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Diversity Dynamics in Static Resource Models

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(Received)

We define three information-theoretic methods for measuring genetic diversity and compare the dynamics of these measures in simple evolutionary models consisting of a population of agents living, reproducing, and dying while competing for resources. The models are “static resource models,” i.e., the distribution of resources is constant for all time. Simulation of these models shows that (i) focusing the diversity measures on *used* alleles and loci especially highlights the adaptive dynamics of diversity, and (ii) even though resources are static, the evolving interactions among the agents makes the effective environment for evolution dynamic.

1. Adaptation as Cause and Effect of Diversity Dynamics

The evolutionary adaptation of a population to its environment can take a range of forms. At one extreme, the environment is static and the agents have a fixed evolutionary learning task, so evolution approaches a stable equilibrium. At the other extreme, the agents’ evolution fundamentally changes the environment in such a way that new evolutionary learning tasks are continually created, thus making adaptive essentially open-ended. To build a baseline for future work on open-ended evolution, here we study relatively fixed adaptive tasks. We discover that even quite simple adaptive tasks are surprisingly dynamic.

Our general methodology is to identify statistical macrovariables that reflect the distinctive properties of evolving systems (cf. Packard 1989; Bedau and Packard 1992; Bedau, Ronneburg and Zwick 1992; Bedau 1994; Bedau and Bahm 1994). One important macrovariable is the genetic diversity of the population. Diversity can be both cause and effect of the dynamics of adaptive evolution in at least three ways:

- I. Diversity Requirement.** Sufficient diversity in the gene pool is a necessary precondition for a population to have the capacity to adapt.
- II. Diversity Reduction.** Adaptation tends to reduce diversity in the gene pool by weeding out the relatively unfit (the survival of the fittest).
- III. Diversity Creation.** Adaptation can also create diversity by promoting traits that permit a variety of different niches to be exploited simultaneously.

2. Static Resource Models

We observe diversity in simulations of simple evolutionary models consisting of many agents that exist together in a two-dimensional lattice of sites with periodic boundary conditions. Overlaying the lattice is a resource field replenished from an external source. Here we consider only *static* resource fields, i.e., fields in which resources are immediately replenished whenever they are consumed, so that the spatiotemporal resource distribution is constant. In static resource models the population has no effect on the distribution of resources. Nevertheless, agents constantly extract resources and expend them by moving and reproducing, so the agents function as the system's resource sinks and the whole system is dissipative. Evolution is resource driven since the agents need a steady supply of resources in order to survive and reproduce.

Each agent moves each time step as dictated by its genetically encoded sensorimotor map: a table of behavioral rules of the form IF (environment j sensed) THEN (do action k), where k is either a random walk to the first empty site or a jump some number (positive or negative) of sites along the x and y axes. The map contains a rule for each detectable environmental condition, one per locus. Only one agent can reside at a site at a time, so an agent randomly walks to the first unoccupied site when its movement makes it "collide" with another agent. Movement expends resources as a function of distance moved. An agent dies if its resource supply becomes empty and reproduces if its supply surpasses a certain level. Children start life with half of their parent's resources, and they inherit their parents' sensorimotor mapping except perhaps for mutations in encoded actions. A given simulation starts with agents with randomly chosen sensorimotor strategies randomly distributed across the environment. Since the model contains no *a priori* fitness function (Packard 1989), the population level fluctuates with the contingencies of extracting resources. For more about these models, see Bedau and Packard (1992), Bedau, Ronneburg and Zwick (1992), Bedau (1994), and Bedau and Bahm (1994). Figure 1 summarizes the parameter values for the simulations reported below.

