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# Balancing Population and Individual Level Adaptation in Changing Environments

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Running head: *Balancing population & individual adaptation*

## **Abstract**

This paper examines the interdependency of population level adaptation (evolution) and individual level adaptation (learning). More specifically, we assume a trade-off between the two means of adaptation, i.e., a higher individual level adaptation can only be achieved by reducing the population level adaptation and vice versa. This trade-off is apparent in computational evolutionary systems, and there is also evidence that it exists in nature. As we show, despite this considered trade-off, there exist environments in which a combined adaptation scheme is optimal. Furthermore, we show that it depends on the environmental dynamics what particular distribution of population and individual level adaptation produces the optimal adaptive behavior. Finally, we show that the optimal balance (i.e., an optimal learning effort) can emerge from evolution.

**Keywords:** Evolution, Learning, Changing Environments, Second-Order-Selection, Adaptation Strategy

# 1 Introduction

In nature species are faced with changing environmental conditions and evolution has found a variety of adaptation mechanisms that seem to be tailored for the particular environmental conditions. The distinction between *individual level* and *population level adaptation* is often used to categorize natural adaptation mechanisms (Ancel & Bull, 2002). Individual level adaptation includes all forms of individual phenotypic changes during an individual’s lifetime, such as development and learning. Population level adaptation represents the evolutionary cycle of selection and genetic variations. We use the terms population and individual level adaptation rather than evolution and learning, because we want to investigate the coupling of two very similar trial-and-error adaptation mechanism that only differ from each other in that one is applied on the population and the other on the individual.

While in some species population level adaptation is the dominant adaptation mechanisms (e.g., bacteria), adaptation in other species relies much more on individual level adaptation. It seems that in nature there exists a trade-off between individual and population level adaptation. Interestingly this trade-off does not only exist *between* but also *within* species, such as, e.g., the well-known trade-off between reproduction (population level adaptation) and survival/longevity (individual level adaptation), see e.g. Levins (1968); Sibly and Calow (1984); Stearns (1989); Mukhopadhyay and Tissenbaum (2007). This trade-off follows from the assumption that organisms have a limited amount of energy which can be spent for the achievement of distinct goals, such as reproduction *or* survival. Such a trade-off could be visualized as in Figure 1. Notice that the figure is a qualitative sketch of such a trade-off and does not refer to particularly measured data.

In evolutionary computation there exists another trade-off between individual and population level adaptation. When coupling an evolutionary algorithm with a local learning procedure it needs to be decided what amount of computational resources are assigned to the local learning procedure. Thus, if the overall amount of computational effort is constant, such a trade-off exists. A high level of local learning (individual level adaptation) implies a low level of evolutionary search (population level adaptation), and vice versa. See Figure 2 for an illustration of this trade-off. There, with 0 individual learning steps, i.e., only 1 evaluation is applied to an individual, 100 percent population adaptation takes place. An increase of individual learning steps from 0 to 1, thus 2 instead of 1 calls to the evaluation function are now needed, reduces the relative number of genetic mutations by 50 percent. If the number of learning steps increases further, the relative number of genetic mutations with respect to the case of 0 individual learning steps, is reduced further. This relative number of genetic mutations can be interpreted as the intensity of population level adaptation.

In this paper we ask under what conditions a mixed adaptation strategy that couples population and individual level adaptation, i.e., an intermediate point on the trade-off curve, produces an adaptational advantage over population or individual level adaptation alone. In particular we consider the coupling of two similar trial-and-error adaptation mechanism on the population and individual level. After briefly reviewing the related work in Section 2, we introduce a simulation model in which adaptation effort can be distributed between population and individual levels while the overall adaptation effort is kept constant (Section 3). Thus, the cost of individual level adaptation is fully accounted for. We will show how the distribution of population and individual level adaptation influence exploration and exploitation (Section 4). Referring to Figures 1 and 2 we ask under what environmental conditions an intermediate point on the trade-off curves (not on the borders) produces an adaptational advantage. We will demonstrate that such cases exist, however such effects can only be observed in changing environments (Section 5). In nature the realized balance of population and individual level adaptation is probably partly determined by natural constraints and partly a result of higher-order adaptation process. We will demonstrate under

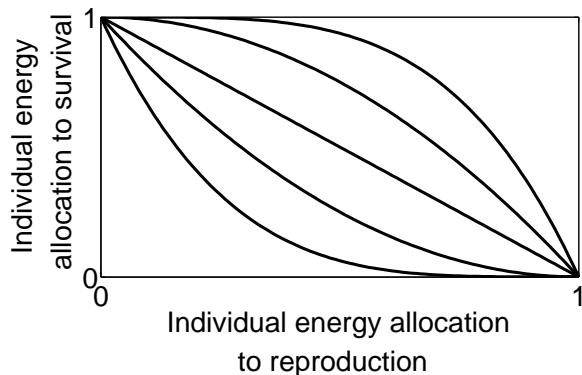


Figure 1: A qualitative sketch of possible trade-offs between reproduction and survival as can be found similarly in many species in nature.

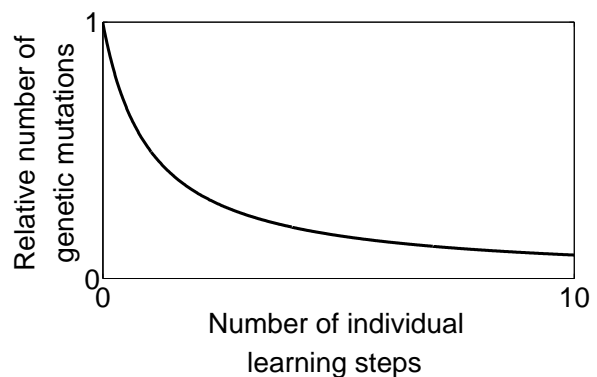


Figure 2: A trade-off between individual and population level adaptation that can be found in evolutionary computation when the overall computational budget is constant.

what constraints an evolutionary (second-order) adaptation of the balance between population and individual level adaptation can take place that leads to a near-optimal adaptation strategy (Section 6). We conclude with a summary and a discussion of the results (Section 7).

## 2 Related Work

In research fields related to the interaction of population and individual level adaptation by far, most efforts have been made to investigate how individual level adaptation influences the population dynamics. A review of the related literature can be found in Paenke, Sendhoff, and Kawecki (2007) and a collection of papers in Belew and Mitchell (1996) and Weber and Depew (2003). In the following, we only briefly summarize the main findings reported in the literature.

There exists an obvious influence of individual level adaptation on the population dynamics under Lamarckian inheritance (Lamarck, 1809) which assumes that the result of individual lifetime adaptation can be directly transferred from parent to offspring. Although some Lamarckian-like inheritance mechanisms exist (Paenke, Sendhoff, Rowe, & Fernando, 2007), the theory of Lamarckian inheritance is rejected in evolutionary biology, e.g., Crick (1970).

However, even in the absence of Lamarckian inheritance, individual level adaptation may change the evolutionary pathways. This effect has first been formulated by Baldwin (1896) and was later named the *Baldwin effect* by G. Simpson (1953). The seminal work by Hinton and Nowlan (1987) demonstrated that the Baldwin effect can indeed guide evolution towards a global fitness optimum. A recently published mathematical framework, called the gain function, explains under what conditions individual level adaptation accelerates or decelerates evolution (Paenke, Sendhoff, & Kawecki, 2007; Paenke, Kawecki, & Sendhoff, 2007). The gain function framework is limited to monotonic parts of the fitness landscape, and the main idea is to determine whether individual level adaptation enlarges or reduces fitness difference between fit and unfit individuals. The reduction of fitness differences caused by individual level adaptation has first been mentioned in the biology literature (Johnston, 1982), and was later termed *Hiding effect* by Mayley (1997). Though in Mayley (1997) the hiding effect is associated with a decrease of the rate of genetic evolution towards the optimum, this relationship does not hold in general. It has been demonstrated empirically on a bi-modal fitness landscape (Mills & Watson, 2006), and mathematically based on random walk

theory (Borenstein, Meilijson, & Ruppin, 2006) that the Hiding effect may accelerate evolution on a multi-modal fitness landscape, since individual level adaptation tends to smooth fitness valleys. The presence of the Hiding effect may also explain the results of a paper recently published in this journal (Curran & O’Riordan, 2006), where the addition of cultural learning to a genetically evolving population increased diversity. Through cultural or any other form of learning, individuals with genetic differences can achieve a similar fitness which results in a higher diversity in the population than in the absence of learning. In another paper (Curran & O’Riordan, 2005), it has been shown that the addition of cultural learning lead to a better adaptation behavior under dynamic environments. An intuitive explanation for this may also be the increased level of diversity induced by the Hiding effect.

When investigating under what conditions a coupling of population and individual level adaptation produces an adaptational advantage, the influence of individual adaptation on population adaptation is an important factor. Though the above work provides some insights into this question, no attempt has been made to fully account for the cost of individual level adaptation, to the best of authors’ knowledge. A few exceptions are in (e.g. Mayley, 1997), where a cost for individual level adaptation is explicitly included in the fitness function which reduces the fitness.

