Importance of Diversity

Reconciling Natural Selection and Noncompetitive Processes

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ABSTRACT: To better understand selection processes in evolutionary systems (ecological to economic to social to artificial systems), the origins and role of diversity are examined in two systems that show increased group functionality (better performance, efficiency, robustness, adaptability, stability, etc.). Diversity was chosen as a clarifying concept, because it appears to have been largely ignored, or misunderstood. One system is a model of group selection within an ecosystem. The other is the group solution of a sequential problem using self-organizing dynamics *in the absence of any selection*. A comparison of the two systems show that while diversity is essential to both, improvement by natural selection is derived from *consuming* diversity, whereas improvement by noncompetitive self-organization is decreased by any reduction in diversity. The resulting perspective is that natural selection is a mechanism that increases the functionality of the individual (or groups within a larger system); noncompetitive self-organization of the system, without need for selection, increases the functionality of the whole above that of the individual or group. The two extreme roles for diversity are reconciled if natural selection is not strongly expressed in these systems—"survival of the fittest" becomes "survival of the adequate"—so that noncompetitive processes can occur. The resulting view of a mature ecosystem is an elastic web of interactions in which natural selection is dormant or retains the status quo. The processes of natural selection for individual or group improvement are activated only if environment changes are sufficient to *break* the elastic interconnections, as might occur in punctuated equilibria.

INTRODUCTION

This paper suggests that a significant revolution is taking place in the fields of ecology, economics, and social sciences; a revolution that is changing our understanding of the processes in these systems. Expression of this change takes many forms, from theoretical understanding to experimental studies. The character of the change is based on the growing observations indicating that the traditional views of these systems (mature ecosystems, developed economies, and interdependent social systems) have processes that have been overlooked:

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- Competition and selection is less important in these mature systems; instead, mechanisms of cooperation and mutualism (mutual benefit for both) are significant.

- Desirable global functionality (better performance, efficiency, robustness, adaptability, increased stability, etc.) are emergent properties from the dynamic interactions of relatively simple constituents—the emphasis is on their dynamic origins.

Within the field of ecology, both observations are best captured by the sustained work of Salthe, summarized in his most recent book[1] and, from a different perspective, by Kauffman.[2] The latter observation is best captured by the group of researchers involved with the study of artificial life[3] in the general field of complex adaptive systems.

This paper focuses on the role of diversity in self-organizing systems, focusing primarily on ecosystems. Although the concept of diversity has always been part of the lexicon of ecologists and social scientists, quantitative understanding of diversity has been limited until recently. The difficulty is that diversity is only meaningful in heterogeneous constituent systems and available analytical tools for evaluating diversity have been lacking. Recent diversity studies have quantitatively advanced by means of simulations of genetic evolution[4] and knowledge systems,[5] and by both analytical solutions and simulations in economics.[6,7] The latter studies initially observed counterintuitive results in nonselective, problem-solving systems, such as the observation that diverse groups solve problems better than individuals when selection is not present. This paper is an attempt to extend this new understanding to the role of diversity in ecosystems.

The following discussion begins with a summary of the traditional viewpoint of natural selection, using as an example from recent literature, a careful simulation of group selection. As a contrasting example, a model problem is presented in which nonselective interaction of randomly generated diversity leads to higher system performance. We then introduce a current ecological opinion that de-emphasizes selective processes, and speculate how the apparently contradictory processes of natural selection and noncompetitive self-organization might be integrated into one model for ecosystems, with the role of diversity as the pivotal concept.

DEFINING CONCEPTS

Because our subject spans many areas of expertise, the following definitions, assumptions, and restrictions establish a common perspective.

An *agent* or *individual* refers to any localized constituent or entity with decision-making or problem-solving ability. It can be a single individual or a subgroup of individuals within a larger system. Decision making or problem solving can be as simple as a deterministic response of a physical subsystem, given an initial state and external boundary conditions (because these systems are typically nonlinear, deterministic chaos is still possible) or a conscious, premeditated act by a complex human problem solver. A sequence of decisions is a *path* through the problem domain, each step requiring that a previous problem be solved in order to proceed. For example, a

path may be the sequence of events that are associated with decay of an organism or the sequence of decisions for an investment strategy. For example, in an ecosytem, nutrients can take many different paths from their initial creation by conversion of sunlight, through use by a lower life form, to more complex life forms, and then to final decay process and recycling.

