# On the Adaptive Disadvantage of Lamarckianism in Rapidly Changing Environments

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**Abstract.** Using a simple simulation model of evolution and learning, this paper provides an evolutionary argument why Lamarckian inheritance - the direct transfer of lifetime learning from parent to offspring - may be so rare in nature. Lamarckian inheritance allows quicker genetic adaptation to new environmental conditions than non-lamarckian inheritance. While this may be an advantage in the short term, it may be detrimental in the long term, since the population may be less well prepared for future environmental changes than in the absence of Lamarckianism.

## 1  Introduction

Natural selection to a first approximation operates with variation that is undirected [1]. Lamarck suggested that the results of lifetime learning could be directly passed on to ones offspring [2]. When would we expect directed variation or inheritance of acquired characters to occur? Recent work reveals a range of mechanisms capable of sustaining heritable epigenetic variation [3], phenotypic memory [4] and neo-Lamarckian inheritance [5], for example: mutational hotspots and adaptive mutations occurring during bacterial stress [6] , chromatin marks that control differentiation in multicellular organisms [7], RNA silencing allowing potential influence by somatic RNA on germ line gene expression [8], inheritance of immune system states by antibody transfer in breast milk [9], and behavioural and symbolic inheritance systems such as food preference, niche construction traditions and all information transmission dependent on language [3]. By these mechanisms, Lamarckian inheritance can occur without breaking the central dogma, i.e. without sequence information having to pass from protein to DNA [10]. In the case of immune system, behavioural and symbolic inheritance systems, information need not be passed from soma to germ line either [11].

So, directed variation is possible, but is it always advantageous to inherit characteristics acquired by ones parent? Evolutionary biology modeling revealed that Lamarckianism would have provided an adaptive advantage in changing environments compared to genetic mutation alone [4]. In randomly changing, and

rapidly changing environments, low to medium values of heritable phenotypic plasticity were optimal, respectively. In slowly changing environments there was a monotonic improvement in fitness as the capacity for heritable phenotypic plasticity increased. Absent in the above model was a distinction between genotype and phenotype, for its intention was not to compare non-heritable phenotypic change, i.e. lifetime learning, with heritable phenotypic change, i.e. lifetime learning plus Lamarckian inheritance. In the field of evolutionary algorithms, researchers experiment with "evolution as it could be". They found when evolving artificial neural networks that Lamarckian inheritance of weights learned in a lifetime was harmful in changing environments but beneficial in stationary environments [12]. Our aim is to compare various combinations of non-directed genetic change, lifetime learning, and Lamarckian inheritance of learnt phenotypes, under variable environmental conditions.

Recently, Paenke et al. developed a general model [13, 14] in a Darwinian framework to explain under which conditions learning accelerates or decelerates evolution in stationary environments. In their model, learning altered the fitness landscape, which could speed up or slow down evolution. In this paper we investigate the interaction between learning, Lamarckian inheritance, and undirected variation, in changing environments. We introduce the model in Section 2, results are presented in Section 3, and discussed in Section 4.

## 2   Model

Inspired by the model of Jablonka et al [4], our model of evolution and learning, allows two environmental states $E_0, E_1$. Two phenotypes $P_0$, $P_1$ are possible, where $P_0$ is better adapted to $E_0$, and $P_1$ is better adapted to $E_1$, i.e.

$$f(P_0|E_0) > f(P_1|E_0) \ , \ \ f(P_0|E_1) < f(P_1|E_1) \ , \tag{1}$$

where $f$ denotes the fitness score. In the simulations of Section 3 fitness scores are set such that $f(P_i|E_i)/f(P_i|E_j) = 2, i \neq j$, i.e. the "fit" phenotype reproduces twice as much as the unfit. The real-valued genotype $x \in [0; 1]$ represents the predisposition towards a phenotype, a low $x$ value corresponds to a genetic predisposition towards $P_0$, and a high $x$ value towards $P_1$. A phenotype is realized stochastically by sampling from a Bernoulli probability distribution with parameter $p$. In the absence of learning, $p$ is defined by the genotype value alone, i.e.