A closer investigation on how to distribute adaptation (or search) effort between population and individual levels has been made in the field of evolutionary optimization, in particular in designing memetic algorithms that couple evolution and local search algorithms. In these algorithms, it has been found that a proper distribution of computational effort between evolution and local search is a critical issue (Hart, 1994; Hüsken & Igel, 2002; Hart, William, Krasnogor, & Smith, 2005; Krasnogor & Smith, 2005). The main argument in favor of memetic algorithms over conventional evolutionary algorithms is that two-level search allows to employ two distinct search techniques, one for coarse-grained (population) search and the other for fine-grained (individual) search, where each technique is particularly well suited for the search space characteristics in which they are applied. Since the techniques used for coarse-grained search are usually very different from those employed for fine-grained, it is difficult to distinguish to what extent the performance improvement arises from simply employing two instead of one search level and to what extent from the specialization of the techniques. Furthermore, memetic algorithms are commonly applied to stationary optimization problems together with a Lamarckian inheritance scheme. Therefore, findings in memetic algorithms cannot be used to answer the question of the present paper which considers a dynamic environment and the coupling of two very similar adaptation mechanisms.

Most observations made from coupling population and individual level adaptation stem from models with a stationary environment. The derived principles are believed to be, more or less, applicable to dynamic environments as well. In this paper, we will, however, demonstrate some principles that can not be observed under stationary conditions but only in changing environments.

In a preliminary study (Paenke, Branke, & Jin, 2007), we have used a simulation model similar to the one used in this paper to investigate how phenotypic adaptation influences genotypic diversity. There we have arrived at a similar conclusion as in Curran and O’Riordan (2006) that phenotypic adaptation influences genotypic diversity. Notice, however, that a higher degree of diversity is not always favorable. Whether diversity leads to an adaptational advantage can be assessed only from the perspective of *what level* of diversity is most appropriate for a given dynamic environment with regard to exploration *and* exploitation capability of the population.

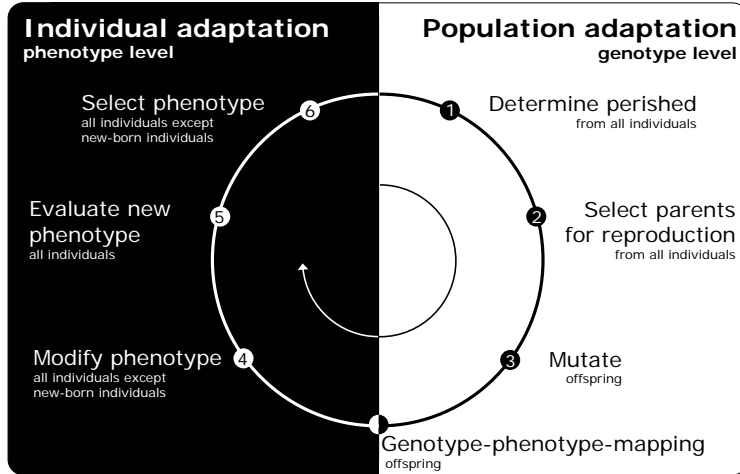


Figure 3: Adaptation loop that takes place every time unit in the analysis model of coupled individual and population level adaptation.

### 3 The Model

A population is composed of  $n$  individuals, each represented by a 3-tuple

$$I = (x, z, t_b), \quad (1)$$

where  $x$  is a one-dimensional real-valued *genotype*,  $z$  is a (variable) one-dimensional real-valued *phenotype*,  $t_b$  is the time when the individual is born. How well an individual's phenotype  $z$  is adapted to the environment at time  $t$  is specified by its *adaptive value* which is given by a time-dependent environment function  $f(z, t)$ . Selection is based on the adaptive values of the individuals and takes place every time step<sup>1</sup>.

Figure 3 shows the loop of individual and population level adaptation, representing one time step in the discrete time model. Adaptation steps 1 to 3 represent population level adaptation (right-hand side of the figure), whereas adaptation steps 4 to 6 represent individual level adaptation (left-hand side of the figure). The genotype-phenotype-mapping represents the transition from individual to population level adaptation. In the following the adaptation steps are described in detail.

#### 3.1 Population Adaptation

**Determine perished (Step 1):** Individuals have a limited lifetime which is specified by the model parameter  $L$ . Based on all individual's time of birth  $t_b$ , lifetime  $L$ , and the current time  $t$

<sup>1</sup>Notice that in evolutionary optimization,  $f$  is commonly called *fitness*. In such algorithms individuals represent solutions to an optimization problem and fitness indicates the corresponding performance. We use the term *adaptive value* instead of *fitness* for the following reason: In biology an individual's fitness indicates the number of its offspring. Thus, it is the result of a lifetime process and can strictly speaking only be assessed posthumously. In most evolutionary optimization algorithms, individuals either do not have a lifetime and its performance indeed correlates with the expected number of offspring, or where they have lifetime (so called memetic algorithms with individual local search) fitness assessment and selection is only applied *after* local search. The usage of the term fitness is in both cases consistent with the biological concept. In the model of this paper, however, selection is applied *during* the individual's lifetime, and the usage of *fitness* as reference to the "temporary basis of selection" would be inconsistent with the biological lifetime concept of fitness.

the number of individuals that reach the end of their life is determined (condition  $t - t_b = L$ ). Let  $m$  be the number of perished individuals in one evolutionary cycle.

**Select parents for reproduction (Step 2):** Based on the individual's current adaptive value  $f(z, t)$ ,  $m$  individuals are selected to produce offspring to replace the  $m$  perished ones. The selection probability is linearly proportional to the current adaptive value. This selection scheme is implemented by the *stochastic universal sampling* algorithm proposed by Baker (1987). The union of the original population with the  $m$  perished individuals removed, and the  $m$  new offspring forms the new population, such that the population size is constant over time.

**Mutate (Step 3):** The genotype of the new offspring is mutated by adding a random number sampled from a normal distribution  $X_{\phi(0, \sigma_G)}$  with mean  $\mu = 0$  and standard deviation  $\sigma = \sigma_G$  to the original (parent's) genotype  $x$ . Formally

$$x' = x + X_{\phi(0, \sigma_G)} \quad , \quad (2)$$

where  $x'$  is the genotype of the offspring.

### 3.2 Genotype-Phenotype-Mapping

This step is only applied to offspring (new-born individuals). Their innate phenotype is developed by applying the identity function to their genotype value, i.e., the innate phenotype equals the genotype value.

Using the formal definition of an individual of Equation 1, the whole process of (asexual) reproduction of an offspring  $I'$  from a parent  $I$  at time  $t$  is given by

$$(I, t) = ((x, z, t_b), t) \mapsto (x', x', t) = I' \quad , \quad (3)$$

where  $x'$  is calculated according to Equation 2. The offspring's lifetime  $L$  is equal to its parent's lifetime  $L$  and the time of birth is set to the current time.

### 3.3 Individual Adaptation

All individuals (except the new-born offspring<sup>2</sup>) try to increase the adaptive value using a simple (individual) adaptation algorithm based on a rudimentary lifetime memory that stores the best phenotype found so far and the corresponding adaptive value that has been achieved at the time when the phenotype value was explored. The individual adaptation procedure comprises the following three steps.

**Modify phenotype (Step 4):** Individuals modify their current phenotype by adding a random number sampled from a normal distribution with mean  $\mu = 0$  and standard deviation  $\sigma = \sigma_P$ . Formally,

$$z_t = z_{t-1} + X_{\phi(0, \sigma_P)} \quad , \quad (4)$$

where  $z_t$  denotes the phenotype in time  $t$ .

**Evaluate new phenotype (Step 5):** The new phenotype (for new-born individuals the innate phenotype) of each individual is evaluated in its current environment. An environment is specified by a time-dependent adaptive value function, i.e., the adaptive value becomes  $f(z_t, t)$ . In this paper we study four different environments, as illustrated in Figures 6, 7, 11, and 12. In addition to the mapping from phenotype  $z$  to the adaptive value  $f$  the time dimension ( $t$ ) is included for

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<sup>2</sup>This exception allows a precise distribution of adaptive value function calls between individual and population level; during the first lifetime unit, only the innate phenotype is evaluated and no modification of it takes place



visualization of the environmental dynamics. This adaptive value becomes the selection criterion for this timestep regardless of whether it is kept or not in the next step.

**Select phenotype (Step 6):** The adaptive value of the new phenotype of each individual is compared to its adaptive value at time  $t - 1$ . If the new adaptive value is lower than the memorized one, the memorized phenotype remains the current phenotype.

### 3.4 Remarks

The implementation of this kind of individual level adaptation can be seen as a (1+1)-*Evolutionary Algorithm* (Schwefel, 1993) and is very similar to the population adaptation mechanism. Notice that in both levels of adaptation the same adaptation step-size is chosen, i.e.,  $\sigma_G = \sigma_P$ , which is intended to avoid a methodological bias towards a particular adaptation mechanism. In all simulation studies of this paper we set  $\sigma_G = \sigma_P = 0.01$ . The default population size is 1000 in this paper.

The model allows to distribute the adaptation effort between individual and population level by setting the lifetime parameter  $L$ . With population size  $n$ , the average generation turnover, i.e., the number of individuals that perish and are replaced, is  $\frac{n}{L}$ . E.g., with  $n = 1000$  individuals,  $L = 20$  causes an average generation turnover of 50 individuals per time unit, i.e., 5 percent of all adaptation steps are genetic mutations and 95 percent are individual learning steps. Setting  $L = 1$  would cause an average generation-turnover of 1000 individuals per time unit, i.e., 100 percent of all adaptation steps are population adaptation steps. The case of  $L = 1$  represents the special case of *pure* population level adaptation, the case of  $L = 10$  represents a case of *coupled* individual and population level adaptation.