A *group* is a collection of agents that solve a common problem, either knowingly or not, cooperating or not, but one that shares a common view and expectations within the system. *Local* and *global* extent describes the degree of proximity of a property to an agent or group of agents. Local extent is limited to the region of the agent; global extent encompasses the system as a whole. Note that local and global are applied to more than just spatial extent. These concepts apply to any system in which the information of the agent is limited to its proximity, including more abstract domains of functional space or knowledge space.[5] The systems of interest are those that have little or no centralized control and are *self-organizing*; that is, their dynamics are such that the system as a whole exhibits self-regulating processes that are largely determined by the properties of the subsystems and the governing processes of the dynamic system. Global properties that cannot be determined from the properties of the constituents are called *emergent*.

Note that in the above definitions, the concept of decision making or problem solving is used outside of its normal context of solving a *posed* problem. Problem solving is extended to describe a change of state of a subsystem as a consequence of internal processes that may not explicitly pose a *problem*. We adopt this liberty in the definition of problem solving in order to apply a common vocabulary to a variety of systems. Our approach is similar to the use of concepts of cooperation and altruism in both cognitive and noncognitive systems in biology.[8]

PERSPECTIVE ON DIVERSITY

Before analyzing of the origin and role of diversity in these systems, a common understanding of meaning of diversity is needed. We offer a working definition and discuss the parameter space for diversity. In this context, diversity of a group is defined to be the degree of unique differences within a group for which its constituents have a common "world view" (see Johnson[5] for a mathematical description). Applying this definition, if all the individuals within a group have identical qualities, then the group has zero diversity, although the qualities of the individuals may encompass all possible variations of the system. If each individual contributes a unique quality not shared by others, then the diversity of a group is a maximum. The restriction to a common construct of the world is necessary, because differences between individuals in a group can arise from different assumptions (world-views) about the system. Although this source of differences may appear to be a source of diversity, we argue that comparisons between different world constructs are not advantageous within a self-organizing system. For example, the approaches to problem solving of a New Yorker and Australian bushman are likely to be mutually exclusive and therefore *unique*, but because these approaches operate in very different environments, it is of questionable meaning to measure their diversity (as defined above) and ask how it correlates to system performance. This is equivalent to saying that meaningful

expressions of diversity to the system dynamics require the unique contributions to be potentially coupled by the system dynamics. Implicit in the above definition is that diversity is a property of a *group* of individuals, not of a single individual. Hence, the common phase, "she has diverse interests" is meaningful only in comparison to a group. Diversity can be a measure of any characteristic of the system *at a given time*, either in function, capability, or information.

Because the systems of interest often have extent (as defined above), diversity can be evaluated either locally or globally. Global definitions of diversity have significance only if the system is coupled globally. For example, if one looks at the correlation between some measure of system performance and some measure of diversity over greater and greater spatial extent, then at some extent, no correlation will be found since the diversity measure is including states that are no longer coupled by the system dynamics. An illustration of this is seen in applying the concept of biodiversity of populations across uncoupled ecosystems, as is commonly, possibly incorrectly, done.

NATURAL SELECTION—COMPETITIVE/SELECTIVE PROCESSES

The dominant model for the advancement of individual functionality within biology is natural selection, often cited as the process of "the survival of the fittest." The role of natural selection in improving the individual fitness is not questioned here, but the exclusive role of natural selection on improving the fitness of the group or global system functionality is questioned. In this section, recent work on multilevel selection is reviewed in order to illustrate the basic relationships between diversity and selection.

Initially, the generally accepted role of diversity within natural selection can be summarized as follows[9]:

- Natural selection requires diversity; without diversity selection cannot occur.

- All other things being equal, the greater the diversity, the greater the selection.

- Selection consumes diversity. For selection to continue, diversity must be replenished, by either mutation or emigration.

