INVESTIGATING THE EFFECTS OF FUNCTIONAL DIVERSITY IN SPATIALLY DISTRIBUTED GEOGRAPHIC DOMAINS

Gary M. Pereira

Department of Geography, San Jose State University San Jose, CA 95192-0116, USA Tel 408-924-5475 Email: gpereir1@email.sjsu.edu

Abstract

Distributed models of autonomous consumer agents on resource landscapes are used to demonstrate the effects of functional diversity. Comparisons between populations of agents with various degrees of diversity in the values of key functional variables indicate that moderate diversity results in the formation of spatial patterns, higher yield, and greater resilience. These results are discussed in the context of previous research, as are their implications for understanding and improving the resilience of geographical 'systems'.

1. Introduction

In contrast to the nearly overwhelming presence of functional and structural diversity within geographic domains, many spatial analytical approaches have remained almost reflexively selective, bounded and categorical. Current approaches to geographical modeling continue to rely heavily on implicit generalizations and classifications, static parameterization of functional characteristics and externalities, and other simplifying assumptions that have less to do with theoretical rationale than with practical difficulties of imagination, representation, computation, and sensor technologies. Interest in the direct effects of various forms of continuous, rather than categorical, diversity in the natural and social sciences has increased of late, as has our ability to model more fully the complexities of geographic phenomena, but little has been done to explore the effects of functional diversity by, for example, comparing the results of enabling various degrees of diversity within models that are otherwise equivalent. A simple study in contrasts between artificial landscapes with different degrees of diversity in the functional characteristics of mobile agents is described here.

Even when diversity is simulated stochastically, one is often tempted to resort to mean values or derived indices when proceeding from one conceptual 'step' to another. As a result, we often cannot distinguish artifacts of our conceptual frameworks from those structures and processes reflecting underlying realities. Geographic models continue to rely heavily on conceptually homogeneous compartments of structure and pathways of flux that are common in all theories of systems, even when broad spectra of functional characteristics can be effectively modeled in distributed, concurrent environments. For this reason, the general approach promoted here has no necessary epistemological kinship with traditional forms of complex *systems* theory. More flexible approaches to the representation of individualized, interactive behaviors can succeed whether or not we see a given geographic phenomenon as systematic, specifiable, separable from its environmental matrix, or even objectively definable. We need not accept a particular aspect of the world as a 'system' because we use systems to model it, any more than a painter would describe the landscape she sees as a painted canvas. The more neutral term 'scenario' is therefore used here where one might expect to find the term 'system', in recognition of common circumstances in which individuals, agents, functions, organizations, and scales are not fully specifiable, reducible, bounded, or systematic, and in which processes or events are subject to numerous historical contingencies, but which nevertheless may be usefully modeled and studied within computational systems.

While diversity is most often described in terms of appearances, the quality of diverse *functional* responses to similar circumstances holds the greater interest. In spatial domains, such functional diversity expresses itself concurrently. In this study, simple and easily reproducible computational experiments are presented in order to illustrate the dramatic effects obtained when functional diversity is represented explicitly in spatially distributed models. The scenarios described here investigate the consumption of common pool resources over spatially distributed domains: an 'archetypal' situation common to the geographic, ecological, and economic sciences. In order to highlight the general nature of these effects, they are simulated within neutral landscapes, without spatial features that may influence the results. Ongoing investigations of functional diversity within other archetypal situations, as well as work on models of real geographical import on real landscapes, are yielding similar results. It is my hope that this work will encourage others to more fully investigate the effects of functional and structural diversity, particularly when the results are to be used in decision making capacities.