## 4 Influence of Lifetime on Population Dynamics

The balance between *exploration* and *exploitation* is the key issue for adaptive systems (Holland, 1992; Eiben & Schippers, 1998). In this section we investigate how a change in the central model parameters lifetime  $L$  (that adjusts the distribution of individual and population level adaptation) influences population dynamics with a focus on the exploration-exploitation balance. There exist two obvious effects of increasing lifetime.

First, as mentioned earlier, *a increase in lifetime  $L$  reduces the average generation-turnover*. Formally, the average generation turnover of a population of  $n$  individuals is  $\frac{n}{L}$ .

Secondly, *an increase in lifetime  $L$  smoothes the effective fitness landscape*. Individual adaptation influences the average adaptive value over an individual's lifetime. We will here call the mapping from genotype to its average adaptive value *effective fitness*. In principle, an increase of individual adaptation intensity can either increase or decrease selection pressure (Paenke, Kawecki, & Sendhoff, 2007; Paenke, Sendhoff, & Kawecki, 2007), however there exist only rare cases where the selection pressure is actually increased. The model of Hinton and Nowlan (1987) is such an example. Borenstein et al. (2006) refer to such scenarios as *extreme fitness landscapes*. In all other cases, an increase in individual adaptation intensity decreases selection pressure, and an increase in  $L$  smoothes the effective fitness landscape.

It is accepted wisdom that the exploration and exploitation ability is strongly influenced by the degree of *diversity*. A second important concept for this paper is the *quasi-species*. In the following we briefly introduce both concepts, diversity and quasi-species, before we present simulation studies.

## Diversity

In Magurran (2005) diversity is described as *the variety and abundance of organisms at a given place and time*. However, it is less clear how to measure it (Cousins, 1991; Magurran, 2005). Numerous diversity indices have been suggested in the biology literature, but it was shown in Routledge (1979) that no single index is universally superior. In artificial life and evolutionary computation, diversity has been studied, too (Morrison & Jong, 2001; Mattiussi, Waibel, & Floreano, 2004). Every diversity index reflects at least one of the two aspects, namely, *richness* and *evenness*. By richness, it is meant how many different elements exist in an element set, e.g., how many species in the ecosystem or how many different genotypes or phenotypes in a species or a local population. Evenness refers to the distribution of a given set of elements with respect to certain element properties. A uniform distribution produces the maximum evenness. Some diversity indices focus on either of the two properties, e.g. the Hurlberts Probability of Interspecific Encounter (Hurlbert, 1971) quantifies evenness. Most indices aggregate both aspects, such as the Shannon entropy (Shannon, 1948; Pielou, 1966) and the Simpson’s index (E. Simpson, 1949). In this paper, we decided to adopt the intuitive and widely used Simpson index (E. Simpson, 1949) for measuring diversity, as recommended in Routledge (1979). The Simpson index reflects the probability for two randomly sampled individuals to fall into the same partition class of a partitioned continuous space and is defined as

$$H = 1 - \sum_{i=1}^m \frac{n_i}{n}, \quad (5)$$

where  $n$  is the population size, and  $n_i$  the number of individuals in partition class  $i$  (out of  $m$  partition classes).  $H$  increases with both evenness and richness which is a desired property. For all studies, we have also used Shannon-Evenness, Hurlberts Probability of Interspecific Encounter, the standard richness measure, and the average Euclidean distance as diversity measures with which we obtained, without exception, qualitatively equal results.

## The Quasi-Species

Here, we briefly introduce the concept of the quasi-species, and refer to Eigen (1971); Eigen and Schuster (1979); Bull, Ance-Meyers, and Lachmann (2005) for a detailed description of this concept.

If the environment is static for a sufficiently long time, the population moves to a local or global optimum where the selection pressure is usually decreasing and the loss of diversity is slowed down. At the same time, mutation keeps introducing new (non-optimal) genotypes to the population. At some point in time the two forces selection and mutation that reduce and increase diversity at the same time are equally strong and cancel each other out. This well-known phenomenon has been termed *mutation-selection balance* in Haldane (1937); Crow and Kimura (1964). Under mutation-selection balance the population forms a “cloud” of genotypes around the so-called *wild-type*. This genotype cloud at mutation-selection balance is called *quasi-species* (Eigen, 1971; Eigen & Schuster, 1979).

The following illustration is inspired by the description of the quasi-species in Bull et al. (2005). Assume that there exist only two genotypes, an optimal and a non-optimal one.  $x$  denotes the fraction of optimal genotypes in the population, implying that  $(1 - x)$  is the fraction non-optimal genotypes.  $h$  denotes the fitness of the optimal genotype in multiples of the non-optimal genotype’s fitness, i.e.,  $h$  indicates the degree of selection pressure.  $p$  denotes the probability that a non-optimal

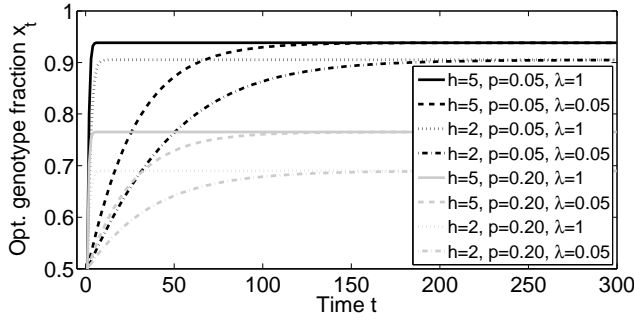


Figure 4: The fraction of optimal genotypes in a simple evolution model over time (Eq. 7). Mutation  $p$  and selection pressure  $h$  determine the mutation-selection-balance (quasi-species formation). Generation turnover  $\lambda$  has no influence in the long run.

genotype mutates to the optimal one, and the same for back-mutation. If reproduction is linear-proportional to fitness, evolutionary dynamics are described by a difference equation, that predicts the increase of the fraction of optimal genotypes over time,

$$x_{t+1} = (1-p) \frac{hx_t}{hx_t + (1-x_t)} + p \frac{1-x_t}{hx_t + (1-x_t)} = \frac{(1-p)hx_t + p(1-x_t)}{hx_t + (1-x_t)}. \quad (6)$$

In absence of mutation ( $p = 0$ ) only the current fraction of optimal genotypes ( $x$ ) and the selection pressure  $h$  determine the composition in the next time step. However, with mutation ( $p > 0$ ) genotypes mutate *to* and *away* from the optimum. Now we include the effect of a reduced generation turnover in the difference equation. If  $\lambda$  denotes the relative generation turnover (the percentage of individuals that are replaced, i.e., in our model  $\lambda = 1/L$ ), we obtain

$$x_{t+1} = (1-\lambda)x_t + \lambda \frac{(1-p)hx_t + p(1-x_t)}{hx_t + (1-x_t)}. \quad (7)$$

Figure 4 shows how, according to Equation 7, the fraction of optimal genotypes evolves over time for different parameters. A lower generation turnover  $\lambda$  leads to a slowed convergence, i.e., slower loss of diversity and later formation of the quasi-species, but has no influence on the mutation-selection-balance. Only mutation  $p$  and selection pressure  $h$  determine the mutation-selection-balance. A low fraction of optimal genotypes  $x$  after formation of the quasi-species can be interpreted as higher diversity, thus a small  $h$  (a smooth fitness landscape), leads to a higher quasi-species diversity. The conclusion that follow from this analysis are summarized in Figure 5. Notice that this model does not account for finite population effects.

Both concepts, diversity and quasi-species, play an important role in the analysis of the following simulation studies.

#### 4.1 Influence of Individual Adaptation on Diversity (Environment 1)

We investigate the influence of lifetime on diversity with a simulation study in Environment 1 which is visualized in Figure 6 and can be formally defined as

$$f_1(z, t) = e^{-z^2}. \quad (8)$$

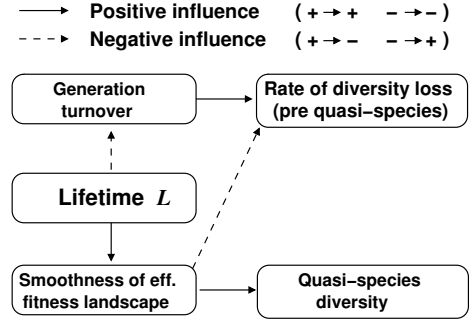


Figure 5: An increase in lifetime causes a decrease in the rate of diversity loss and an increase in quasi-species diversity.

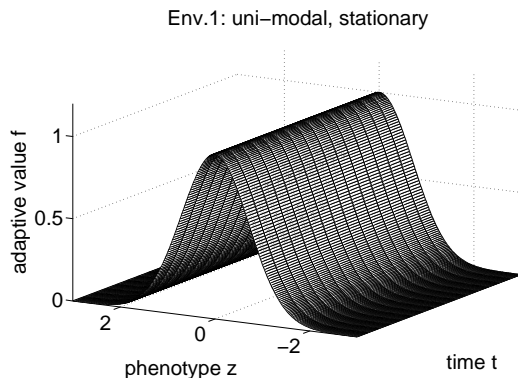


Figure 6: Environment 1: A uni-modal, stationary Gaussian function.