These statements are clear about the role of diversity within natural selection, but only for selection within one level and within one niche or collection of closely related niches. Selection between multiple levels (individual, group, metagroups) introduces interdependencies that can lead to more complex behavior. Group selection is one common explanation of the origin of cooperative (altruistic) behavior or processes. The argument is that if selection operates between groups, then traits that are disadvantageous to the individual but advantageous to the group can be selected and propagated.

A definitive paper on multilevel selection was published recently by Pepper and Smuts[8] and it presents an agent-based ecological model. The work addresses the need to develop the simplest model that illustrates cooperative behavior from group selection. Peppers and Smuts examine the development of observed altruistic behavior in two separate simulations: alarm callers in predator–prey systems and feeding restraint in foraging systems. Mutation is not considered in this work, thus they

examine the amplification of preexisting traits. The authors summarize that "…the model has shown that the groups emerging through the behavior of individual agents in patchy environments are sufficient to drive the evolution of group-beneficial traits, even in the absence of kin selection."[8] They observe that "[b]ecause of its within-group disadvantage, cooperation can only spread though an advantage in founding new groups. Successful groups must be able to export their productivity from the local area, so that their reproductive success is not suppressed by local population regulation."[8] In the absence of "patchiness" or spatial heterogeneity, individuals with the cooperative traits inevitably lose out to their selfish counterparts in this model.

Trait variation, synonymous here with diversity within and between groups was examined by Pepper and Smuts by looking at different patch sizes and separations of patches. They observed that:

> Smaller trait groups in turn increased the strength of between-groups selection relative to within-group selection by changing the partitioning of genetic variance. Selection at any level requires that the units being selected vary genetically, and all else being equal, the strength of the selection increased with the genetic variance among units. In a sub-divided population, all variance among individuals can be partitioned into within- and between group components, and the proportion of the total variance found at each level strongly affects the relative strength of the within- versus between-group selection. The smaller groups are, the more variance is shifted from within to between groups, and thus the stronger the between group component of selection becomes relative to the within group component. Because small isolated patches reduced trait group size, both small patches and large gaps facilitated the evolution of both forms of cooperation. (Ref. 8.)

The simulation results confirm the three roles of diversity listed at the start of this section. Expression of group selection in the simulations does not alter these roles, with the exception that diversity is increased between groups and reduced within groups.

ORIGINS OF DIVERSITY IN A COMPETITIVE SYSTEM

Much has been written in trying to explain the source of observed bio-, social-, and economic-diversity, but little quantitative proof of the mechanisms involved, or discussion of the role of diversity have been offered. The basic argument[10] is that to minimize the use of scarce resources, material, or energy an individual or group will fare better if it can avoid direct competition with other individuals by creating a new niche, whether spatially or functionally. By occupying and adapting to the new niches, the system as a whole expresses greater diversity. Furthermore, the occupation of new niches can create additional diversity by the subsequent adaptation of individuals that are interdependent with the original relocator. Therefore, according to this argument, the existence of unexploited niches provides the driving force for increased diversity.

This argument is an explanation only for nonlocal diversity; it does not explain the observed diversity within a given niche, only that between niches. There appears to be no satisfactory explanation for both local and global diversity in the simple application of natural selection. For more complex models, new mechanisms for diversity may arise. As an ecosystem becomes more complex, there exist mechanisms within group selection that might result in higher diversity within the group.

As populations begin to specialize in function and consequently become more interdependent, a population may function better as a mutualistic entity than as competing groups—for example, the best house builder is a group of specialists and not any one of the specialists (plumber, carpenter, roofer, etc.).[11] Presumably, this diverse, mutualistic entity gains a selective advantage. In the discussion section, we revisit a model with more complex processes, along with the role that diversity plays within a broader perspective.

SIMULATIONS OF NONCOMPETITIVE SELF-ORGANIZATION

We next examine a quite different system than the ecosystems considered above, in order to investigate mechanisms for diversity creation and its importance to global functionality. The following is a summary of a detailed study.[5] We wish to address the question: what is the simplest demonstration of increased global performance of a group above that of the individual? By simplest, we mean the least number of assumptions, processes, or rules.

