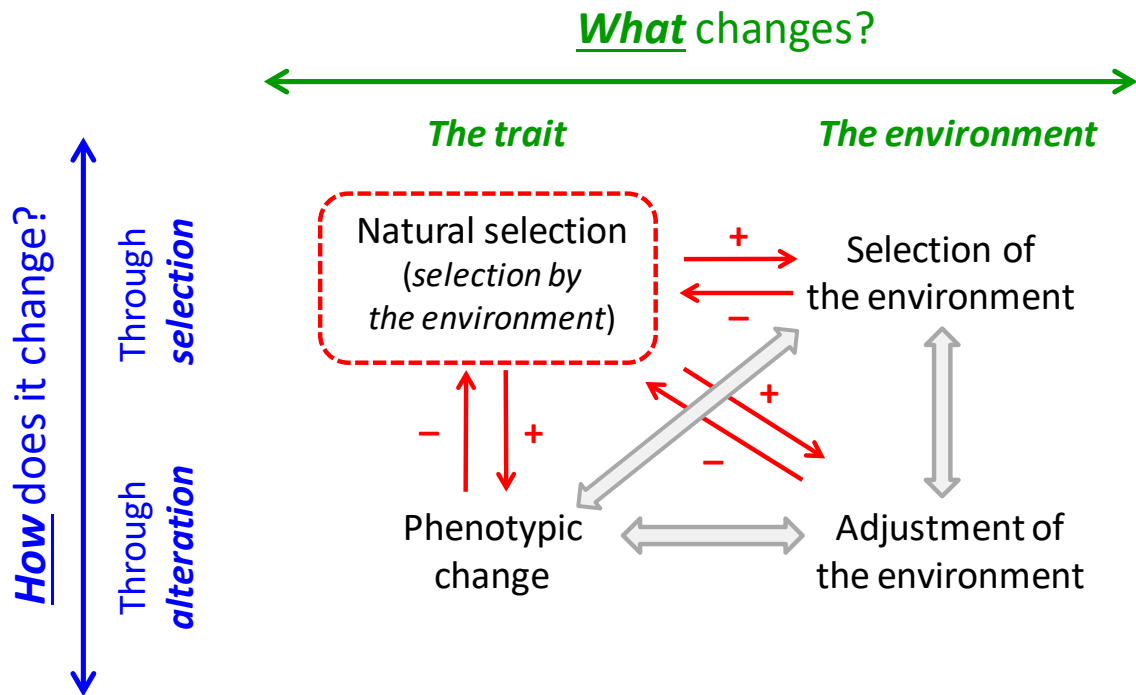
641 **Highlights**

642 • Individuals and populations can increase their fitness in at least four distinct
643 ways. We place these processes in a classifying framework that highlights their
644 similarities and differences. This is based on what changes (the phenotypic trait, or the
645 environment), and how it changes (via alteration, or via selection).

646 • The framework places major stress on the ability of individuals to adaptively
647 change their environments, via “adjustment of their environment” and “selection of
648 their environment”.

649 • While the distinct processes are not new, some are frequently confused or
650 overlooked.

651 • The framework is valid for any ecological context (including sexual and social). It
652 therefore has the potential to be applicable to any research field, and to draw attention
653 to underexplored research topics. In particular, little is known about the relative
654 contributions of the four processes to adaptation, and how they interact.