1.1 Functional diversity and resilience

The resilience of an ecosystem can be described as directly relating to the magnitude of disturbances it can absorb while maintaining its integrity (Holling 1973). In addition, it has been related to "the degree to which the system is capable of self-organization" and "the degree to which the system can build capacity for learning and adaptation" (Folke et al. 2002). It is therefore not surprising that the concept of functional diversity and its possible relation to resilience and survival has long been studied in the biological and ecological sciences. Holling (1996) uses the term 'functional diversity' to describe the effect of competing species that respond differently to external variability: "their risks and benefits are spread widely to retain overall consistency in performance independent of wide fluctuations in the individual species." Social and ecological resilience are increasingly seen as being both conceptually related and practically interdependent (Adger 2000; Peterson 2000), and the idea of using the functional diversity of natural processes to enhance the resilience of human economic and social processes to which

they are tied has long been employed. Indeed, it forms a guiding principle of ecological engineering (Odum and Odum 2003). These efforts often imply nondeterministic and somewhat 'inefficient' approaches. For example, ecosystem regeneration cannot often be accomplished with a single precise set of species. Instead, larger, more diverse sets of species are introduced, with the expectation that some may succeed and other will not. The precise result is unpredictable, but the goal of ecosystem resilience is often attained. If a more tightly controlled and optimized policy of species introduction were used, success would be less likely, even though the process may appear to be more efficient and rational.

The ability of substantially different structures to perform similar functions under a variety of conditions, which in biology has been assigned the unflattering term 'degeneracy' (Edelman and Gally 2001) has often been overlooked in standard normative evolutionary science. However, degenerate structures can be found at every biological scale, and they often come into play under conditions of stress and collapse. Current understanding of evolution does not reflect 'survival of the fittest', but rather 'survival of the sufficiently fit'. The principle of competitive exclusion is widely flaunted in the biological world. As a result, multiple alternative solutions to problems of survival often coexist. Even when such alternative, 'degenerate' functionalities lie dormant under normal circumstances, they may provide extraordinary opportunities for resilience and survival under conditions of collapse. The possibility that similar principles hold in geographic domains relevant to hazards and social and environmental resilience is certainly deserving of investigation.

Indeed, functional diversity has recently become an important topic at the interface of ecology and economics (Matutinović 2001; Rammel and van den Bergh 2003), artificial life, and theories of complexity (Johnson 1999, 2000). Anecdotal and informal theoretical discussions of the positive effects of functional diversity and intentional 'sloppiness' in the management of changing geographical scenarios (de Vries, Thompson, and Wirtz 2002) are beginning to benefit from this interdisciplinary discussion. Unfortunately, the term 'diversity' has become needlessly politicized within the social sciences, as many of us have paradoxically come to rely on certain static categorizations (of race, ethnicity, and belief, for example) while ignoring or suppressing other forms and definitions of social diversity. Such tendencies are being countered by recent calls from thinkers like Nobel Prize-winning economist Amartya Sen for more open consideration of all forms of social identity and diversity. The economic, ecological, and decision sciences have been exploring various aspects of functional diversity that may point the way to pragmatic implementation of new insights in decision making contexts. Allen, Strathern, and Baldwin (2004) describe several models of functional diversity in economic evolutionary settings, including one simulating the effects of a diversity of competing strategies among fishing fleets in the Canadian Atlantic fisheries, concluding that in such a dynamic environment no single optimal strategy exists. Strategies that yield the greatest catch in the short term lead to global collapse. Indeed, "we need to turn off our rationality, our clever economic calculations and our directed, intentional behaviour in order to continue fishing and find ways of returning to behaviour that is simple." Surprising claims with regard to functional diversity are increasingly found in the decision sciences. Hong and Page (2004) have shown both analytically and through simulation that diverse groups of less-than-optimal problem solvers may outperform less diverse sets of more highly competent problem solvers. They discuss the implications of this work in the context of standardized testing, organizations, and management.

Unfortunately, much of the recent modeling of 'complexity' in highly distributed spatial environments has not taken functional diversity into account. Such models continue to rely on very rigorously categorized, even binary, global attributes. Nevertheless, such foundational work is very useful for purposes of comparison. For example, scenarios of dynamic, distributed spatial complexity without functional diversity have been analyzed and modeled in terms of such paradigms as self-organized criticality, or SOC (Bak 1996), and the less well known 'highly optimized tolerance', or HOT (Carlson and Doyle 2000). Both of these conditions are characterized by scale-free statistical distributions like those found throughout natural and human domains. They can be linked to measures of production, risk, crisis, collapse, and resilience in environments without structural defenses (SOC) and with designed or otherwise optimized structural defenses (HOT). The consistency of SOC with the statistics of many natural phenomena has encouraged several authors (e.g., Bak 1996; Batten 2000; Buchanan 2000) to speculate that SOC may explain the dynamics and formation of social and economic as well as natural systems. Although little progress seems to have been made in the application of SOC to geography, and none with regard to HOT, both of these approaches seem to have validity in geographic domains and deserve further work. However, it will be argued at the conclusion of this paper that the kinds of self-organization that occur in the presence of functional diversity produce patterns that are more highly organized and productive than those created under SOC conditions, as well as more adaptive and resilient than either SOC or HOT.