The idealized system examined is the solution of a sequential problem (see FIGURE 1, insert) that has many optimal and nonoptimal solutions, solved by agents that have identical capabilities and do not interact. Although this maze problem is
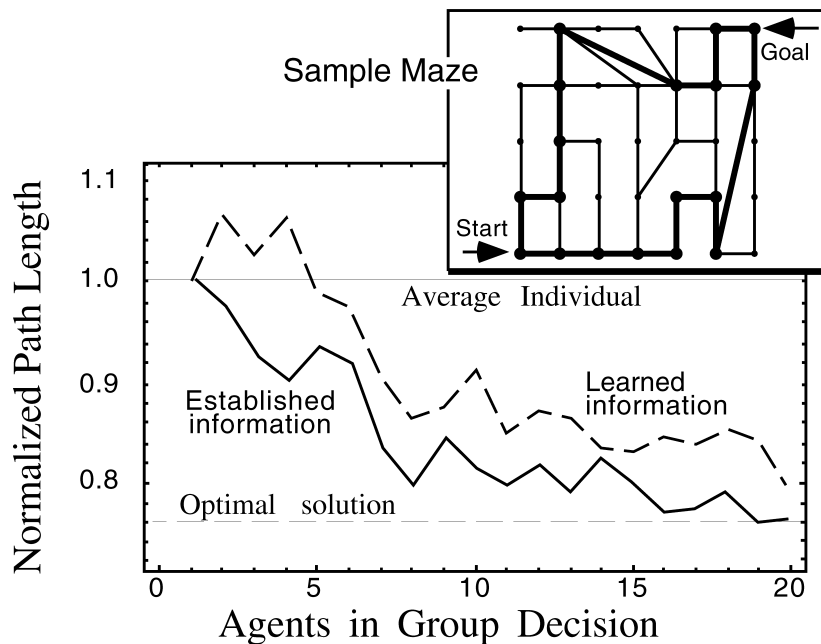

FIGURE 1. A sample maze (**insert**) with two of the 14 minimum paths highlighted and the simulation results (**main figure**) showing the effect of the group size on the path length, normalized by the average individual path length, about 12.8.

quite simple from a global perspective, it serves as a representation of more complex processes: the solution of a problem that has many decisions points and many possible solutions, and that is more difficult than that solvable optimally by one individual. It is argued that a more realistic landscape does not change the underlying processes that are observed in this simple model.

The solution process for a single agent is separated into a *learning phase* and an *application phase.* In the *learning phase* simple rules of movement are used to explore and learn about the problem domain. Because the agents have no global sense of the problem, they initially explore the problem until the goal is found. The learning process can be thought of as an agent exploring the maze randomly and leaving "breadcrumbs" behind to aid in its search for the goal, thereby avoiding fruitless paths. In the *application phase*, learned information (the bread crumbs) is used by the agent to solve the problem again, typically with a shorter path as a consequence of eliminating unnecessary loops. Essentially, in the application phase, the agent follows the path with the most breadcrumbs.

Because the initial search is random, a collection of individuals shows a diversity of experience (knowledge of different regions of the maze), diversity of preferences (different preferred paths at any one location in the maze), and diversity of performance (different numbers of steps), even though each agent has identical capability. This is the source of diversity in the population: by virtue of the domain having multiple optimal and nonoptimal solutions, a diversity of experience, preferences, and performance is created.

In the repeated solution to an unchanging problem domain, we tend to remember only that information needed to solve a problem, and to forget extraneous information associated with unused paths. Here, the equivalent effect is for the agent to remember only *established* information along paths used by individual, thereby *forgetting* unused paths. The process of "forgetting" unused information does not change the performance of an individual agent, because both the learned and established information produces the same path during the application phase, discounting random choices between paths of equal preference. Therefore, an established individual experience is created from the learned experience by retaining the information just used in an individual solution, and forgetting unused information.

