Traversing Fitness Landscapes by Changing Environments

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Introduction

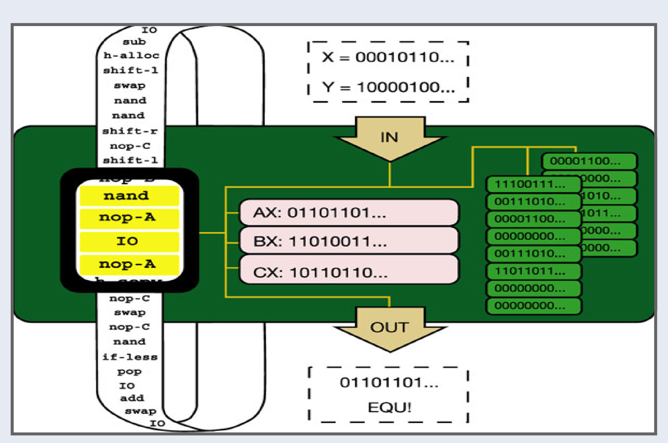
Since its introduction by Sewall Wright (1932), the fitness landscape has been a popular metaphor for describing how populations evolve. In these landscapes, where elevation represents fitness, populations move via small, mutational steps. Selection drives populations uphill (improving their fitness), while drift allows populations to wander. In cases of strong selection, a population can become trapped on a sub-optimal peak, unable to further improve its fitness. Wright's explanation for how populations escape these sub-optimal peaks involves genetic drift. However, an understudied mechanism for escaping sub-optimal peaks is the effect of changing enviroments (Fisher 1932). A population trapped on a sub-optimal peak with respect to one environment can move to a new position when the environment (and thus landscape) changes. Switching back to the reference environment, the population may be in a position to climb a different (and perhaps higher) peak.

We are interested in how populations evolve in changing environments. One approach would be to determine fitnesses for all genotypes in all environments (i.e. determine the topology of all lanscapes). Unfortunately, the enormous number of possible genotypes makes this impossible. Therefore, we take a top-down approach that involves repeatedly evolving populations where the environment can be manipulated with fine precision. This requires a fast-evolving system that is well understood and tractable. The two systems that we have used thus far are *Escherichia coli* and Avida. For this poster, we focus on the Avida portion of the study.

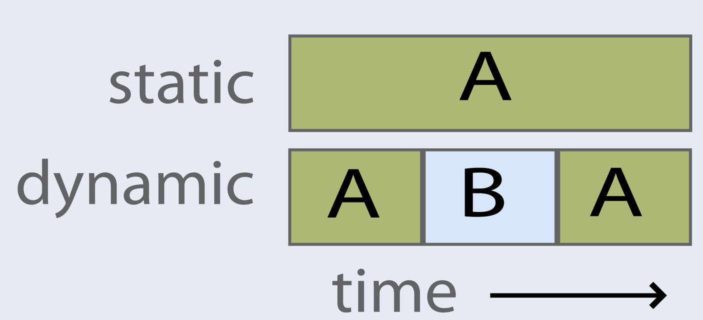
Methods

Avida is a computer program that contains an evolving population of organisms (Avidians). The fitness of an Avidian is determined by how quickly it replicates. Avidians can replicate faster by performing certain tasks. The environment determines which tasks are rewarded.

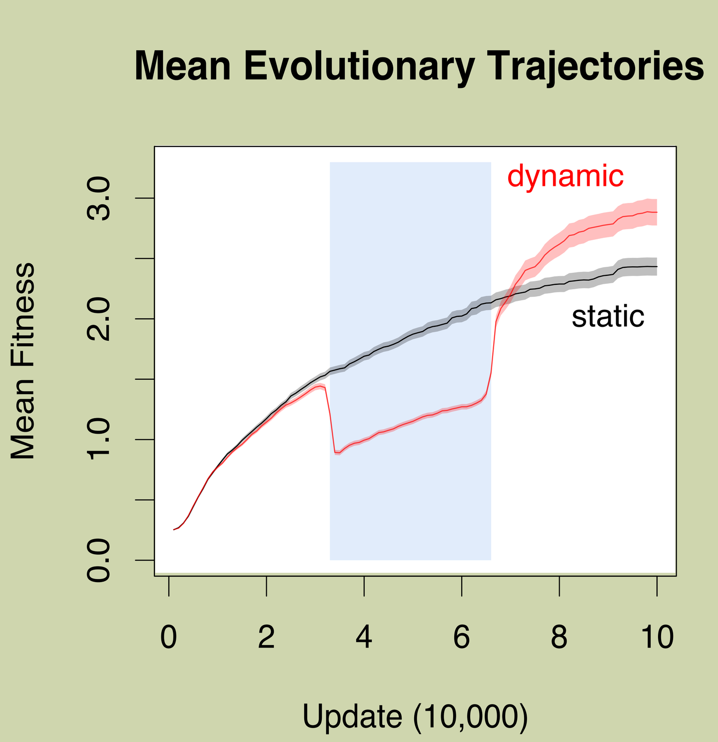
In our **Static Regime**, the environment remains constant for the duration of the run. In contrast, the **Dynamic Regime** spends the first third of the run in a reference environment (A), the middle third in a different alternative environment (B) and then returns to the reference environment (A) for the last third (see figure below). Every run is initially seeded with a same ancestor (which can perform none of the tasks) and spans the same duration.