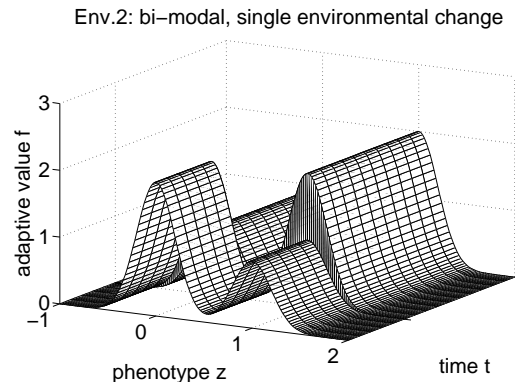


Figure 7: Environment 2: A uni-modal Gaussian function, where the optimum moves from 0 to 1 at time 1000.

$f_1$  is a Gaussian function centered at  $z = 0$ . Environment 1 is stationary, i.e., the mapping from  $z$  to  $f$  is independent of  $t$ . In the following simulations the population is initially distributed uniformly on  $[-2; 2]$ . Figure 8 shows the population dynamics of typical evolutionary runs. Each of the thick black dots represents the genotype of one individual at a time, each of the thin gray dots represents a phenotype. Notice that for this visualization we reduced the population size to 100.

With a lifetime of  $L = 1$ , i.e., pure population adaptation, the population quickly converges to a stable state which is known as *quasi-species*. With a lifetime of  $L = 1$ , the quasi-species formation takes only about 5 time units. In case of  $L = 20$ , i.e., coupled population-individual adaptation, it takes far longer and the quasi-species is less stable. After 500 time units the diversity seems to be slightly higher with coupled population-individual adaptation than with pure population adaptation. From these observations we derive the following hypotheses:

1. Higher lifetime slows the speed of genotypic diversity loss.
2. Higher lifetime increases quasi-species diversity.

A second simulation study confirms these hypotheses. Figure 9 shows how (Simpson) diversity<sup>3</sup> averaged over 500 independent evolutionary runs evolves over time. The thin black line shows the average genotype (equals phenotype) diversity in case of pure population adaptation ( $L = 1$ ). The case of coupled population-individual adaptation ( $L = 20$ ) is denoted with a thick black line showing the average genotype and a thick gray line showing the average phenotype diversity, respectively. The trajectory resulting from an additional experiment is shown as dashed line. In this additional experiment, all individuals had a lifetime of  $L = 20$  but individual lifetime adaptation was disabled, thereby avoiding the smoothing of the effective fitness landscape (Hiding effect). Thus, an individual's phenotype value was equal to its genotype throughout its lifetime. This additional experiment allows to separate the influence of reduced generation turnover and fitness landscape smoothing (cf. beginning of this Section).

From Figure 9, we can see that with a higher lifetime ( $L = 20$ ), the rate of genotypic diversity loss is indeed lower than with pure population adaptation (compare the slopes of the thin and the thick black lines). The extent to which this is caused by the reduced generation turnover is

<sup>3</sup>cf. Equation 5. Notice that for the Simpson index ( $H$ ) the space is discretized into partition classes  $(-\infty; -3], (-3; -2.75], (-2.75; 2.5], \dots, (2.75; 3], (3; +\infty)$ .

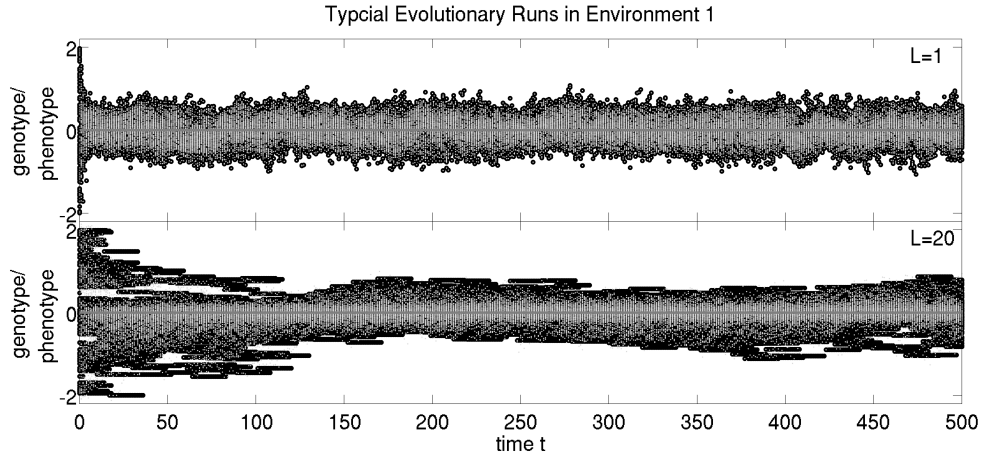


Figure 8: Adaptational dynamics of a typical evolutionary run in Environment 1 in case of pure population adaptation (lifetime  $L = 1$ , top panel) and coupled population-individual adaptation (lifetime  $L = 20$ , bottom panel). Each of thick black dots represents the genotype of one individual (out of a population of 100 individuals) at a time, each of the thin gray dots represents a phenotype.

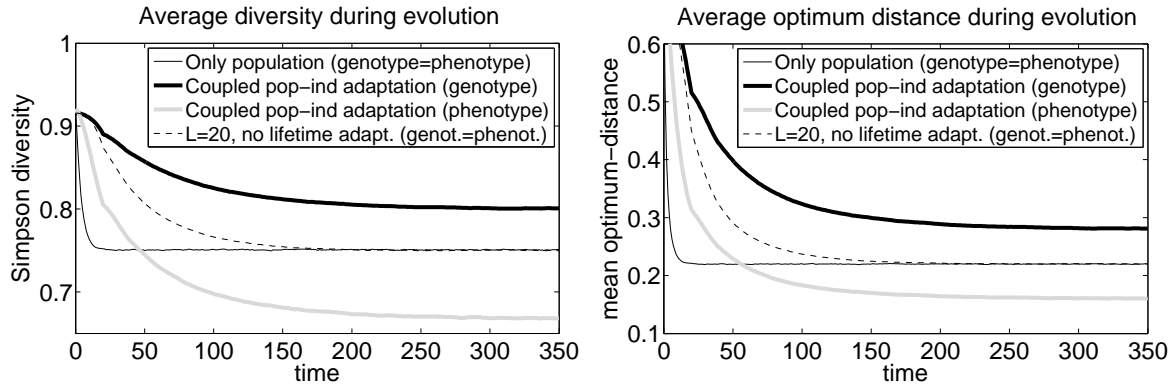


Figure 9: Evolution in Environment 1. Left panel: Comparing the average diversity evolution in environment 1 in case of *pure population adaptation* ( $L = 1$ ) and *coupled population-individual adaptation* ( $L = 20$ ). Coupling population and individual adaptation causes a slower genotypic diversity loss (compared to pure population adaptation). Coupled population-individual adaptation also results in a higher genotypic quasi-species diversity and a lower phenotypic quasi-species diversity than pure population level adaptation. Right panel: Mean distance to the optimum. After formation of the quasi-species, the population with coupled population-individual adaptation has on average a smaller phenotype distance to the optimum but a larger genotypic distance.

represented by the difference between the thin black line and the dashed line. The extent to which the increased rate of genotypic diversity loss is caused by the smoothing of the effective fitness landscape is represented by the difference between the slopes of the dashed line and the thick black line.

Meanwhile, we notice that a higher lifetime ( $L = 20$ ) leads to a more diverse quasi-species (the average time of the formation of a quasi-species - all curves remain more or less constant - is around 15 in case of  $L = 1$  and 300 in case of  $L = 20$ ). The explanation for the higher quasi-species diversity is that  $L$  causes a smoothing of the effective fitness landscape that shifts the mutation-selection balance.

Although the phenotype is strongly dependent on the genotype, phenotypic diversity is much lower here. An explanation for this finding is that genetically different individuals may adapt to a similar phenotype during lifetime which directly reduces phenotypic quasi-species diversity. The latter argument is further supported by additional simulation results presented on the right panel of Figure 9, where the population mean distance, again averaged over 1000 independent simulation runs, to the genotypic and phenotypic optima, respectively, is shown. The population with coupled population-individual adaptation has on average a smaller phenotype distance to the optimum despite a larger genotypic distance.

Contrary to this findings, the experimental results in (Curran & O’Riordan, 2006) showed that a population with individual level adaptation (cultural learning) can have a higher *phenotypic* diversity than a population that does not employ individual level adaptation. However, Curran and O’Riordan (2006) come to the same conclusion as our study, with regard to *genotypic* diversity, namely, that a population employing coupled population and individual level adaptation maintains a higher genotypic diversity than one with pure population level adaptation. Thus, it is likely, that in the simulation model of (Curran & O’Riordan, 2006) individual adaptation (cultural learning), reduces the genotypic (respectively innate) diversity of a population less than in our model. Furthermore, since in (Curran & O’Riordan, 2006) genotype and phenotype were represented in different domains, the authors had to employ different diversity indices for genotype and phenotype level which prohibits a direct comparison of genotypic and phenotypic diversity.

To summarize, an increase in the degree of individual level adaptation ( $L$ ), a) slows down the loss of genotypic diversity, and b) causes a higher genotypic quasi-species diversity, but a lower phenotypic quasi-species diversity.

With regard to exploration, a high diversity is desired, however, with regard to exploitation a high adaptation velocity (loss of diversity) is desired. The following section shows how exploration and exploitation are affected by an increase in individual level adaptation.