The process of forgetting information has been argued as a form of selection in these simulations, but two points can be made. As we shall observe, there is only a quantitative effect of using established or learned information, so the basic conclusions of the simulations are not pivotal on the inclusion of this effect or not. The consideration of effect of forgetting is introduced, as we shall see, to clarify the correlation between diversity and performance: higher diversity leads to higher performance. Secondly, selection in a biological context means that the individual is removed from further contribution to the gene pool, not just part of their gene contribution. There is no equivalent removal of the agent in the current simulations. Indeed, the individual's performance is unchanged by the process of forgetting.

Information for a group of individuals is then constructed by forming a linear combination of each individual's experiences at each node in the maze. That is, the breadcrumbs from each individual in a selected group are summed for each decision point (node) in the maze. Then the same application rules as used for the individual are applied to the group information to find a group solution. As seen in FIGURE 1,

the group solution always outperforms the average individual for larger groups and the solution using the established individual information performs better than the learned information. Furthermore, for groups of size above 20, the optimal solution is found, although nothing in the agent's rules seeks a minimal path length. FIGURE 2 shows one mechanism that provides a reason for the fact that the group does better than any agent: individual information is combined to indicate a shorter path for the group (follow the maximum number of bread crumbs at each intersection). The dynamics of the group solution are chaotic in detail. For example, the specific path of a group is sensitive to the addition of one individual, even for arbitrarily large groups. Nevertheless, the global solution for the group, any path of minimum number of steps, is stable. This illustrates the desired feature of chaotic dynamics that leads to a responsive and robust system, but not at the expense of the quality of the global solution.

To better understand the role and importance of diversity in this simple model, quantitative measures of diversity were examined. The best measure found defines diversity as the degree of unique information in a collection of agents, based on a node-by-node comparison of preferences, as defined in a previous section. Groups contributing *established* rather than *learned* information exhibit higher diversity, although less information is available. Moreover, as observed in FIGURE 1, the groups based on established information perform significantly better than those based on learned information. Furthermore, this measure of diversity also indicates the degree of insensitivity to noise. In the process of combining information for the group, if valid information from an agent is replaced by random information (the number of breadcrumbs is randomly changed), this is a test for the stability of the group solutions. It was found that groups with low diversity were very sensitive to noise, whereas groups with high diversity were not—up to 90% of the valid information can be replaced before a group path degenerates to a random walk—the worst solution of all methods.
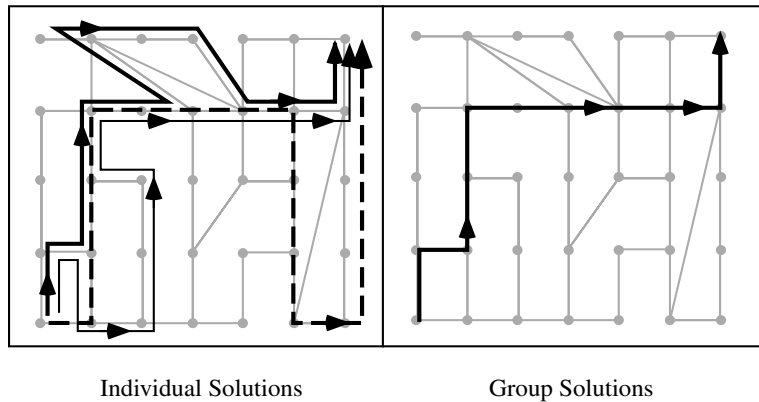

Individual Solutions   Group Solutions

FIGURE 2. One mechanism for the better performance of the group. Note that the path length of the group is better than that of any agent.

All of the above studies assumed that the agents do not share information while learning or applying information; they are completely independent, except that they solve a problem with a common world view. If the effect of information exchange is included, so that the individual can benefit from the experiences of other agent while learning the maze, we find that improved individual performance is achieved. Not unexpectedly, groups made up of these shared-learning agents, converge with fewer agents to a minimum path length, much faster than observed in FIGURE 1. However, improved performance is not without a cost. Shared learning results in individuals with similar information and, therefore, the group exhibits low diversity. Consequently, the stability of the group is degraded, often severely.