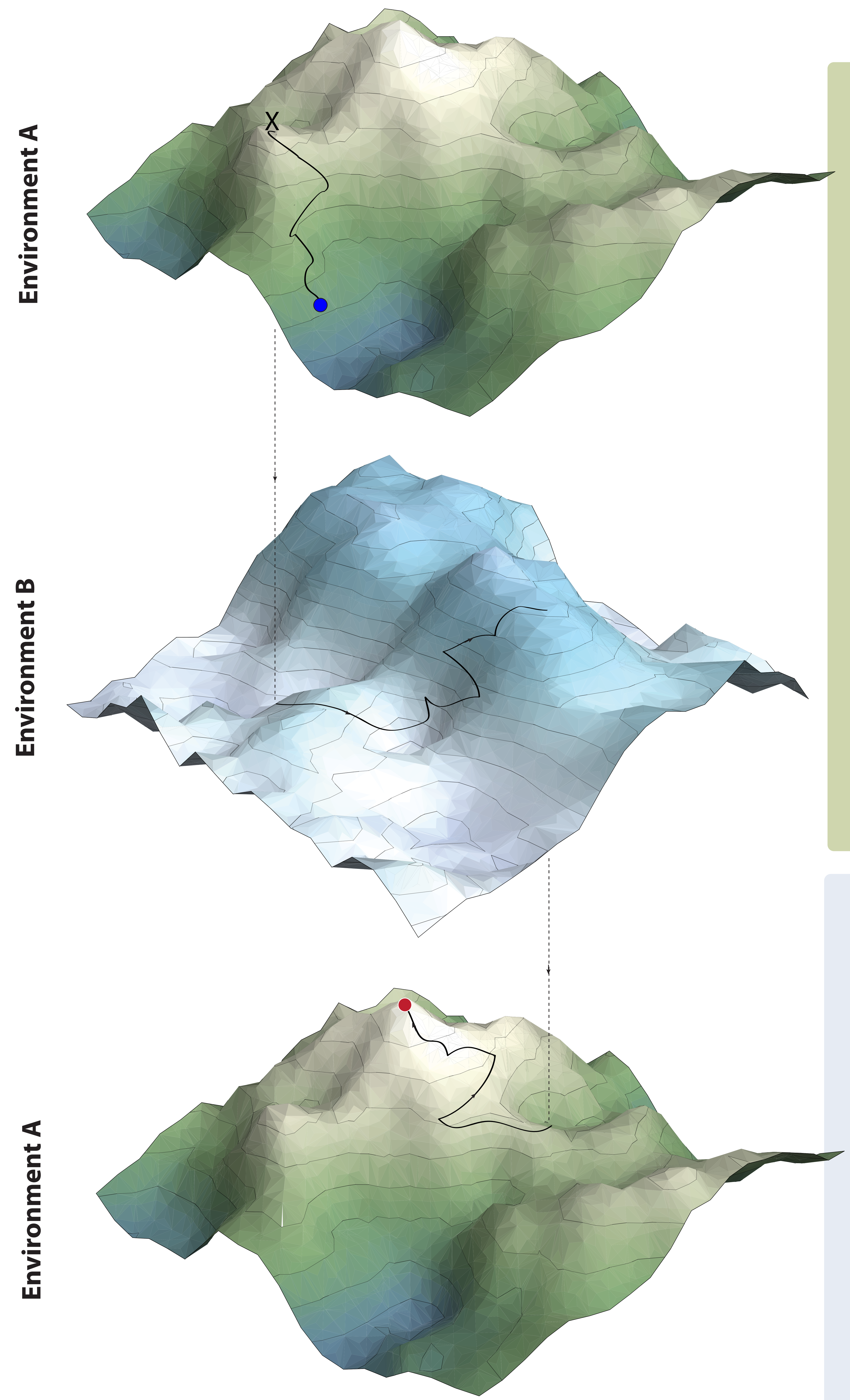
A visual representation of an Avidian's anatomy (from Lenski et. al, Nature 2003).