## 4.2 Influence of Individual Adaptation on Exploration and Exploitation (Environment 2)

Figure 7 shows Environment 2 which is defined by the time-dependent adaptive value function  $f_2$ ,

$$f_2(z, t) = h e^{-\left(\frac{z - z_{\text{opt}}(t)}{\sigma_{\text{opt}}}\right)^2} + e^{-\left(\frac{z - (1 - z_{\text{opt}}(t))}{0.25}\right)^2}, \text{ with } h > 1, \quad (9)$$

$$\text{and } z_{\text{opt}}(t) = \begin{cases} 0, & \text{if } t < 10000 \\ 1, & \text{else,} \end{cases}$$

where  $h$  is a height factor that determines the difference of relative adaptive value between local and global optima. For instance,  $h = 2$  means the global optimum is twice as high as the local optimum. This environment is designed in such a way that the basins of attraction of the two optima have

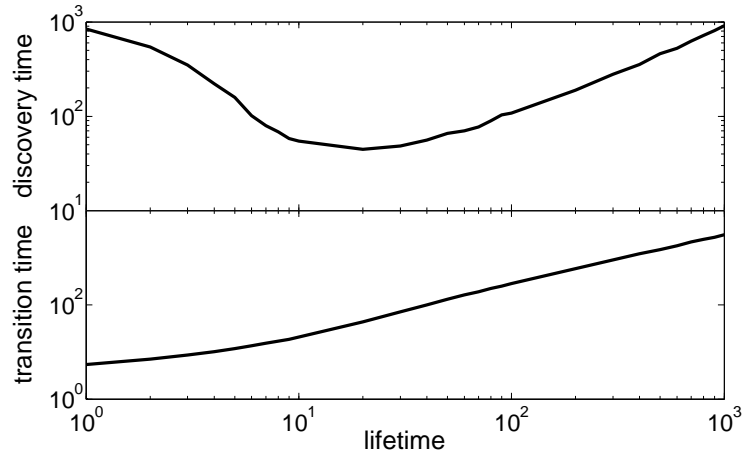


Figure 10: Evolutionary dynamics in Environment 2. The discovery time is an indicator for exploration, where transition time indicates exploitation ability. The discovery time, and the transition time, averaged over 1000 evolutionary runs, suggest that there exists a non-trivial optimal lifetime with regard to the exploration-exploitation balance.

an equal size between the optima, i.e., in the interval  $[0; 1]$ . This is realized by adjusting  $\sigma_{\text{opt}}$  with respect to  $h$ . The respective  $\sigma_{\text{opt}}$  can be derived numerically (we omit the technical details here). In this environment the adaptive value function changes only a single time in  $t = 10000$ . Then, the global optimum changes from 0 to 1 where it remains for the rest of the simulation time. The population is expected to form a quasi-species state around the optimum 0 well before  $t = 10000$ . The evolutionary dynamics immediately after the change at  $t = 10000$  provides insights into how the balance between population and individual level adaptation affects exploration and exploitation in this model.

The population dynamics in Environment 2 is investigated with the following experiment. For a range of constant lifetime settings, evolution was run for 1000 times and in each evolutionary run we measured the following two performance indicators:

- *Discovery time*: The time the population needs to reach the interval  $[0.5; 1.5]$  with at least one individual after the environmental change, i.e., the time needed to *discover* the neighborhood of the global optimum. The discovery time can be seen as an indicator for the exploration ability.
- *Transition time*: The time the population needed to populate the neighborhood of the global optimum (interval  $[0.5; 1.5]$ ) after the discovery with at least 50 percent of the population. The transition time can be seen as an indicator for the exploitation ability.

Figure 10 shows the two properties for the tested range of lifetime settings.

The discovery time is first decreasing with an increasing lifetime. This is due to an increase in genotypic quasi-species diversity (cf. Section 4.1). The larger the diversity, the more likely it is to discover a neighboring optimum. When the lifetime increases further, the discovery time starts to increase at some point. This phenomenon can be explained as follows: Despite a further increase in genotypic quasi-species diversity, the generation-turnover decreases with increasing lifetime, thus reducing the number of “trials” to find the new optimum. The latter effect seems to be stronger than the former for large lifetimes and vice versa. The discovery time is an indicator for exploration.

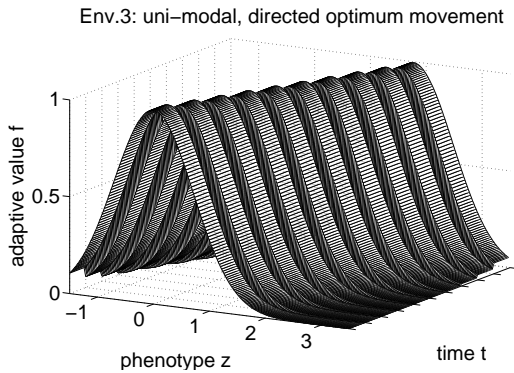


Figure 11: Environment 3: A unimodal Gaussian function that moves gradually in positive  $z$  direction, where  $T$  (the length of the change interval) determines the velocity of this movement.

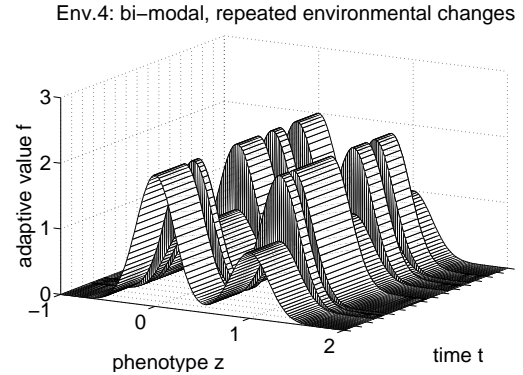


Figure 12: Environment 4: The mapping from phenotype to adaptive value at a time is identical to Environment 2, however, in Environment 4 the optimum changes *periodically* with an expected *change interval* of length  $T$ .

The transition time increases monotonically with the lifetime. This is due to the decreasing generation-turnover, i.e., the less individuals are replaced the longer it takes to populate the new optimum. The transition time is a measure for exploitation.

If the environment changes periodically, the interplay between discovery (exploration) and transition (exploitation) determines the overall adaptation success of the population, as the following section will show.

## 5 Existence of An Optimal Balance

In this section, we present simulation results of the model in Environments 3 and 4. We show that for Environment 3, the optimal adaptation is achieved when no individual level adaptation is included. An increasing degree of individual level adaptation which consequently decreases the population level adaptation, deteriorates the whole adaptation capability of the population. In contrast, we show that for Environment 4, increasing individual level adaptation at the expense of population level adaptation first brings about an adaptational advantage. However, with too much individual level adaptation, this advantage vanishes which means that there exists an optimal balance between population and individual level adaptation.

### 5.1 Pure Population Level Adaptation is Optimal (Environment 3)

Figure 11 shows Environment 3, that is defined by the time-dependent adaptive value function  $f_3$ ,

$$f_3(z, t) = e^{-(z - z_{\text{opt}}(t))^2} \quad \text{with } z_{\text{opt}}(t) = 0.2 \lfloor t/T \rfloor . \quad (10)$$

The uni-modal function that maps phenotype to adaptive value moves gradually in positive  $z$  direction where  $T$  (the length of the change interval) determines the velocity of this movement.

The following experiment demonstrates that pure population adaptation is the best adaptation strategy in Environment 3. For three different settings of the change interval,  $T \in \{1, 10, 100\}$ , representing rapidly changing, moderately changing, and slowly changing environments, we compare the two different settings  $L = 1$ , representing pure population adaptation, and  $L = 20$ , representing coupled population-individual-level adaptation. Figure 13 shows the population mean adaptive



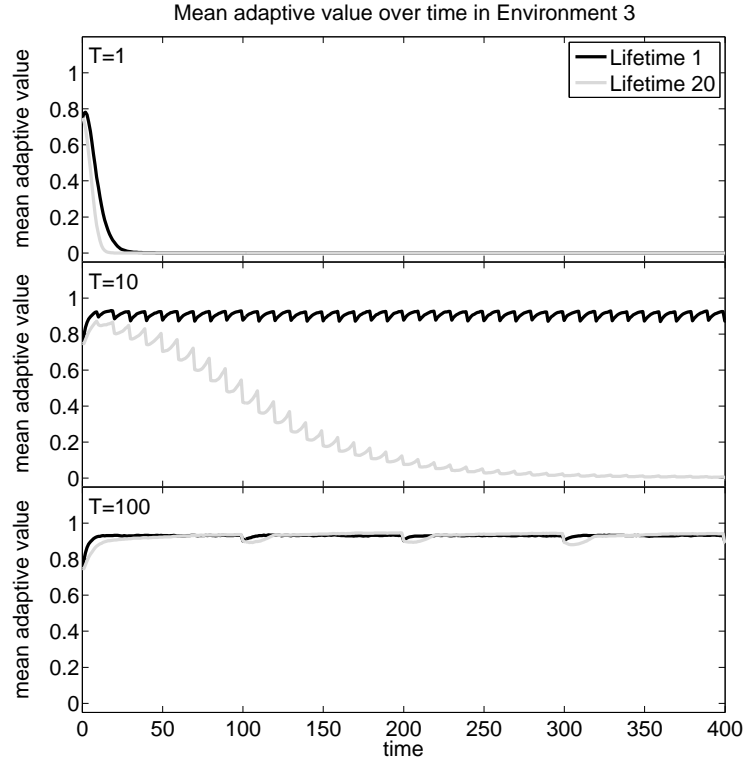


Figure 13: Evolution of the population mean adaptive value in Environment 3 for selected settings. If the environment is changing too quickly ( $T = 1$ ), neither of the populations (with  $L = 1$  and  $L = 20$ ) can maintain a high mean adaptive value. However, for an intermediate change rate ( $T = 10$ ), the population with pure population adaptation ( $L = 1$ ) has an advantage.

value, averaged over 100 independent simulation runs, for the first 400 time units of evolution. In the rapidly changing environment where the change interval equals 1, the population mean adaptive value is going down to zero quickly in both settings  $L = 1$  and  $L = 20$ , although slower in case of  $L = 1$ . On the contrary, in the slowly changing environment with change interval 100 a high mean adaptive value level of the population is maintained for both  $L = 1$  and  $L = 20$ . However, in the environment with an intermediate change velocity (change interval 10) the population mean adaptive value is decreasing in case of coupled population-individual-level adaptation with  $L = 20$  while it remains at a high level with pure population adaptation at  $L = 1$ .