3. Measures of Diversity

The diversity measures are based on the frequency of alleles at loci across the population. Following Bedau, Zwick, and Bahm (1995), we distinguish three distributions. The simplest is the frequency distribution $P(a_k, l_j)$ of the alleles a_k that exist and the loci l_j that exist across the population, i.e., the distribution collecting the frequency of the k^{th} allele and the j^{th} locus, for all alleles and loci of all individuals. Second, to reflect the relative use, and hence relative adaptive significance, of the various loci, we consider the distribution $P_{\text{used}}(a_k, l_j)$ of frequencies with which the allele a_k and the locus l_j have actually been *used* in the immediate past. Third, since a well-adapted population generally encounters a non-random distribution of the environmental conditions present in the world, to reflect the diversity of alleles with respect to the actual distribution of local environments we consider the distribution $P_{\text{env}}(a_k, l_j)$ of frequencies of the alleles a_k at those loci that *could* be used in the actual world, i.e., the loci corresponding to the types of local environments that actually exist, weighted by the frequency with which those types of environment are present in the world. (In static resource models, of course, the existing environmental conditions, and their frequency, never change.)

We assume these distributions are normalized, e.g., $\sum_{i,j} P_{\text{env}}(a_k, l_j) = 1$, and treat the frequencies as probabilities. Furthermore, we create one-dimensional distributions by

Table 1. Summary of three families of information-theoretic measures of diversity.

\mathcal{D}	Uncertainty of existing alleles.
\mathcal{W}	Uncertainty of existing alleles at a given locus, averaged over existing loci.
\mathcal{B}	Mutual information between existing alleles and existing loci.
$\mathcal{D}_{\text{used}}$	Uncertainty of used alleles.
$\mathcal{W}_{\text{used}}$	Uncertainty of used alleles at a given locus, with an average weighted by a locus's use.
$\mathcal{B}_{\text{used}}$	Mutual information between used alleles and used loci.
\mathcal{D}_{env}	Uncertainty of existing alleles, weighted by the frequency with which the corresponding environmental conditions exist in the environment.
\mathcal{W}_{env}	Uncertainty of existing alleles at a given locus, with an average weighted by the frequency with which the corresponding environmental conditions exist in the environment.
\mathcal{B}_{env}	Mutual information between existing alleles and loci, weighted by the frequency with which the corresponding environmental conditions exist in the environment.

collapsing along the locus or allele dimensions, e.g., the frequency $P(a_k) = \sum_j P(a_k, l_j)$ of alleles a_k that *exist* in the population, irrespective of locus, or the frequency $P_{\text{used}}(l_j) = \sum_k P(a_k, l_j)$ with which the loci l_j are *used*, irrespective of which allele is used. Finally, from these distributions, we can calculate components of genetic diversity, using the scheme of Bedau, Zwick and Bahm (1995), summarized in Table 1.

4. Observations of Diversity Dynamics

We observed the dynamics of the diversity measures in a variety of static resource models; here we focus on two. The *resource strip* is a world devoid of resources (a “desert”) except for a narrow strip, one site wide and 80 units high, that runs across the desert. In this environment agents can use only four loci—those corresponding to the von Neumann neighborhoods sensed when on the strip, immediately to its left, immediately to its right, or in the desert. The *resource block* is a world devoid of resources except for one block, 20 sites wide and 80 units high, in the middle of the desert. In this environment agents can use fourteen loci—those corresponding to the von Neumann neighborhoods sensed in the middle of the block, at its edges or corners, or in the desert.

In the resource strip environment, adaptation is largely a matter of coordination. It is not sufficient to be able to navigate the strip; in order to minimize the likelihood of colliding with other agents and being bumped into the desert, one must move in concert (same direction, same speed) with the other agents on the strip; as we will say, the population must “flock” together. In addition, as the resource strip becomes more populated, agents increasingly collide and get bumped into the desert, so desert survival (i.e., finding and getting back onto the resource strip) becomes increasingly important. These adaptations tend to reduce diversity.