$$p(P_1) = x \ , \ \ p(P_0) = 1 - x \ . \tag{2}$$

If learning is adaptive, it must increase the probability of realizing the fit phenotype of the current environment ($P_0$ in $E_0$, $P_1$ in $E_1$). The following mapping satisfies this condition

$$p(P_1|x, E_0, L) = \phi(x, L) \ , \ \ p(P_1|x, E_1, L) = 1 - \phi(1 - x, L) \ , \tag{3}$$

with

$$\phi(x, L) = \begin{cases} = 1 \, , & \text{if } L = 1 \\ = x^{1/(1-L)} \, , & \text{else} \end{cases} \ , \tag{4}$$
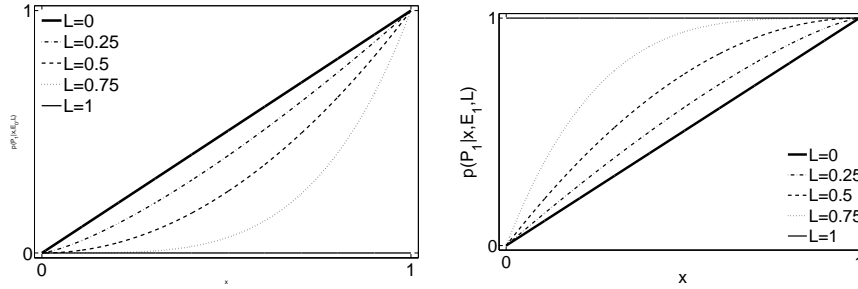
**Fig. 1.** Influence of the learning parameter $L$ on the probability to express phenotype $P_1$ for genotype value $x$, in Environments $E_0$ (left panel) and $E_1$ (right panel).

where $L \in [0;1]$ is a learning parameter. Thus, learning $(L > 0)$ increases the "predisposition" towards the fit phenotype. The larger the $L$, the larger this increase. Note, that the probability to express phenotype $P_0$ is the counter-probability of realizing $P_1$, i.e. $p(P_0|x, E_i, L) = 1 - p(P_1|x, E_i, L), i \in \{0, 1\}$. Fig.1 illustrates the relationship as specified in Equation 3 for different $L$ values.

In each generation, each of 100 individuals reproduces (asexually) an expected number of $f/\bar{f}$ offsprings ($f$ is the individual's fitness, $\bar{f}$ the population mean fitness), such that the population size is constant over time. The offspring's genotype $x'$ depends on the parent's genotype, its learning-induced increase in predisposition, and a Lamarckian parameter $\lambda$, in particular $x' = \lambda p + (1 - \lambda)x$. Pure Lamarckianism is given if $\lambda = 1$ and no Lamarckianism is present if $\lambda = 0$. See Fig.2 for illustration of this implementation of Lamarckianism. A low mutation rate (realized by adding a Gaussian random number with mean $\mu = 0$ and standard deviation $\sigma = 10^{-4}$, cut off at the genotype space boundaries) may further influence the offspring's genotype. In some of the experiments the Lamarckian parameter $\lambda$ and/or the learning parameter $L$ evolves as well. In these cases each individual has an additional gene that stores its $\lambda$ respectively $L$. The average time between two environment changes is specified by a parameter $T$. The actual change periods are either deterministic (cyclic changes) or probabilistic. How well the population adapts is measured as the mean fitness of individuals in the population averaged over time. To avoid an initialization bias, only fitness from generation 1000 to 2000 is sampled. Three experiments have been carried out, which are described in the next section.