The explanation is straight-forward: If the environment changes slowly ( $T = 100$ , bottom panel in Figure 13) both adaptation strategies (pure population adaptation with  $L = 1$  and coupled population-individual level adaptation with  $L = 20$ ) allow to follow the monotonic movement of the optimum, although small differences in the rate of adaptation to the population with  $L = 1$  produces a slightly better adaptive behavior. In the environment with an intermediate change velocity (change interval 10, middle panel in Figure 13) the population mean adaptive value is decreasing in case of coupled population-individual-level adaptation with  $L = 20$  while it remains at a high level with pure population adaptation at  $L = 1$ . This means, that at some change velocity above  $T = 10$ , the coupled population-individual level adaptations strategy fails, i.e., the population can not follow the moving optimum. If the dynamics are monotonic as in this example, pure population adaptation is the best adaptation strategy. A higher degree of (lifetime-included) diversity is not needed for adaptation, and is actually detrimental because of its negative side-

effects on the exploitation of a new optimum. If the environment changes even quicker as in case of  $T = 1$  (top panel in Figure 13) neither of the two adaptation strategy allows to follow the optimum, although with pure population adaptation, the optimum is lost later.

## 5.2 Intermediate Degree of Individual Adaptation is Optimal (Environm. 4)

Figure 12 shows Environment 4 which is defined by the time-dependent adaptive value function  $f_4$ ,

$$f_4(z, t) = h e^{-\left(\frac{z - z_{\text{opt}}(t)}{\sigma_{\text{opt}}}\right)^2} + e^{-\left(\frac{z - (1 - z_{\text{opt}}(t))}{0.25}\right)^2}, \text{ with } h > 1, \quad (11)$$

$$\text{and } z_{\text{opt}}(t) = \begin{cases} 0, & \text{if } (z_{\text{opt}}(t-1) = 1 \wedge X_{\text{Uni}[0;1]} < \frac{1}{T}) \vee \\ & (z_{\text{opt}}(t-1) = 0 \wedge X_{\text{Uni}[0;1]} \geq \frac{1}{T}) \\ 1, & \text{else,} \end{cases}$$

where  $X_{\text{Uni}[0;1]}$  is a random number drawn from a uniform probability distribution on the interval  $[0; 1]$ . In Environment 4, the mapping from phenotype to adaptive value at a time is identical to Environment 2, however, in Environment 4 the optimum changes *periodically* with an expected *change interval* of length  $T$ . The actual time between changes is uniformly, stochastically distributed and can vary strongly.

The following experiment investigates the evolutionary dynamics in this environment for a height factor of  $h=2$  and a height factor of  $h = 5$  with a range of constant lifetimes for the environmental change intervals 20, 50, 100, 200. The genotype population is initially distributed uniformly on  $[-0.5; 1.5]$ . The overall adaptation quality is assessed by measuring the mean population fitness over time and over 200 independent evolutionary runs. The results are shown in Figure 14.

From these results, we see that the slower the environmental change, the higher is the mean adaptive value for the population. For a height factor of 2 (left panel), the optimal lifetime is around  $L = 75$  for an expected change interval of  $T = 200$ , however, for change intervals lower than that ( $T \in \{20, 50, 100\}$ ), the optimal lifetime is at the boundary of the tested range ( $L = 1000$ ). There seems to be a threshold for the rate of environmental change below which an intermediate lifetime is optimal. For a height factor of 5 (right panel), this threshold lies between an expected change interval of 20 and 50. For a change interval of  $T = 20$ , a maximally high lifetime  $L > 1000$  is optimal, for slower changing environment  $L = 25$  (in case of  $T = 50$ ) and  $L = 30$  (in case of  $T = 100$  and  $T = 200$ ) is optimal. The existence of a threshold for the rate of environment change below which an intermediate lifetime is optimal has been confirmed in several other settings of  $h$ .

Figure 15 shows the population dynamics of typical runs in Environment 4 for the non-trivial optimal balance between population and individual level adaptation. As an example, we study the case when the height factor equals 5 and the change interval is set to 200, corresponding to the dotted line in the right panel of Figure 14. Figure 15 shows four different degrees of individual level adaptation for this setting, a low degree of individual level adaptation ( $L = 1$ ) which produces a rather low mean adaptive value, an intermediate degree of individual level adaptation ( $L = 30$ ) which produces approximately the maximum mean adaptive value and high degrees of individual level adaptation ( $L = 200$  and  $L = 1000$ ) which produce rather low mean adaptive values. The thick gray line shows the trajectory of the global optimum, the thick black dots shows the genotype values, and the smaller gray dots show the phenotype values present in the population at a time.

With  $L = 1$  (pure population adaptation) the population quickly converges to the global optimum. The population maintains diversity with mutation-selection balance, however, this degree of diversity is not sufficient to discover another global optimum. This shows that the discovery

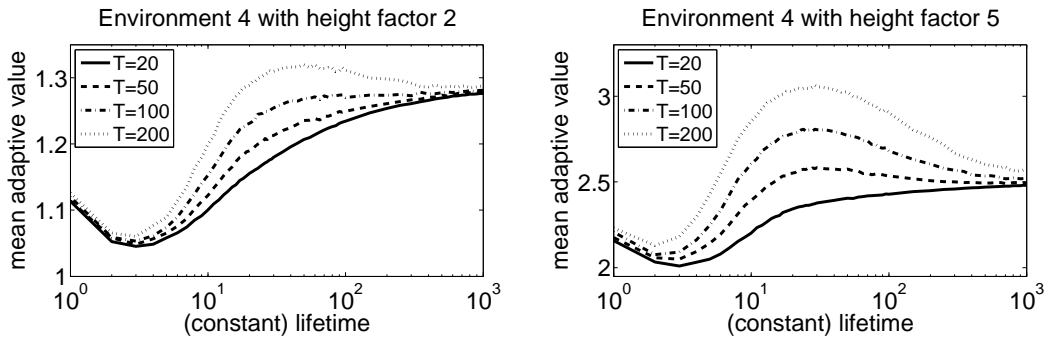


Figure 14: Mean adaptive value for different constant lifetimes in Environment 4 for change intervals  $T \in \{20, 50, 100, 200\}$  and height factors 2 (left panel) and 5 (right panel), respectively. There exists an optimal lifetime that depends environmental dynamics and height differences between local and global optimum.

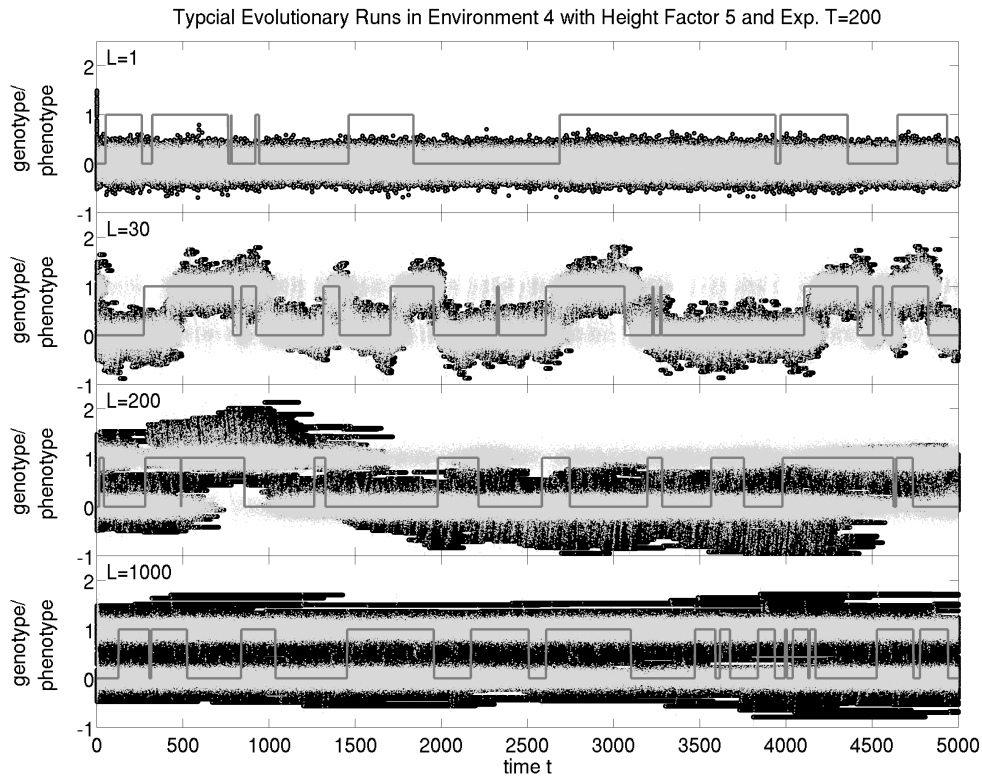


Figure 15: Typical evolutionary runs in Environment 4. The thick gray line shows the global optimum, the thick black dots shows the genotype values, and the smaller gray dots show the phenotype values present in the population at a time. With  $L = 1$  (pure population adaptation) the population only occasionally discovers a new global optimum. For long lifetimes  $L = 200$  and  $L = 1000$  the population is not flexible enough to move the majority of individuals to the current global optimum before the next environmental change. Only in the intermediate case of  $L = 30$ , a good balance between exploration and exploitation is achieved, and as a consequence, the population follows the environmental dynamics.

time is too long for the given dynamics. In some other evolutionary runs, a population transition occurred occasionally. Next, we consider the cases  $L = 200$  and  $L = 1000$ .