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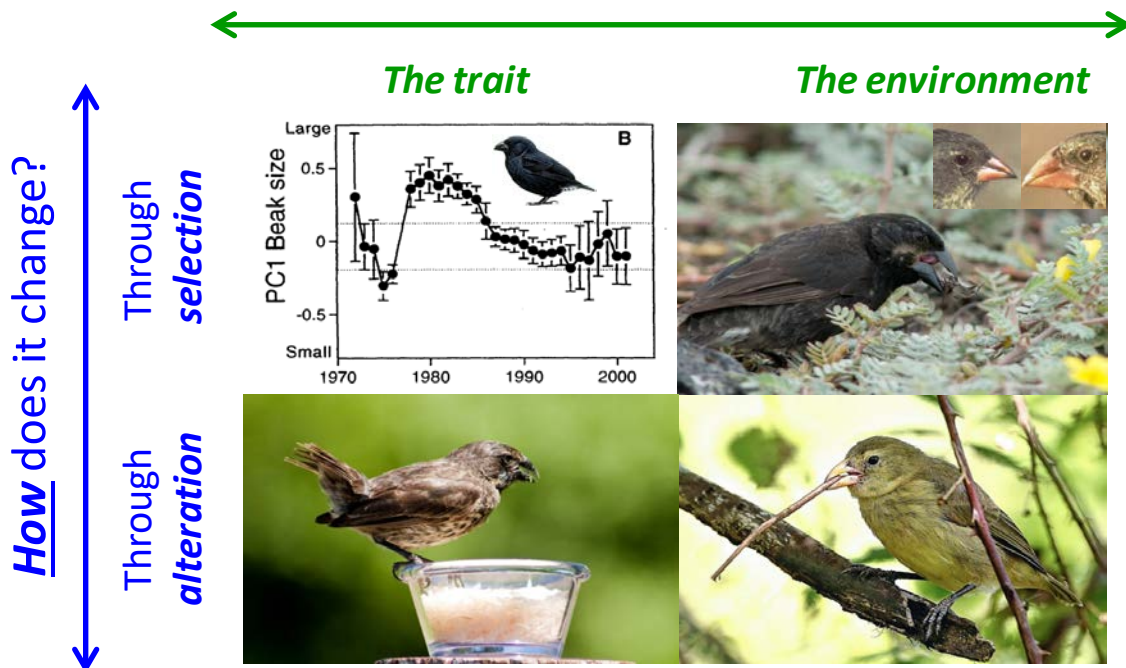
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Figure 1. A classification of the distinct processes to improve fitness. Natural selection will favour the evolution (origin and continuous fine-tuning) of processes that allow individuals to increase their fitness (i.e. to avoid being selected against, positive red arrows). Once natural selection has driven the evolution of these individual processes, they subsequently act to reduce opportunity for natural selection (negative red arrows). To increase fitness, individuals can either change their traits, or their environments (horizontal axis). Next, they can do so via selection, or via alteration (vertical axis). These options combine into four different processes. All can contribute to greater mean population fitness (Box 3). They can do so by themselves, or in interaction with one or more of the other processes, both at within-generation time scales and at between-generation (evolutionary) time scales (double-headed grey arrows). Increasing fitness via natural selection on traits can only operate at the population level, whereas the other three processes to increase fitness are only open to individuals. With selection of the environment, individuals select among a set of environments (i.e. individuals do the selecting). In contrast, with natural selection the environment selects among a set of phenotypes (i.e. individuals are selected upon), and could therefore be seen as selection by the environment.

What changes?



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Figure 2. An example of applying the framework to adaptation and feeding ecology in Darwin's finches. Top-left: Darwin's finches are most famous for their evolutionary responses in population mean bill size to temporal changes in food availability as driven by differential mortality and survival, i.e. natural selection. [From 54. Reprinted with permission from AAAS]. However, food intake and fitness can also be increased via other, individual-level, processes. Bottom-left: some finches have recently started to feed on novel food items, like rice provided by humans (photo by Luis de León). Such behavioural plasticity (a responsive, environment-dependent component of phenotype change) has probably played a historical role in finch adaptation, with some populations feeding on exotic food items like seabird eggs, seabird blood, ticks, afterbirths, decaying fish, dead seabirds, and undigested faecal remains [55]. Bottom-right: the Woodpecker finch uses small sticks and cactus spines (a constitutive, phenotype-independent component of adjustment of the environment) which are adjusted for the task of prying insect larvae out of decaying wood (photo by Peter W. Hills, © of www.worldbirdphotos.com). Top-right: Medium ground finches may show a lot of variation in bill depth within a single population (inset. [From 54, reprinted with permission from AAAS]). It has been suggested [56] that males with deeper bills, which therefore can crack larger seeds, tend to settle in areas that are richer in the large-seeded *Tribulus* plant (a responsive, phenotype-dependent component of selection of the environment) (photo by Andrew Hendry). Note that these three individual solutions may affect natural selection: natural selection on bill size is reduced in urban environments providing novel foods [57] and likely also reduced when using tools, or when selecting environments that provide the right food given an individual's bill.