## 3 Results

### Experiment 1

The results of this experiment are presented in Fig.3. We simulate evolution for a range of combinations of the Lamarckian parameter $\lambda$ and change interval $T$, for learning parameters $L = 0.5$ and $L = 0.75$, and we compare the case of
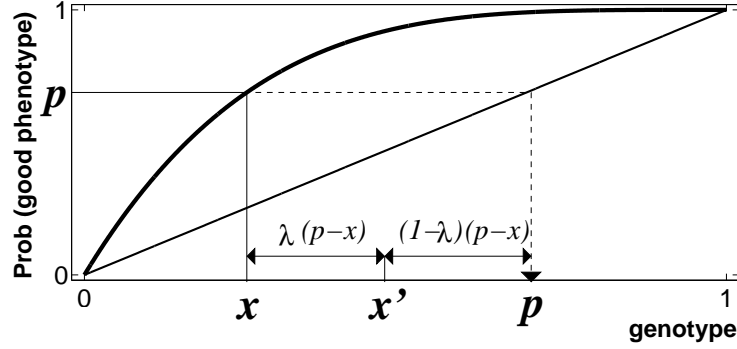
**Fig. 2.** Implementation of Lamarckianism: Learning increases the probability of realizing the optimal phenotype from genetic predisposition $x$ to $p$. Depending on the Lamarckian parameter $\lambda$ its offspring benefits from this increase directly because it inherits a value $x'$, with $x \leq x' \leq p$, where $\lambda$ determines how close $x'$ is to $x$ and $p$.

probabilistic to the case of deterministic environmental changes. In particular we combine $T \in \{1, 5, 10, \cdots, 95, 100, 200\}$ and $\lambda \in \{0, 0.05, \cdots, 0.95, 1.0\}$. The results are shown in four figures (see Fig.3), each showing all combinations of $\lambda$ and $T$. The mesh plots show for each combination of $T$ and $\lambda$ the mean population fitness, averaged over time and over 25 independent evolution runs. The following findings are qualitatively consistent over all settings: With small $T$, i.e. in rapidly changing environments, the maximum mean population fitness is produced for $\lambda = 0$, i.e. without Lamarckianism (see the thick gray line). However, with large $T$, i.e. slowly changing environments, the maximimum mean population fitness (thick gray line) is produced with $\lambda = 1$, i.e. pure Lamarckianism. The minimum mean population fitness (thick black line) is produced with pure or high level of Lamarckianism ($\lambda$ around 1) in rapidly changing environments, and without or low level of Lamarckianism ($\lambda$ around 0) in slowly changing environments. Interestingly, for intermediate $T$, the lowest adaptation success is found for intermediate $\lambda$. For example, in the top-left panel, for $T = 20$ the minimum mean population fitness is produced with $\lambda = 0.4$. The curious fitness valley disappears for very low or high $T$. A geometric explanation for this fitness valley is provided at the end of this section. Although qualitatively consistent, the observed effects are weaker with higher mutation rates (not shown). In summary, Lamarckianism results in higher mean population fitness than Darwinian inheritance in slowly changing environments and a lower mean population fitness in rapidly changing environments. For a given level of environmental change, the minimum mean population fitness is produced by an intermediate level of Lamarckianism. The slower the environment changes, the lower the level of Lamarckianism where this minimum occurs (see also end of this section for a geometrical explanation).
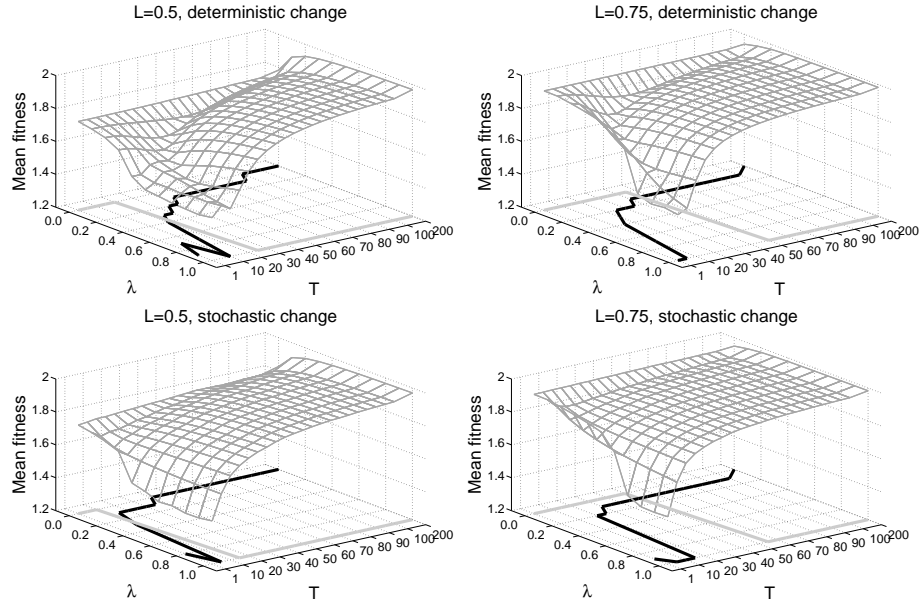
**Fig. 3.** Experiment 1: Mean fitness in evolution with different Lamarckianian parameters $\lambda$ and environmental change intervals $T$. The thick black line shows where, for a given $T$, the minimum occurs for $\lambda$. The thick gray line is the corresponding maximum. Panels in the left column correspond to $L = 0.5$, panels in the right column correspond to $L = 0.75$. Upper row panels are based on deterministic, lower row panel on probabilistic environmental changes.
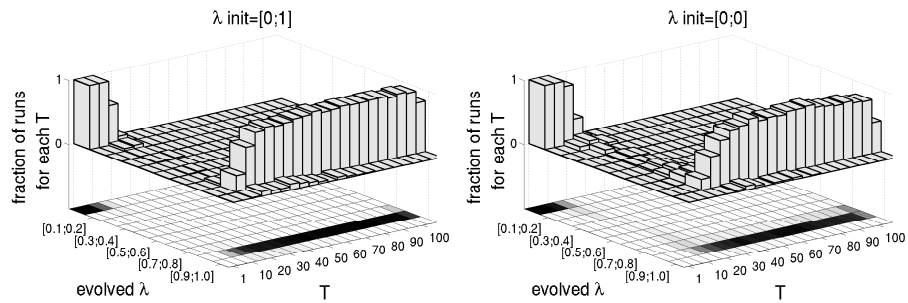