By contrast, the resource block can support a larger population if subpopulations follow *different* strategies. To survive on a resource block, one must stay on the block, as follows: when in the middle of the block you detect a uniform environment and move in a given direction at a given speed until you detect an edge, at which time you jump back into the middle of the block. Although some degree of coordinated flocking will minimize collisions that might bump you into the desert, the optimal population will not flock

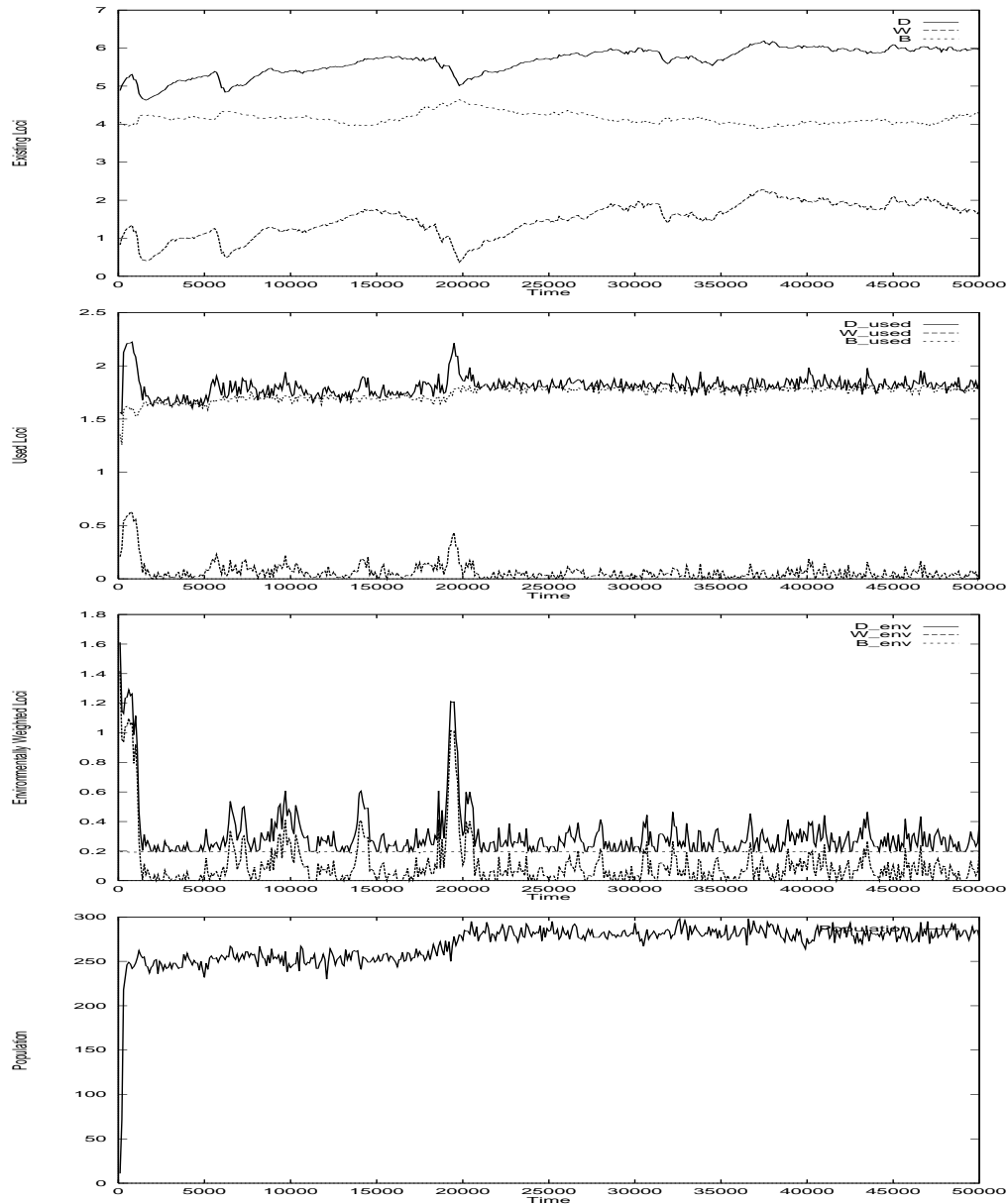


Figure 1. A simulation of the one-resource-strip world, showing (i) \mathcal{D} , \mathcal{W} and \mathcal{B} dynamics, (ii) \mathcal{D}_{used} , \mathcal{W}_{used} , and \mathcal{B}_{used} dynamics, (iii) \mathcal{D}_{env} , \mathcal{W}_{env} , and \mathcal{B}_{env} dynamics, and (iv) population level dynamics. The world contains 128×128 sites with an initial population of 1000 agents. Each agent can detect whether food is present at the five sites in its von Neumann neighborhood, so its sensorimotor map contains a behavioral rule for each of the $2^5 = 32$ detectable environmental conditions. At each time step an agent pays “metabolic taxes” consisting of thirty plus two times the number of sites traversed during the last move, and it can extract 80 units of resources from its current site. An agent reproduces when its internal resource supply exceeds 2000 units, and each IF-THEN rule in a child’s inherited sensorimotor strategy mutates with probability $p = 0.01$.