Computational models of complex distributed spatial scenarios can improve our understanding of some of the most general characteristics of crisis, collapse, and resilience, and of the roles diversity may play in enhancing resilience. A key hypothesis guiding the work presented here is that a diversity of autonomous actors in any domain implies a diversity of ideas, resources, options, approaches, and responses, which if wisely and flexibly negotiated provide greater resilience to external threats and more sustainable internal dynamics than comparable situations where such diversity is absent or discouraged.

2. Experimental design

Current approaches to the dynamic modeling of spatially distributed phenomena, involving for example cellular automata and mobile agents, apply sets of global rules to a diversity of spatially localized attribute values. Different agent types may operate in conformity with different sets of rules. At the level of individual cells or agents within any particular type, diversity is represented only through variability in attribute values, but not through any significant differences in the behavioral rule bases of each individual. For example, the evolution of landscape attributes in a cellular model may depend on the states of neighboring locations, but the rules of evolution are the same everywhere. All members of a species or breed in an 'individual based' or 'agent based' model are generally assumed to behave in accordance with one schemata.

It is within these restrictions that the models described in this paper express diversity. They represent a necessary first step in this effort, and serve to illustrate the degree to which the results of currently popular models can provide greater insight with relatively minor modifications to their computational and experimental design. Discussion of more profound representations of behavioral diversity is left to a later time. For now, let us concentrate on a traditional method of computational experimentation: we establish certain base, or control, models lacking functional diversity, and then we introduce diversity in the values of certain key variables, comparing their results with the base models and with each other, through simple processes of sensitivity analysis.

2.1 Modeling environment

The agent based models discussed here are implemented within the NetLogo modeling environment (Wilensky 1999). The current version of this environment seems to be free of artifacts, is easy to use, and performs a variety of functions that are useful in serious research (Tisue and Wilensky 2004). Many kinds of dynamic activity on a raster landscape surface may be simulated within NetLogo. The direct use of georeferenced spatial data remains problematic, although loose coupling of NetLogo with geographic information systems can be accomplished through file sharing processes. Each spatial grid location in NetLogo is an agent with specifiable characteristics. The landscape by default has periodic edge properties, which can be negated. Mobile agents may assume arbitrary point, linear, or areal positions within this landscape, and they may interact with the landscape, with one another, and with nonspatial observer agents or other global functional agents. Agents may inherit behaviors and properties from parents and from species level organization. Each individual mobile and landscape agent may have unique values for variables that control behavior, and each can change in fundamental ways.

This environment is being used by the author to study the effects of functional diversity in scenarios that simulate diffusion, competition for common pool resources, and other 'archetypal' situations found in geographical domains wherein the inherent functional diversity of both landscape and mobile agents can be adjusted. Here, a set of distributed models describes simple but surprising results obtained when functional diversity is introduced into simple spatial ecological or economic models of resource consumption.

2.2 Model characteristics

All of the models described in this paper represent localized consumption of a landscape resource by mobile agents. At each time step, each cell of the landscape resource transfers energy to the agents that consume it. The resource cells regenerate at a constant rate to a maximum potential value. The level of energy resource present at each time step

within each landscape cell is portrayed in Figures 1 and 2 as a gray shade, with white representing the highest possible value. Consumer agents expend energy at some metabolic rate, and in some versions they also expend energy in proportion to their movement. A consumer agent reproduces if sufficient energy is available, and dies if its energy falls to zero. It cannot remain stationary or within a particular cell for very long, since the metabolic consumption of even one agent exceeds the regeneration rate of the resource cell. Agents in these models are afforded a myopic version of bounded rationality, moving at each time step in the direction of greatest resource availability among the cell locations immediately adjacent to their current location. Spatially, consumer agents are points that can lie anywhere within the grid cells. The landscape consists of 80x80 such cells and may be set up with or without periodic boundaries. Model details and code are available from the author.