**Fig. 4.** Experiment 2: Evolving the Lamarckian parameter $\lambda$, initialized uniformly on $[0; 1]$ (left panel), and starting without Lamarckianism, i.e. $\lambda = 0$ for all individuals (right panel), in case of deterministic environmental changes and with $L = 0.5$.
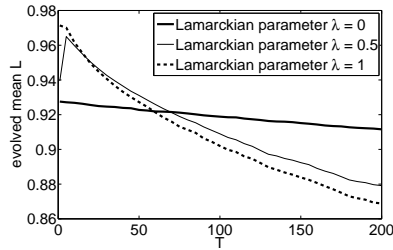
**Fig. 5.** Experiment 3: Evolving the learning parameter $L$ while the level of Lamarckianism $\lambda$ is constant. The figure shows the evolved mean $L$, in the cases pure Lamarckianism ($\lambda = 1$), intermediate level of Lamarckianism ($\lambda = 0.5$) and no Lamarckianism ($\lambda = 0$).
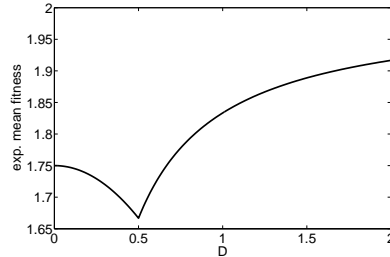
**Fig. 6.** Geometrical explanation for the fitness valley for intermediate $\lambda$ at intermediate $T$ encountered in Experiment 1 (cf. Fig 3). The figure shows Equation 6 with $L = 0.5$. A mean fitness minimum occurs at $D = 0.5$ (cf. text).