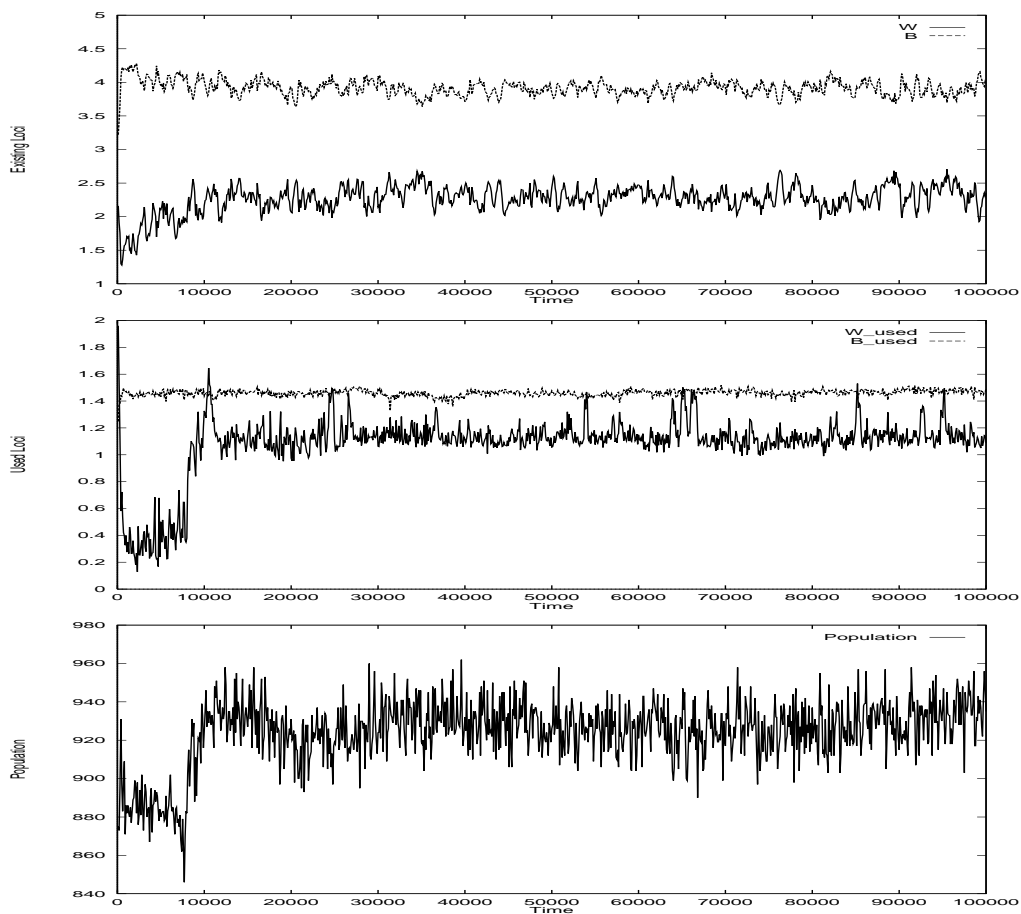


Figure 2. A simulation of the one-resource-block world, showing (i) \mathcal{W} and \mathcal{B} dynamics, (ii) $\mathcal{W}_{\text{used}}$ and $\mathcal{B}_{\text{used}}$ dynamics, (iii) population level dynamics. Except for the resource field, all model parameters are as in Figure 1.

together. If all agents follow the same strategy, they will all move across the block in the same direction, say, south, and then jump north when they detect the southern edge, forming a flow that cycles over the southern side of the block, and leaving the northern side as a “niches” that could be occupied if an appropriate subpopulation evolved an appropriate strategy, e.g., moving north on the block and jumping south at the northern edge. So, resource block populations can be larger when they contain subpopulations following *different* strategies, and diversity will *increase* when the population adapts into different niches. This illustrates how adaptation can create diversity.

Diversity and population level simulation data substantiate these arguments. The population level in Figure 1 shows two adaptations on a resource strip: a population explosion as flocking evolves, and a second increase at around time 20,000 when the population comes to random walk in the desert (a good strategy for returning to the strip). The within-locus diversity drops during both adaptations; $\mathcal{W}_{\text{used}}$ shows the adaptations especially clearly. $\mathcal{W}_{\text{used}}$ also dramatic *rises* just before it drops, showing that population’s used loci become significantly more diverse at the outset of the random walk adaptation.

This is the the diversity precondition for adaptation. The random walk adaptation can occur only if that allele enters the gene pool (through a random mutation) and then spreads. $\mathcal{W}_{\text{used}}$ increases when the random walk subpopulation initially grows. Then, when this subpopulation increasingly dominates the population, $\mathcal{W}_{\text{used}}$ starts to drop. Focusing on used alleles and loci allows us to see this adaptive diversity dynamic. Since desert environments dominate the resource strip worlds, \mathcal{W}_{env} emphasizes the desert locus diversity and so and clearly shows the diversity precondition and reduction of the random walk adaptation.