Figure 1. The modeling interface for this study consists of switches, sliders, and indicators for model structure and operation; graphs of important global statistics; and a dynamic representation of the model landscape.

Generally, consumer agents are afforded different degrees of freedom in certain functional variables. At any particular moment in a simulation lacking any diversity, all consumer agents roam the landscape at a single velocity, or exhibit a single metabolic rate. In otherwise equivalent simulations exhibiting functional diversity, populations of consumer agents roam the landscape with a variety of velocities, or exhibit a variety of metabolic rates. Two different types of diversity models are implemented with respect to reproduction and the persistence of diversity. In one, a distribution of values in the diversity variable (e.g., agent velocity) is given to the initial population of mobile agents, but the descendant(s) of each agent must assume the value of its parent. This represents a sort of 'static' diversity. In the other type of diversity model, all descendants over all time steps assume values from a distribution whose central value is that of the parent. Clearly, this latter type represents a more dynamic sort of diversity, which allows for (and does indeed result in) statistically measurable adaptation to changing circumstances.

In most of the models investigated here, only a single 'species' of consumer agent is present on the landscape. The initial number of randomly located individuals could be varied, but remains constant over all simulations intended for comparison with regard to diversity. However a number of models were investigated in which two separately tracked 'species' of consumer agents are simultaneously present on the landscape. The two species represent different degrees of diversity in the key variable, but they are otherwise equivalent. These models are designed to investigate any competitive advantage afforded by diversity. Of course, the initial numbers of individuals of each species is always equal.

At each time step, global statistics are compiled, graphed, and saved for further analysis. Among these are the total numbers of consumer agents within each active population, the total energy transferred from the landscape to all consumers during that time step, and the distributions of values among the variables afforded diversity (portrayed as histograms like the one near the top left of Figure 1). Central to studies of consumption and production are indicators of efficiency, which are often used as objectives for optimization. Here a simple index called 'yield' is calculated at each time step, defined as the quotient of total energy consumed during that time step over the total current number of consumer agents, for each species.

3. Results

The results discussed here are preliminary, but they are stable and repeatable. The initial number of consumer agents placed randomly about the landscape is found to have little or no influence on the results of the simulations in which dynamic equilibrium conditions were achieved. The various combinations of values in variables influencing energy production, consumption, and transfer do influence the outcomes. Under most conditions investigated, population densities achieve dynamic equilibrium conditions after about one to two hundred time steps. In other cases, extinction of consumer populations occurs, as the result either of over-population and global famine, or internal over-consumption of available energy. Since these investigations are designed to explore the effects of agent diversity and do not represent real world conditions, energy balance variables were initialized to avoid such extinctions. A wide range of variable combinations yield dynamic equilibrium conditions. Diversity experiments were conducted under various conditions. While quantitative results differ between such energy balance combinations, qualitative differences within each combination of simulations under different 'diversity'

conditions are the same. In other words, these results are robust with regard to different energy flux conditions.

3.1 Pattern formation

Perhaps the most dramatic and unexpected effect of the introduction of a diversity of consumer agent velocities concerns the appearance of wavelike patterns of consumption over the landscape. When all agents and their descendents move with a single velocity, the resulting patterns of landscape energy values have either no visible pattern or have ephemeral patterns that display nearly scale-free size-frequency distributions, very much like those of computational SOC 'forest fire' models (Figure 2a). When an initial population is given a diversity of velocities (e.g., a normal distribution with a mean of 1.0 cell per time step (cps) and a standard deviation of 0.05), and each descendent of that initial population must maintain the precise velocity value of its parent, with no further diversity, the patterning is more pronounced but also ephemeral. However, when each agent and all descendents over all generations may assume one of a variety of velocities (again a normal distribution with a mean of 1.0 cps and a standard deviation of 0.05), more pronounced wavelike patterns arise, and these patterns remain stable over time. Each wave oscillates with resource availability, but the patterns themselves are stable as families of mobile agents travel back and forth across them. These qualitative results are consistent over many runs, regardless of changes in initial population numbers. Since average velocities can vary over time in this model, it doesn't matter what the initial velocities are; as long as some individuals survive, average velocities soon migrate toward a stable region - in most cases, about 1.0 cps. The non-diverse cases and the case for which diversity was frozen after the first generation are therefore also set to 1.0 cps for valid comparison.