Results: multiple runs

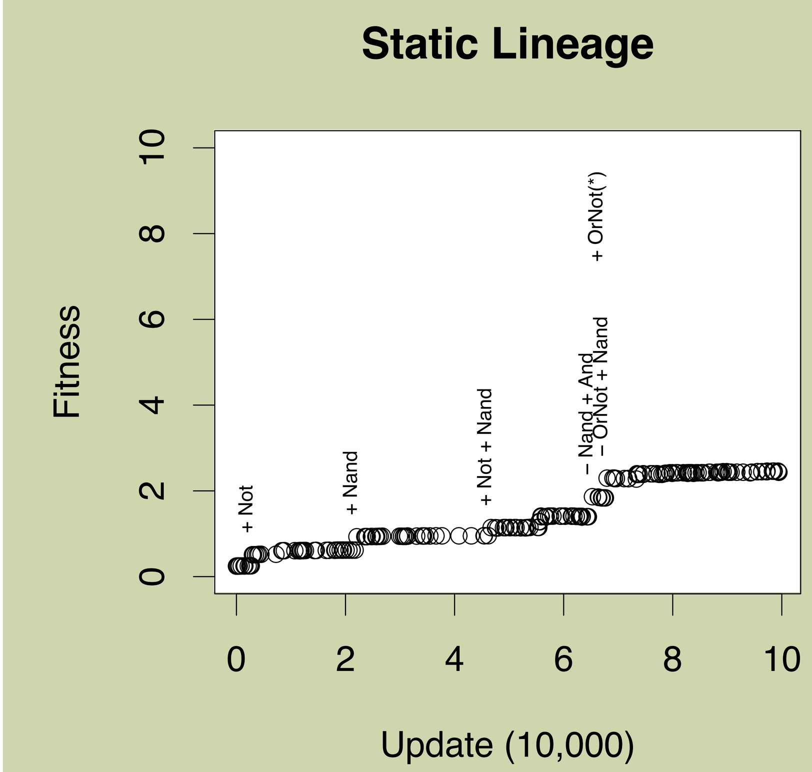


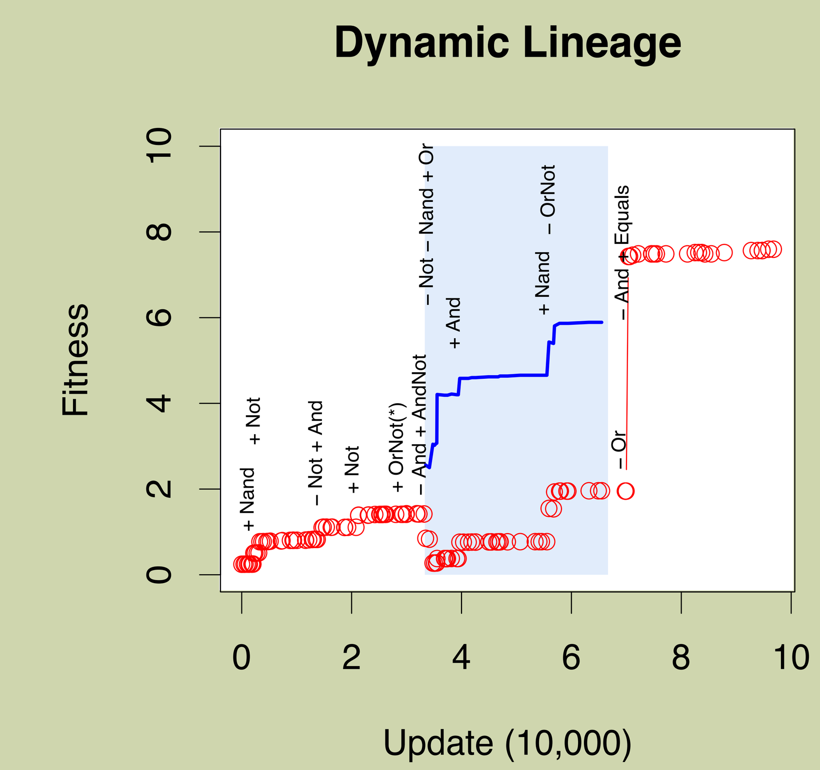
Comparison of evolutionary outcomes due to shifting environments. 'Update' is an arbitrary time unit equal to the time required to execute ~ 30 instructions. The fitness of each individual is measured relateive to the reference environment (rewarding the tasks Not, Nand, And & Equals). The black line is the mean fitness of 407 runs, evolved only in the reference environment. The red line is the mean fitness in the reference environment of 404 runs, evolved under a dynamic regime. Under the dynamic regime, Avidians experience the alternative environment (rewarding Not, Nand, And, OrNot, Or & AndNot). Shading around the black and red lines indicates standard error. The blue region represents the alternative environment (only applicable to the dynamic regime). At the conclusion of the run, the differences in fitness are statistically significant (Welch's t-test, $p < 0.001$).