On the resource block, by contrast, diversity rises. What stands out in the time scale used in Figure 2 is a sharp population increase around time 10,000—an example of adaptation creating diversity through exploiting a new niche. Both \mathcal{W} and $\mathcal{W}_{\text{used}}$ show corresponding rises, but only $\mathcal{W}_{\text{used}}$ sharply rises exactly when the adaptation occurs. \mathcal{W} shows that genetic diversity continually changes throughout the period from 1000 to 10,000, but $\mathcal{W}_{\text{used}}$ shows that most of this change is not adaptive.

Finally, note that, while \mathcal{B} dynamics are ambiguous, each main adaptation in Figure 1 corresponds to a significant rise in $\mathcal{B}_{\text{used}}$. Thus, these adaptations significantly increase the information the used alleles and used loci contain about each other, and $\mathcal{B}_{\text{used}}$ is correlated with fitness in resource strip worlds. In the resource block worlds, however, adaptation into new niches is *not* associated with a rise in between-locus diversities.

5. Conclusions

Even in very simple static resource models we see many kinds of diversity dynamics: (I) diversity requirement, (II) diversity reduction, and (III) diversity creation. Weighting the diversity measures by the extent to which alleles and loci are *used* depicts how diversity is both cause and effect of adaptation especially effectively. Furthermore, our simple static resource models underscore the idea that the environment to which an agent must adapt includes the population of other agents with which the agent interacts. Even if agents interact only by colliding, interactions can still dominate an agent’s adaptive challenge. The shape of an agent’s fitness landscape depends on what strategies other agents use, and this changes as the population evolves. Out of a completely static resource distribution a dynamic environment for evolution emerges.

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