## Experiment 2

The results of this experiment are presented in Fig.4. This experiments aims to test whether the optimal level of Lamarckianism $\lambda$ (cf. thick gray line in the top-left panel of Fig.3) evolves if each individual has its $\lambda$ encoded in the genotype. Note, that a second-order adaptation process is necessary for this. Fig.4 presents the results of a set of evolutionary runs. For each $T \in \{1, 5, 10, \cdots, 95, 100, 200\}$, evolution was run 100 times with mutation $\sigma = 0.0001$ for $x$ and $\lambda$, and with learning parameter $L = 0.5$. The lenghts of the bars in Fig.4 represents the fraction of runs that resulted in a mean $\lambda$ in the interval $[0; 0.1], [0.1; 0.2] \cdots [0.9; 1.0]$. The left panel of Fig.4 shows the case in which the initial population was distributed uniformly on the entire $\lambda$-range. In rapidly changing environments ($T \leq 10$), the majority of the runs produce a small $\lambda$, and for slower changing environment ($T \geq 15$) a large $\lambda$. Comparing this to the results of Experiment 1 (top-left panel of Fig.3), we see that the optimal $\lambda$ indeed evolves in a second-order process. In another experiment (Fig.4, right panel) evolution starts without Lamarckianism ($\lambda = 0$) for all individuals. In this case, a large $\lambda$ is only evolved for $T \geq 25$. The likely reason for this difference is the observed fitness valley for intermediate $\lambda$ in case of intermediate levels of environmental change. Apparently, the population can not cross the fitness minimum for $T$ around 20. In an additional experiment (results not shown) the learning rate $L$ was evolvable as well. In the absence of learning cost, a high $L$ quickly evolved and suppressed the evolution of the Lamarckian parameter $\lambda$ in slowly changing environments: With very high learning ability, there was only weak selection pressure for a large $L$ in slowly changing environments, which leads to the evolution of only intermediate levels of $\lambda$. In summary, in most cases, a near-optimal level of Lamarckianism evolves as a second order process. However, in cases where there is a population mean fitness minimum for intermediate levels of Lamarckianism (see Experiment 1), the globally optimal level of Lamarckianism does not always evolve.

**Experiment 3**

The results of this experiment are presented in Fig.5. The aim of this experiment is to test if Lamarckianism influences the evolution of learning ability $L$. Holding the level of Lamarckianism $\lambda$ constant during the evolution, we evolve $L$, for a wide range of $T$, and compare the cases "no Lamarckianism" ($\lambda = 0$), pure Lamarckianism ($\lambda = 1$) and an intermediate level of Lamarckianism ($\lambda = 0.5$). Comparing the two extreme cases no ($\lambda = 0$) and pure ($\lambda = 1$) Lamarckianism, we see that in quickly changing environments ($T < 60$) a larger mean $L$ evolves with pure Lamarckianism, and in slower changing environments a lower mean $L$ evolves with pure Lamarckianism than without Lamarckianism. The case of intermediate level of Lamarckianism ($\lambda = 0.5$) lies between the two extremes cases, but is closer to the case of $\lambda = 1$. So, Lamarckianism suppresses the evolution of learning ability in slowly changing environments and facilitates the evolution of learning ability in quickly changing environments. An explanation for this is that for large $T$, there is a relatively low selection pressure for high $L$ in case of Lamarckianism, because a high $\lambda$ alone allows good adaption. For small $T$, however, we have shown that Lamarckianism is detrimental, and there is a relatively high selection pressure to evolve a high $L$ that can compensate for the Lamarckian disadvantage. In summary, where Lamarckianism provides an adaptive advantage (slowly changing environments) a lower learning ability is evolved because there is less selection pressure for it, but where Lamarckianism provides an adaptive disadvantage (rapidly changing environments) a higher learning ability is evolved because there is stronger selection pressure for it, i.e. learning compensates the disadvantage of Lamarckianism here.

**Geometric explanation for the fitness valley**

In experiments 1 and 2, we found that for a given $T$, the minimum mean population fitness is produced by an intermediate $\lambda$. A possible explantion is outlined in the following: With a very low mutation rate we assume that genotype changes within time $T$ are mainly induced by Lamarckianism and that mutation-induced random genetic changes are negligible. We further assume that the population mean fitness is well represented by the expected fitness of the population mean genotype. Thus, population mean fitness can be expressed w.r.t. the population mean distance to the optimal genotype, which we denote $d$. Assume that initially $d = 0.5$ and between two environmental changes (within one $T$), this distance is reduced by a distance of $D$, where $D$ depends on the level of Lamarckckianism $\lambda$ and the learning parameter $L$, i.e. $D(\lambda, L)$. In our model, we know that $\frac{\partial D}{\partial L} \geq 0$ and more importantly for this analysis $\frac{\partial D}{\partial \lambda} \geq 0$, i.e. $D$ is increasing with $\lambda$. Let us first consider the case where ($0 < D \leq 0.5$), such that the population never reaches the optimum within $T$ or just immediatly before the environmental change at $T$, e.g. because $\lambda$ is too small: At the time, just before an environmental change occurs, the population has a distance $d = 0.5 - D$ to the optimum. Immediately after the environmental change this distance becomes $d = 0.5 + D$ since the optimal genotype has changed (from 0 to 1 or from 1 to 0). Since the