How does the performance of the group depend on the individual performance? Two studies were done, one in which the mazes were made more complex with the individual's capability held constant, and another in which the maze was held constant and the individual's capability was varied. From these studies the following conclusions were drawn. (1) A simple maze to a good individual solver is a trivial problem and no improvement is obtained by a group solution. (2) More difficult global problems require larger groups. (3) An extremely difficult problem to an individual with fixed capability leads to a random individual solution that shows no group advantage. The latter conclusion is significant; it suggests that harder and harder problems cannot be solved by larger and larger groups of individuals. Equivalently, the individual must have some capability (i.e., not random) that can be amplified in groups. This observation is also related to the assumption of having a common world view. A different world view in the above simulations is equivalent to solving a maze with different connectivity between the nodes (i.e., each agent sees a different set of possible paths at each node), while still having the same common goal. Although not demonstrated in the simulations described above, it is expected that a group of agents with "capability" above a random walk would perform poorly as a group, because the information that each contributes does not correspond to a common world view and, hence, will not be compatible and cannot be amplified. Therefore, different world views and limited individual capability both lead to no better group performance over the average individual.

DISCUSSION: THE ROLE OF DIVERSITY

There are two main observations from the above noncompetitive simulations. First, they illustrate how diversity can arise in groups of agents *of identical capability* when a system has options of equal likelihood or fitness. Second, they illustrate how random creation of diversity can contribute directly both to global performance and robustness, above that of an individual and in the absence of any selection from the population. Both of these observations are in direct contrast to the processes observed in natural selection when applied to a single level. In this section, we try to reconcile the two extreme approaches to higher functionality, represented by the two models summarized above.

In both models, diversity is a prerequisite for improvement: without diversity, there can be no improvement. For natural selection, this improvement is for the group by increasing the capability of the individuals in the group; for nonselective

self-organization it is for the group, assuming shared learning is not present. However, this is where the similarity ends. Once the necessary functionality is achieved by natural selection, the immediate need for diversity is lost. Thereafter, having diversity at a current time becomes an investment for the future. When selection processes operate at a single level, diversity does not directly contribute to current system performance; only past diversity contributes to the current performance and then only by the reduction of diversity in the selection process. Indeed, diversity can be argued to lower the group performance in a natural selection viewpoint by the inclusion of individuals with poorer fitness. By direct contrast, diversity in the noncompetitive system directly contributes to performance and robustness.

The above differences between the two extremes for self-organizing systems can be reconciled if the predominance of natural selection and competition in ecosystems and, in general, all self-organizing systems is relaxed. Initially, it is possible to adopt a less competitive view of ecosystems, where "the survival of the fittest" is replaced by "the survival of the adequate,"[12] also referred to as "soft-selection."[13,14] Essentially, this is a statement that, in mature ecosystems significantly greater expression of random variation is likely and there is no need to select among this diversity. This is equivalent to the observations in the noncompetitive simulations that the source of diversity originates from indeterminacy in the solution space; one path is, at an individual level, as successful as another. For ecosystems, this argument requires that there exist multiple paths of near equal fitness. Mature ecosystems in nature are observed to have rich interdependencies.[15] These interdependencies create many alternative paths for energy, material, and information. Consequently, global system function is not dependent on a single critical path, as in, for example, the many alternatives for transforming sunlight.

The flexibility to express random diversity is not a sufficient argument for high diversity alone, because it begs the question about why such flexibility exists. The noncompetitive simulations provide insight into this question. The existence of multiple paths leads to a chaotic, but robust system. Ecosystems are chaotic in the same sense as the present study: a small change in initial conditions, or the addition of noise, results in a different set of paths or a different distribution of paths through the system. An example of the chaotic but robust nature of evolutionary systems is the recent theories of "frozen accidents,"[2,16] in which the details are chaotic, for example, the specific base-pairs in DNA, but where the global need is still satisfied—the need to develop an encoding system for passing on information to offspring. Another example is the material–energy path in an ecosystem: a slight difference in predator location can result in, say, a wolf consuming a dying deer, instead of bacterial decay, but in either scenario the global need for recycling nutrients is achieved. As observed in noncompetitive simulations, this chaotic property leads to the responsive nature of the system and prevents the failures due to senescence.[1] Nevertheless, the system is also robust in the sense that the global solution is stable and not sensitive to random details or localized failures.