With a high degree of individual level adaptation ( $L = 200$ ), population adaptation has only weak influence on the overall adaptation process. The genotypes (black dots) remain relatively wide-spread in genotype space and individuals are able to adapt to one of the two optima during the lifetime. Due to the high degree of diversity maintained throughout the simulation time, discovery time is very short. The transition time, however, is too long to move the majority of individuals to the current global optimum before the next environmental change. With  $L = 1000$  this is even more evident: Because of the extremely low generation turnover, selection takes place rarely in this case, and population adaptation is practically disabled.

However, in the intermediate case of  $L = 30$ , the population follows the environmental dynamics successfully. Individual and population level adaptation is well balanced. As a result, it is possible for the population to discover a new optimum after an environmental change and to transit to the new optimum in a relatively short period of time. This gives the population an adaptational advantage over the populations with a too low or too high degree of individual level adaptation.

The example of Environment 4 has shown that there exist dynamic environments in which adding individual level adaptation to the population can result in better overall population adaptation. However, too much or too little individual level adaptation results in worse population adaptation.

### 5.3 Summary

Shifting the balance between population and individual adaptation influences the exploration-exploitation balance. What balance between exploration and exploitation is optimal depends on the type of environmental dynamics and the frequency of environmental change.

In Environment 3 which is an example of monotonic dynamics, pure population adaptation is the best adaptation strategy. In such environments, diversity is not needed for adaptation, and actually, diversity is detrimental because of its negative side-effects on the exploitation of a new optimum.

In Environment 4 which is an example of an environment where fitness valleys need to be crossed, however, a coupling of population and individual level adaptation produced an adaptational advantage. An intermediate degree of individual adaptation was optimal here in the case of moderate environmental change rate. The intermediate degree of individual level adaptation allowed to maintain a sufficiently high degree of diversity, but the transition to a new optimum was still possible in a reasonable time. If Environment 4 changes too quickly to allow discovery of a new optimum *and* transition to it, a large lifetime is the optimal adaptation strategy.

## 6 Evolution of the Optimal Degree of Individual Adaptation

The previous Section has shown that there is a potential advantage of coupling population and individual level adaptation in dynamic environments even if the cost of individual adaptation is fully accounted for. Unlike the Baldwin effect, the positive coupling effects observed here can only be found in dynamic environments. In nature this balance can not be set externally, instead it is either constrained by natural laws, an emergent property of the evolution, or a mix of both. Similarly, in computational evolution the optimal balance between population and individual levels may not be known in advance and it is then desired that the right balance is found in a self-organizing way. In the following, we will show under what conditions a near-optimal overall adaptation behavior can evolve. Note that this requires a second-order adaptation process.

## 6.1 Extension of the Analysis Model

The analysis model used in this section is an extended version of the one introduced in Section 3, where an individual was formally defined in Equations 1 to 4. Individual lifetime  $L$  is the central parameter that determines the distribution of population and individual level adaptation. In the extended model  $L$  is now individually encoded in the genotype. Thus the 3-tuple in Equation 1 becomes the 4-tuple  $I = (x, z, t_b, L)$  and the process of (asexual) reproduction of an offspring  $I'$  from a parent  $I$  at time  $t$

$$(I, t) = ((x, z, t_b, L), t) \mapsto (x', x', t, L') = I' , \quad (12)$$

where  $x'$  is calculated according to Equation 2, and the offspring's lifetime  $L'$  is calculated as

$$L' = \begin{cases} L + 1, & \text{if } 0.00 \leq X_{\text{Uni}[0;1]} < 0.05 \\ L - 1, & \text{if } 0.05 \leq X_{\text{Uni}[0;1]} < 0.10 \wedge L > 1 \\ L & , \text{ else} \end{cases} , \quad (13)$$

where  $X_{\text{Uni}[0;1]}$  is a random number drawn from a uniform probability distribution on the interval  $[0; 1]$ . Thus, individual's lifetime  $L$  is now subject to mutation and selection, and evolution can select on the trade-off between population and individual level adaptation.

## 6.2 An Initial Experiment of Lifetime Evolution

We apply the extended model to Environment 4 as defined in Equation 11 with a change interval of  $T = 200$ . Adaptation step-sizes are again set to  $\sigma_G = \sigma_P = 0.01$ . Recall that the optimal balance between population and individual level adaptation has been found to be a lifetime around  $L = 30$ .

According to the formal definition in Section 6.1 the lifetime is encoded in the genotype of each individual. In the initial population the lifetimes are assigned randomly to the individuals with respect to a uniform probability distribution over  $[1; 5]$ , lifetime mutation is realized according to Equation 13.

Figure 16 shows the result of the first 100000 time-steps of 30 independent simulation runs. The left panel shows the evolution of population mean lifetime, averaged over the 30 simulation runs with error-bars. The right panel shows the corresponding standard deviation of the lifetime within the population, again averaged over the 30 simulation runs with error bars. The mean lifetime increases to a value far beyond the optimal lifetime of 30 and seems to grow infinitely. The variation of lifetime within the population is relatively small (see right panel).

Apparently, the optimal lifetime does not evolve in a higher-order adaptation process. How can the infinite growth of lifetime be explained?

To answer this question, we assume in the following that a population of  $n$  individuals with genotypes  $\{x_i\}_{i=1\dots n}$  and lifetimes  $\{L_i\}_{i=1\dots n}$  is given whose corresponding phenotype (that changes over time) has on average an adaptive value of  $w(x_i)$ ;  $\bar{L}$  denotes the mean lifetime of all individuals in the population. The average number of perished individuals is  $n/\bar{L}$ , and the average expected number of offspring of individual  $x_i$  at a time,  $r(x_i)$ , can be calculated as

$$r(x_i) = \frac{n}{\bar{L}} \frac{w(x_i)}{\sum_{j=1}^n w(x_j)} = \frac{n}{\bar{L}} \frac{w(x_i)}{n\bar{w}(x)} = \frac{w(x_i)}{\bar{L}\bar{w}(x)} , \quad (14)$$

where  $\bar{w}$  is the mean adaptive value of the population. The expected number of offspring of individual  $x_i$  over its entire lifetime,  $R(x_i)$ , is given by

$$R(x_i) = \frac{L_i}{\bar{L}} \frac{w(x_i)}{\bar{w}(x)} . \quad (15)$$

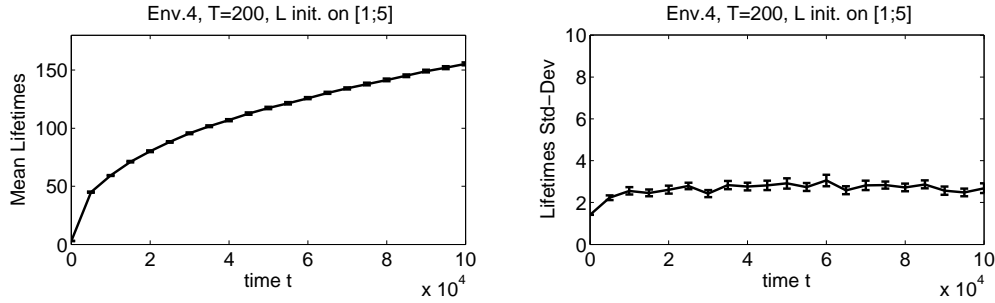


Figure 16: Evolution of lifetime in Environment 4 with expected change interval 200 and height factor 5. The optimal lifetime with respect to mean population adaptive value is around 30 for this setting. Simply encoding lifetime parameter  $L$  leads to an unbounded increase of the average lifetime.

This equation shows that the expected number of offspring increases with the lifetime. In other words, individuals with a longer lifetime have an implicit reproductive advantage, because they have more opportunities to produce offspring. Thus, in a long run individuals with extremely long lifetimes overwhelm. Extremely long lifetimes are not only biologically infeasible but are also disadvantageous with respect to overall population adaptation, as we have shown earlier.

The evolution of a very long lifetime can be attributed to the fact that there exists no *individual* trade-off between average reproduction probability and the lifetime of individuals. In nature such a trade-off does exist as discussed in the Introduction. In the following, we show how a trade-off between reproduction and lifetime can be implemented in our simulation model and how this trade-off influences the evolution of lifetime.