population always moves back and forth between these two states, the expected fitness over time is approximately

$$\bar{f}(D, L) = \frac{1}{D} \int_{0.5-D}^{0.5+D} f_{\exp}(d, L) \ \mathrm{d}d \, , \tag{5}$$

where the expected fitness of $d$ is $f_{\exp}(d, L) = 2 - \phi(d, L)$ (cf. equations 3 and 4). This assumes, that the fit phenotype's fitness is twice the unfit phenotype's fitness. Equation 5 can be reformulated with straight-forward calculations. Substituting $n$ for $(1/(1 - L))$, we obtain

$$\bar{f}(D, n) = \begin{cases} 2 + \frac{(0.5-D)^{n+1}}{2D(n+1)} - (0.5+D)^{n+1} & \text{if } 0 < D \leq 0.5 \\ 2 + \frac{1}{2D} \frac{2n+1}{n+1} - \frac{1}{D} & \text{if } 0.5 < D \leq 1 \\ 2 - 0.5^n & \text{if } D = 0 \, . \end{cases} \tag{6}$$

The first case $(0 < D \leq 0.5)$ corresponds to the above described scenario, where the population never reaches the optimum within $T$. In the second case $(0.5 < D \leq 1)$, the population reaches the optimal genotype within $T$ and stays there until the next environmental change (having the maximum fitness of 2 during this time). Thus, for $(0.5 < D \leq 1)$, we obtain $(0.5/D) \cdot \bar{f}(0.5, n) + ((D - 0.5)/D) \cdot 2$, which produces the second case of Equation 6 after some straightforward calculations. The third case $(D = 0)$ corresponds to $\lambda = 0$ (no Lamarckianism). Here, the mean fitness over time is simply the expected fitness of $d = 0.5$, i.e. the population does not move. Figure 6 illustrates Equation 6 for $L = 0.5$. It shows a minimum at $D = 0.5$. For a given constant $L$, $D$ only depends on $\lambda$ and we know that $D$ is increasing with $\lambda$. Thus, the mean population fitness $\bar{f}$ is decreasing for small $\lambda$ and increasing for large $\lambda$, producing a minimum for intermediate $\lambda$. This provides a possible explanation for the occurence of the fitness valley for intermediate $\lambda$ at intermediate $T$ in experiments 1 and 2.

To summarize the main argument of this geometrical explanation: With a low mutation rate, the population's mean genotype movement is mainly dependend on the level of Lamarckianism, i.e. Lamarckianism allows quick genotype movement. A (Lamarckianism-induced) quickly moving population may be less fit than a population that is not or hardly moving (without Lamarckianism): While a quickly moving population has the advantage of approaching a recently changed fitness optimum, it potentially has an adaptive disavdantage when the next environmental change occurs, since it is farther away from the new optimum than the population that has moved less. In our model this disadvantage indeed occurs, and the disadvantage is even larger than the adaptive advantage of approaching a new optimum. Thus, the population mean fitness is decreasing for increasing level of Lamarckianism. If, however, the level of Lamarckianism increases further and exceeds a certain threshold, the population can move very quickly to the new optimum and stay there at a high fitness level (until the next environmental change occurs). Thus, at intermediate levels of Lamarckianism, the population mean fitness is increasing with the level of Lamarckianism.

# 4 Discussion

This paper predicts that Lamarckian inheritance should be less common in natural environments that oscillate rapidly, compared to stationary environments. The disadvantage of Lamarckian inheritance in rapidly changing environments is explained by the movement of the mean genotype. With Lamarckian inheritance, genotype movement is faster than with genetic mutation alone. In rapidly oscillating environments, Lamarckianism increases the integral of genotype distance from the optimum. The advantage of Lamarckian inheritance in slowly changing environments is because the genotype converges to the optimum more rapidly than by random mutation alone. A curious finding at intermediate levels of environmental oscillation is that a minimum value of mean population fitness is associated with a particular value of Lamarckian inheritance. This is in contrast to the monotonic changes in mean population fitness observed at very high and very low rates of environmental change. This fitness valley may prevent the evolution of Lamarckianism from scratch even though high levels of Lamarckian inheritance are a global optimum.