In order to ascertain whether consumer agents actually move substantially in correlation with these wavelike patterns over the course of a run, and whether boundary conditions would affect the patterns themselves, the landscape is modified in one set of models so that it would no longer be periodic (Figure 2c). In a sense, periodic landscapes are useful in that they simulate infinite landscapes. However, since consumer agents in the periodic landscape merely reappear on the edge opposite the one they exit, it is difficult to determine whether wide-scale behaviors are affected by modeling artifacts. The landscape in Figure 2c is bounded by a permanent lack of resources. When mobile agents are afforded directionality toward resources, they merely avoid the boundaries. It is clear that the general type of patterning is not affected by boundary conditions. It is also clear that no macro-level directionality exists in the population of mobile agents.



Figure 2. Typical snapshots after dynamic equilibrium is achieved. Resource availability is indicated by gray shades for a population of mobile agents descended from a single consumer, wherein (a) all consumers roam with a velocity of precisely 1 cell per time step; (b) consumers roam with a distribution of velocities, centered at 1 cell per second but with a standard deviation of 0.10; and (c) same conditions as b except that landscape boundaries are not periodic. The wavelike patterns in both b and c are dynamic but spatially stable and emanate from the locations of particularly successful initial parent consumers.

By portraying agents with directional arrows and visually examining sequences of time steps (Figure 3), it becomes clear that wave fronts initially form around small successful populations of consumer agents even before dynamic equilibrium is achieved. Agents whose velocities roughly match the velocity of the wave front (whose wavelength is related to the regeneration rate of the landscape cells) travel coherently toward the crest of these waves, as each agent seeks cells of highest resource availability in its immediate neighborhood. Traveling waves are formed as landscape cells regenerate in the wake of these front echelons of consumer agents. But since the agents travel with a diversity of velocities, some will travel at velocities significantly different from that of the wave front. In such cases, it becomes increasingly likely that they will begin seeking resources among cells that are regenerating in the wake of a wave front. Bearing in mind that consumer agents are continuously expiring in roughly the same proportions that they are being generated, local conditions variously favor agents with higher or lower velocities, as different stages of each traveling wave passes through a particular localized region. In total, there is no macro-directionality to these agents, although those that travel with the wave front do so more coherently than those that travel against it.

Most importantly, such dynamics cannot be generated without the possibility of a continuous diversity in agent velocity. When all agents have the same velocity, and this velocity matches the regeneration rate of the landscape, a single traveling wave may form around the descendants of each initial parent, but this wave expires as it reaches the edge of a non-periodic boundary or quickly degenerates into randomness in a periodic landscape. If the initial population is afforded a diversity of velocities but each descendent must adopt the velocity of its parent, similar results are obtained. But if each

newly born generation of agents is characterized by a diversity of velocities, many of them are successful (in terms of affecting landscape resource pattern and producing offspring in turn) no matter what the local conditions may be: a situation of coherent moving agents at the crest of a wave with velocities matching the regeneration rate, or a less coherent situation of regeneration in the wake of this crest. Moreover, if the regeneration rate of the landscape is changed by the experimenter (even in the course of a simulation); the patterns formed will change, but they will continue to exist. These characteristics links pattern formation with both yield and resilience, discussed below.



Figure 3. Close-up snapshot of a portion of a landscape with conditions like those in Fig. 1b or 1c, wherein the positions and directionalities of mobile consumer agents are indicated by arrows.