### 6.3 Lifetime Evolution with a Trade-Off between Reproduction and Lifetime

In the previous section we have shown that the reproductive advantage increases with lifetime in absence of a negative effect of lifetime on reproduction (Equation 15). In order to neutralize this undesired effect we introduce a trade-off between average reproduction probability and lifetime. Lifetime  $L_i$  reduces the probability to reproduce as follows,

$$w_L(x_i) = \frac{w(x_i)}{L_i} , \quad (16)$$

where  $w_L$  is the new basis of selection. The corresponding expected number of offspring,  $R_L$ , becomes

$$R_L(x_i) = \frac{L_i w_L(x_i)}{\bar{L} \bar{w}_L(x)} = \frac{w(x_i)}{\bar{L} \bar{w}_L(x)} , \quad (17)$$

where  $\bar{w}_L(x)$  denotes the population mean with respect to  $w_L(x)$ . Equation 17 shows that the expected number of offspring is independent of the individual lifetime  $L_i$ .

#### Evolution of the Optimal Lifetime in Environment 4

With this model modification, simulated evolution was run once again for Environment 4 under otherwise identical conditions as in Section 6.2. The result is presented in the top-row panels of Figure 17. Now, an average lifetime between 30 and 35 evolves which is close to the optimal lifetime of 30 as found in the experiment with Environment 4 (Section 5.2) where the lifetime was predefined and kept constant during evolution. In a follow-up experiment the population starts to evolve with

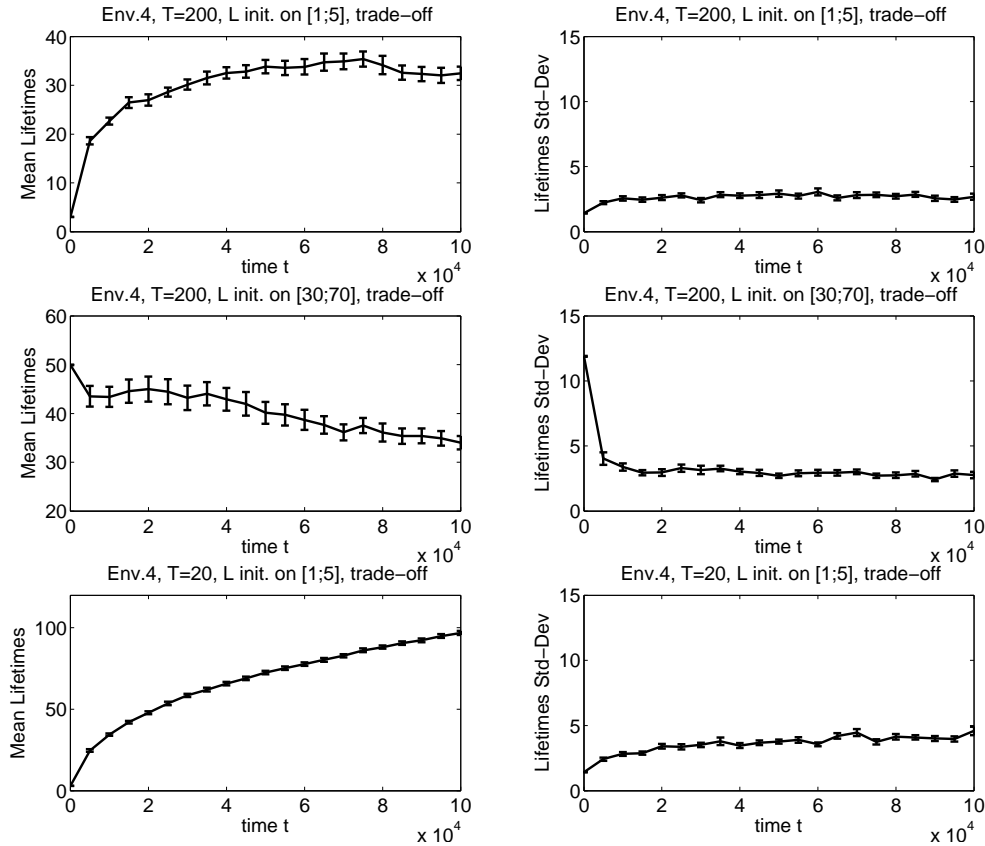


Figure 17: Evolution of lifetime in Environment 4 with a trade-off between reproduction and lifetime. A near-optimal lifetime evolves in a higher-order adaptation process (around 30 in the settings that correspond to the panels in the two top rows) independent on the distribution of lifetimes in the initial population. Also, if the optimal lifetime is very large as in the case that corresponds to the bottom-row panels, the population evolves a mean lifetime towards the optimum (at a change interval of 20, cf Figure 14).

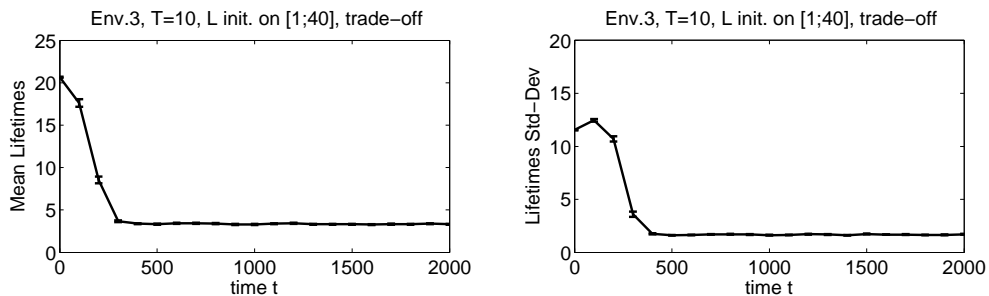


Figure 18: Evolution of lifetime in Environment 3 with an expected change interval 10 and a height factor 5. The optimal lifetime with respect to mean population adaptive value is  $L = 1$  for this setting, i.e., pure population adaptation. A near-optimal lifetime indeed evolves.

lifetime randomly initialized on  $[30; 70]$  (according to a uniform probability distribution, i.e., with an average lifetime of 50). The result is shown in the middle-row panels of Figure 17. Again, the population evolves a near-optimal lifetime.

In the third experiment with the model that incorporates the trade-off, the population is again initialized with lifetimes uniformly distributed on  $[1; 5]$ , however, now the environment changes on average every 20 time units. The result is presented in the bottom-row panels of Figure 17. Now, the average population evolves a lifetime of 100 during the first 100000 time steps of evolution and even longer lifetimes in succeeding time steps (not shown). This corresponds to the findings of Section 5.2 where a very long lifetime turned out to be optimal if the environment changes with an expected change interval of 20.

For all experiments we also show the variation of the lifetime present in the population (measured as standard deviation, see panels in the right column of Figure 17). The variation is low in all experiments, indicating that there is a stable population movement towards the optimal lifetime, and that the population mean lifetime (shown in the panels of the left column) do not “average out” the actual population dynamics.

### Evolution of the Optimal Lifetime in Environment 3

Finally, we look at the evolution of lifetime in Environment 3. There, the adaptational challenge was to follow a quickly moving optimum. We found that population adaptation alone, i.e.,  $L = 1$  is the best adaptation strategy for this dynamics (cf. Figure 13). Figure 18 shows the evolution of lifetime in Environment 3 with an environmental change interval of 10. We see that in this example as well, evolution finds a near-optimal degree of population-level adaptation (near  $L = 1$ ).

## 7 Summary and Discussion

A trade-off between population and individual level adaptation, where the cost of individual level adaptation is taken into account, is evident not only in biological but also in computational evolutionary systems. In this paper, we presented a simulation model that allows to distribute a given amount of adaptation effort between individual and population level adaptation. Shifting the balance between population and individual adaptation influences the exploration-exploitation balance.

Using computer simulations we have shown that in an environment with monotonic dynamics (Environment 3), pure population adaptation is the best adaptation strategy. In such environments diversity is not needed for adaptation and can actually be detrimental because of its negative side-effects on the exploitation of a new optimum.

In contrast, in another environment (Environment 4), where the population has to cross fitness valleys repeatedly, we have shown that increasing the degree of individual level adaptation, thereby allowing the maintenance of a higher degree of diversity necessary for exploration, is of adaptational advantage. If, however, the degree of individual level adaptation increased further which further increases the diversity, exploitation capability will be weakened. In this case, the population is able to discover a new optimum, but is not able to exploit it before the environment changes again. Thus, an intermediate degree of individual level adaptation which allows for a balance between exploration *and* exploitation of a new optimum, is the optimal adaptation strategy. We believe that this finding is not limited to environments in which the global optimum switches between only two values, because in the case where an intermediate lifetime was optimal, the transition from the old to the new optimum occurred mostly after quasi-species formation, i.e., at a time when the population has completely moved to one optimum and has “forgotten” the old one.



To investigate if the optimal balance between individual and population level of adaptation evolves, we extended the simulation model, where the lifetime was also genetically encoded, allowing evolution to self-organize the distribution of population and individual level adaptation. However, without considering an individual's trade-off between lifetime and reproduction, an infinitely increasing lifetime evolved. We then revised our model further to incorporate an individual trade-off between lifetime and reproduction which is biologically more plausible. With this revised model, we could observe the (second-order) evolution of a near optimal distribution of population and individual level adaptation.

Our study has investigated the evolution of a distribution of population and individual level adaptation purely from the adaptational advantage point of view, though in nature, other factors and constraints may also play a role. Nevertheless, we believe that our findings are inspiring in understanding natural evolution, as well as in inspiring new ideas in the field of artificial evolutionary systems, where the adaptation of the exploration-exploitation balance to changing conditions is of crucial importance.

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