A follow-up experiment in which learning rate was evolvable, showed us that the introduction of Lamarckian inheritance in rapidly oscillating environments increases selective pressure for better learning mechanisms, whilst introduction of Lamarckian inheritance in slowly oscillating environments decreases the selective pressure for learning mechanisms. Note that this finding is limited to instances where environmental changes occur cyclically such that the genotype is able to establish itself in an area where a high fitness under several environmental conditions is experienced. In nature, simple binary oscillating environments involve geophysical rhythms such as diurnal and seasonal cycles. If however, the environment were to change in a non-oscillating path, e.g. a continuously increasing temperature or in a co-evolutionary setting, then Lamarckianism may be beneficial even in rapidly changing environments. We have not modeled non-oscillating environmental changes.

Recently it has been proved for several conditions that directed phenotype plasticity helps to cross a fitness valley by smoothing the fitness landscape [15]. This positive effect stems from a non-Lamarckian inheritance mechanism and would not be observed with Lamarckian inheritance. Our model does not cover this type of adaptive disadvantage of Lamarckianism. It also does not include dependencies between Lamarckian mechanisms and learning mechanisms as one would find them in cultural evolution, a Lamarckian-like inheritance mechanism, where a high learning ability is actually a prerequisite for this form of Lamarckianism, to appear. Neither does the model include a cost of learning, which can certainly influence the balance between Lamarckianism and learning ability.

In future we will carefully extend the analysis model in order to cover various aspects of the interaction of evolution and learning under Lamarckian inheritance.

## Acknowledgments

## References

1. S.J. Gould, editor. *The Structure of Evolutionary Theory*. The Belknap Press of Harvard University Press, 2002.
2. J.B. Lamarck. *Philosophie zoologique ou exposition des considrations relatives l'histoire naturelle des animaux*. UCP (reprinted 1984), 1809.
3. E. Jablonka and M. Lamb. *Evolution in Four Dimensions - Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. MIT Press, 2005.
4. E. Jablonka, B. Oborny, I. Molnar, E. Kisdi, J. Hofbauer, and T. Czaran. The adaptive advantage of phenotypic memory in changing environments. *Philos Trans R Soc Lond B Biol Sci.*, 29(350):133–141, 1995.
5. E. Richards. Inherited epigenetic variation  revisiting soft inheritance. *Nature Reviews Genetics. Advanced online publication*, 2006.
6. P. Foster. Adaptive mutation: Has the unicorn landed? *Genetics*, 148:1453–1459, 1998.
7. R. Holliday and J.E. Pugh. DNA modification mechanisms and gene activity during development. *Science*, 187:226–232, 1975.
8. Z. Lippman and R. Martienssen. The role of rna interference in heterochromatic silencing. *Nature*, 431:364–370, 1986.
9. H.B. Slade and S.A. Schwatrz. Mucosal immunity: The immunology of breastmilk. *Journal of Allergy and Clincal Immunology*, 80:348–356, 1987.
10. F.H.C. Crick. Central dogma of molecular biology. *Nature*, 227:561–563, 1970.
11. A. Weissman. *The Germ-Plasm: A Theory of Heredity*. Walter-Scott, 1893.
12. T. Sasaki and M. Tokoro. Comparison between Lamarckian and Darwinian evolution on a model using neural networks and genetic algorithms. *Knowledge and Information Systems*, 2(2):201–222, 2000.
13. I. Paenke, T.J. Kawecki, and B. Sendhoff. On the influence of lifetime learning on selection pressure. In *Artificial Life 10*, pages 500–506, 2006.
14. I. Paenke, B. Sendhoff, and T.J. Kawecki. Influence of plasticity and learning on evolution under directional selection. *American Naturalist*, 2007. in press.
15. E. Borenstein, I. Meilijson, and E. Ruppin. The effect of phenotypic plasticity on evolution in multipeaked fitness landscapes. *Journal of Evolutionary Biology*, 19(5):1555–70, 2006.