When traversing a fitness landscape, populations may become trapped at sub-optimal peaks. The representation of a rugged landscape is shown in the figure above. In the top portion of the figure, the **blue dot** represents the ancestral population. The black line indicates the evolutionary trajectory of that population over time. The point marked with an "x" is a sub-optimal peak where the population becomes trapped. A change in the environment can produce a different landscape, like that seen in the middle portion of the figure. In the new landscape, the population may not be trapped, allowing for movement across the landscape. If this population is returned to the original environment (and landscape), the population may be in a position to climb a different (perhaps higher) peak, marked with the **red dot**.

Results: single runs





The evolutionary history of two sample runs from the Mean Evolutionary Trajectories data. The circles represent every distinct individual in the line of descent (distinguished by mutation). The words represent gain (+) or loss (-) of the ability to perform the task (asterisk denotes gain of unrewarded ability). For example, Avidians typically acquire the ability to perform the logic function 'Not' (negation of a single input) early in its evolutionary history.

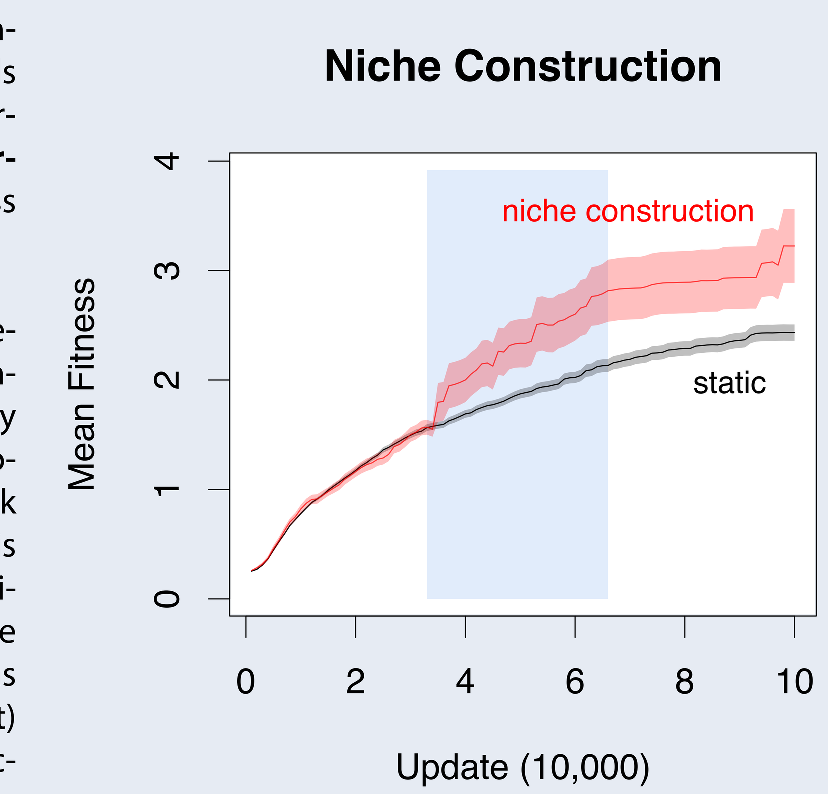
Two lineages are shown–a static run and a dynamic run. The points are the fitnesses measured relative to the reference environment. The dark blue line in the dynamic run is the fitness measured relative to the alternative environment.

Discussion & Future Directions

In a related study, Kashtan et al. (PNAS 2008) found that populations exposed to varying environments reach global optima faster than when the environment is held constant. Our findings are consistent with their results, in that exposure to different environments can improve fitness.

We are exploring other types of changing environments. One type of alternative environment rewards only those tasks that are not rewarded in the reference environment. Preliminary results in these **Orthogonal Environments** show improved fitness relative to static evolutionary runs.

Another type of alternative environment involves rewarding the same tasks as the reference environment, except that tasks are rewarded in a frequency dependent manner. In other words, rewards are proportional to the rarity of the ability to perform a task in the population. The landscape in this scenario is dependent on the location of the population. Acquisition of a new ability alters the landscape–a bit like walking around on a waterbed (also referred to as **Niche Construction**). Preliminary analysis (see right) has shown that niche construction may be an effective way to search the landscape.



Acknowledgements

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