A final result in the noncompetitive simulations was not unexpected, but it does complete the global view of an ecosystem: the global performance, including robustness, is directly coupled to the performance of the individual. An ecological example of this is that if all populations that convert sunlight to useful forms of energy did this only erratically or with lower efficiency, then the global system as a whole would

be less productive and robust. This suggests that from a global perspective, natural selection is needed to make the individual adequate to the global task of survivability. However, because of the complexity of typical evolving systems, particularly in the degree of redundancy, it is difficult to argue about what is essential and what is adequate for survivability. We can conclude only that some degree of individual performance is necessary and that natural selection is the likely mechanism for providing the functionality.

The above speculations result in a powerful, multilevel perspective that can be simply stated. Natural selection is responsible for improvement or adjustment of the relative performance of the individual. However, once an interdependent, multiple-level system develops, then the need for selection is reduced, as noncompetitive processes for global performance start to function. Because both self-organizational processes require expression of high diversity; this creates an optimal system in which either process can operate as required.

One aspect of diversity that has not yet been discussed is the trade-off between diversity and its associated advantages, and the development of a common (and sometimes universal) functionality or approach. In ecosystems, these *cohesions* across populations can reduce diversity by limiting the potential space for random variation. An extreme example of this standardization in living systems is provided by the universal adaptation of the DNA/RNA coding system—one of the few exceptions to the *rule* of biodiversity. In the noncompetitive simulations, the effect of information exchange during the learning phase captures this concept. The reduced diversity of the system and its associated decrease in robustness, is a trade-off for the improved performance of the individual and small groups. This might be a mechanism for the beginning of an expression of specialization. Possibly, in a more complex simulation in which groups can differentiate, this cohesion effect could actually lead to higher system diversity and its accompanying advantages, as different populations define their own uniqueness, an analog to speciation.

What remains unanswered in the above argument is, by what processes do global system functionality, such as robustness, start to operate? It appears that desirable emergent global properties occur in many ecological, economic, and social systems but it is not clear how the properties in the individuals that result in these emergent global properties come into existence. There are two views of their origin. One is the view that the system itself contains these *structural* aspects and organisms form and exist within this structure.[1] The other view is that there are mechanisms for the global coevolution of the necessary traits to propagate the global system.[2] Our present understanding does not resolve these issues.

CONCLUSIONS

The role of diversity, defined as the degree of unique contributions of individuals to a group, is compared in two extremes for achieving higher system functionality, natural selection and noncompetitive self-organization. Although both processes require diversity to function, there is a fundamental difference in the mechanisms by which diversity is activated. Natural selection consumes diversity to yield improvements for a later time; noncompetitive self-organization yields improvements at the current time without selection from the population. The two extremes are argued to

be compatible in ecosystems if there exist many alternative paths (energy, mass, or information flow) of near equal fitness. This flexibility is argued to occur in mature ecosystems.

The resulting viewpoint of such an ecosystem is that it is not static, but has *elastic* interconnections between many entities and processes. Interconnections are chaotic in detail, but globally robust. The response to moderate changes in the environment is the readjustment of these elastic interrelationships, but not their failure. The role of natural selection is largely dormant as a process for improving individual or system functionality. Where active, natural selection operates at the level of rejecting the least fit mutations and preserving the existing interconnections. If a sufficiently rapid environmental change occurs, then there is a catastrophic breakdown of this stable elastic web, which in turn precipitates a high degree of natural selection and a reformation of a new elastic system, based on significantly different interrelationships between new functional forms. We speculate that this process may be the true origin of the proposed punctuated equilibria. The advantage of this viewpoint is that it does not require the questionable assumption of reproductive isolation.[17] The true test of the above speculations requires a sufficiently complex simulation that contains randomly mutualistic interdependence, combined with mutation, and natural selection.

ACKNOWLEDGMENTS

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