To summarize, when populations of consumer agents are afforded a diversity of velocities, they organize the landscape into wavelike patterns of consumption. This occurs over a wide range of energy flux conditions. The highest densities of consumers are along the 'crests' of these waves, where resource availability is greatest. Agents with different velocities move in other directions as the landscape behind them regenerates. No such patterns are formed when the velocities of all agents are precisely the same. Such landscapes may be entirely random in their resource availability, or they may be similar to self-organized critical landscapes described elsewhere.

3.2 Yield and density

When consumer agents are afforded various degrees of diversity in the values of velocity with which they move about the landscape, results consistently show that higher yields (average instantaneous consumption of landscape resource per individual) are gained through a moderate diversity in the velocities of agents within that population. This is clearly indicated through comparative time series of the yield index, but in order to illustrate this effect more effectively, phase portraits tracking the values of total yield and agent population over all time steps are constructed. Such graphs can communicate the dynamics of joint variables more clearly than simple graphs (Figure 4).



Figure 4. Phase portraits provide an alternative representation of the time series of two coupled variables, as shown in this small segment of a model run. If the connective trajectories are removed, the time-generated scatterplot delineates the dynamical attractors resulting from different conditions, as in Figure 5.

As stated previously, the quantitative values depend on the values of energy flux variables, but as long as such values remain the same over all simulations produced for the analysis of a particular kind of functional diversity, the results are very similar. Figure 5 illustrates the effects of different levels of diversity in consumer agent velocities. In all cases, phase portraits portray data obtained after dynamic equilibrium is achieved (thus delineating the attractor), but not data obtained during the initial period of the simulation (somewhere within the basin of attraction). In the simulations portrayed, velocity diversity is achieved in terms of normal distributions with varying deviations around the mean value. Similar results are obtained with different types of distributions.

Several points can be made regarding these results. First, it is clear that a small to moderate degree of velocity diversity increases yield substantially. However, further increases in velocity diversity have no substantial impact on yield. Indeed, excessive diversity results in somewhat reduced yield (not portrayed). Secondly, a slight overall increase in consumer agent population size occurs with a moderate degree of velocity diversity. Finally, the shape of the attractor changes with different degrees of diversity. With no velocity diversity, moments when the population is relatively high correspond to slightly greater yield. This effect becomes more pronounced with moderate diversity. However, as diversity is increased to 0.10 the correlation disappears, and then actually becomes negative as it is increased to 0.15.



Figure 5. Attractor states differ under different conditions of consumer velocity diversity (deviation). Each phase portraits encompasses 1000 time steps after dynamic equilibrium is achieved in simulations like those shown in Figure 2, with consumer velocity diversity conditions indicated as standard deviation around 1 cell per time step. These portraits indicate that higher yield is achieved at similar population densities with greater velocity diversity, and that the instantaneous values of population and yield correlate differently with different diversities. Results are robust and repeatable over many runs.

It is not surprising that increased yield is associated with the wide-scale selforganization of the landscape into wavelike patterns of regeneration. More highly organized landscapes present better opportunities for production; this is the basis of agriculture, for example. Even when known threats and instabilities exist, these can be minimized through defensive structures (as in HOT). But when agents maintain the capacity for 'degenerate' behaviors, which may not be entirely optimal or even rational under given current conditions, yield remains high and resilience is improved, if self-organization is allowed to occur.

3.3 Resilience

Results regarding resilience under different conditions of diversity are not fully discussed here. Various experiments were performed with populations of single species of consumer agents whereby energy variables were changed mid-simulation, after dynamic equilibrium conditions are achieved. Generally, it was found that populations exemplifying diversity in either velocity or metabolic rates are somewhat more resilient to global collapse after sudden, detrimental changes to resource availability or energy flux conditions than populations without such diversity. Diverse populations are certainly more resilient than non-diverse populations under gradually changing conditions of resource availability. This is not surprising, since the adaptive capacity of diverse populations can often keep pace with such conditions. Non-diverse populations, by contrast, often experience rapid decline and extinction when critical thresholds pertaining to energy flux balances are exceeded.

In experiments with two competing sets of agent populations, the population with greatest diversity in either velocity or metabolic rates is more likely to achieve and maintain dynamic equilibrium under adverse conditions than populations with less diversity. A population with no diversity among individual agents will often not survive when in competition with a more diverse population, even if it does achieve equilibrium on the identical landscape without the presence of the competing diverse population (Figure 6). These results certainly have significance with regard to evolutionary dynamics. They also may point the way to more pragmatic responses to environmental change, and may highlight the potential importance of preserving localized biodiversity, for example, in agriculture. In scenarios of competing populations characterized by different degrees of functional diversity, the population with the greater diversity maintains higher population densities, although both populations generally survive.



Figure 6. Two initial populations, each of ten randomly placed consumer agents, compete and develop in a model otherwise equivalent to the previous models. If all members of one population have a precise velocity of 1 cell per time step and/or a precise metabolic rate, and the other population is afforded a diversity of values in either velocity or metabolic rate, the former population will often not survive beyond the initial transient period. Without the presence of the competing, diverse population, the former population would survive and achieve dynamic equilibrium.

4. Discussion

In normative science, diversity is often overlooked in favor of analytic mean-field solutions. However, sciences that examine structurally and functionally complex non-stationary domains, like geography, must do a better job of representing and examining the effects of functional diversity. Here, we have briefly demonstrated the effects of simple manifestations of diversity on spatiotemporal pattern formation and resilience in common pool distributed resource environments. Detailed analyses of all results are not included here, since the models are not meant to represent real world situations. Instead, we have compared selected results, since those left undiscussed to not contradict the general results. The impact of various degrees of functional diversity on otherwise equivalent situations is significant. Diversity not only results in the formation of wide-scale patterns; it increases yield and improves resilience.

The results regarding patterning, yield, and resilience can be situated in relation to SOC and HOT conditions. Various researchers have found evidence of SOC in the dynamics of many physical, biological, and geographic phenomena. Ephemeral organization and dynamically stable scenarios with generally improved yield occur at the 'edge of chaos', as localized collapses keep systems from crossing critical thresholds and prevent total collapse from occurring. If a geographic domain is structurally defended from known threats, it can be optimized for higher production or yield, a situation that can be associated with HOT. However, neither of these theoretical constructs considers the functional diversity present in the real world.

Let us compare SOC and HOT with the sort of consumption scenarios investigated in this paper (Figure 7). If a population is randomly distributed on a landscape, it becomes more vulnerable to extinction through overconsumption as its density increases. The percolation of collapse through this resource can become nearly global as its density surpasses a critical density value p_c. SOC is characterized by a power law distribution of minor and major (but less than global) collapses and regeneration that maintain dynamic stability in many natural circumstances at densities just short of p_c. Structural defenses in HOT environments allow densities and yields (defined as production minus any diversions required for defense or survival) to surpass SOC thresholds. However, such scenarios remain vulnerable to global collapse resulting from the failure of defensive mechanisms or the advent of threats for which they are not designed. It is suggested here that complex domains characterized by functional diversity among individuals in a population or locations in a landscape may self-organize in ways such that yields comparable to those achieved in HOT are possible, but with less risk.



Figure 7. Schematic representation of the locations of attractors in the space of yield versus density, for generalized production and consumption scenarios. SOC implies self-regulation of population densities below a critical threshold. HOT can exceed this threshold, but remains vulnerable to conditions unforeseen in its design. Functionally diverse populations

can result in greater yields than SOC, and their adaptive natures make them less vulnerable to collapse than HOT.

High yield is generally associated with coherent patterns of production and consumption. In low-yield, random environments, no stable patterns occur. In SOC environments, localized patterns are generated, but they are ephemeral. In HOT environments, patterns are explicitly designed. The scenarios described in this paper result in patterns that are wide-scale and generally stable, but are not the result of explicit design or optimization. Instead, they express the self-organizing capabilities of diverse populations of autonomous agents, even absent explicit communication between these agents. In addition, high yields result, and the population may be more resilient and adaptive to unforeseen threats than in HOT environments. If we broadly consider SOC as characteristic of the 'natural' world and HOT as characteristic of anthropogenic design, further investigations of functional diversity may yield practical results that could shed light on the generation and avoidance of geographical collapse in any domain.

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