

CONTAGIOUS DISTURBANCE AND ECOLOGICAL RESILIENCE

By

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CONTAGIOUS DISTURBANCE AND ECOLOGICAL RESILIENCE

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Managing the consequences of anthropogenic transformation of the biosphere requires understanding the processes that create, maintain, destroy, and restore ecological organization. In this dissertation I examine the ability of contagious disturbance processes, such as fire and insect outbreaks, to create and destroy ecological resilience.

Using computer models I examine the consequences of changes in fire regime on the organization of two specific ecosystems. I demonstrate that in north Florida forests both wildfire and the current management practice of periodic controlled burning are insufficient to maintain the landscape, but a policy that applies controlled burns based upon the vegetative condition of an area could be effective.

I compare the responses of climate and fuel-accumulation driven models of fire in the boreal forest. I demonstrate that climate models are more sensitive to climate change than fuel accumulation models, but are more vulnerable to abrupt reorganization. I use these specific explorations to construct two general conceptual models: the first of contagious disturbance, and the second of ecological resilience.

My model of contagious disturbance defines disturbance agents, stress accumulation and release, chain reactions and evolutionary epidemics as four key sub-types

of contagious disturbance. I identified initiation, reproduction, contagion, virulence, and recovery as the five key properties of a contagious disturbance regime, and show how a change in the relationship of these variables alters the behavior of contagious disturbances. These models provide general insights into the consequences of specific ecological organizations, allowing qualitative predictions to be made about the behavior of a poorly understood disturbance process.

My model of cross-scale resilience proposes that ecological resilience is generated by diverse, but overlapping, functions within a scale and by apparently redundant species that operate at different scales. The distribution of functional diversity within and across scales allows regeneration and renewal to occur following ecological disruption over a wide range of scales. The consequences of species or ecological process loss may not be immediately visible, but it decreases ecological resilience to disturbance or disruption. It produces ecosystems that are more vulnerable to ecological collapse, and reduces the variety of possible alternative ecological organizations.

INTRODUCTION

Ecological Reorganization

The Earth is currently undergoing a biospheric reorganization, as the expansion of human constructed or dominated ecosystems at the expense of natural ecosystems is altering climate, mineral cycles, land cover, and biotic communities (Vitousek et al. 1997). Human ecological expansion is mainly occurring at the meso-scale, between the global and the local. The meso-scale is the scale at which people live and transform ecosystems through activities such as agriculture, human settlement, and forestry (Harris 1984). It is these activities that drive much of global change and it is through changes to these activities that people will experience much of the impacts global change.

Anticipating and coping with the surprises that these anthropogenic transformations will bring requires an understanding of how the interaction of ecological dynamics across scales shapes ecological organization (Kates and Clark 1996). It requires understanding the processes that create, maintain, and restore resilient ecosystems, as well as understanding the processes that disrupt and destroy them. In this dissertation, I examine the cross-scale relationship between ecological resilience and disturbance.

Resilience and Disturbance

Ecological resilience is the ability of a system to persist despite disruption (Holling 1973). Ecological resilience assumes that an ecosystem can exist in alternative self-organized or 'stable' states. It is a measure of the amount of change or disruption that is required to transform a ecosystem from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures.

A disturbance is an event that disrupts the functioning of an ecosystem. A disturbance process produces disturbances at a frequency slower than the time it takes the disturbed system to recover. I differentiate between contagious and non-contagious disturbances. Non-contagious disturbances have a fixed temporal frequency and spatial impact that is externally imposed upon the disturbed system. Contagious disturbances are disturbances that propagate through a system, such as fire or a flood. Consequently, their size and behavior emerges out of the interaction of the disturbance process and the system being disturbed. In this dissertation I disregard non-contagious disturbances and focus upon contagious disturbances, because contagious disturbance processes connect ecosystems across scales.

Disturbance and resilience are intimately intertwined with one another. Disturbance disrupts ecosystems. This disruption can overwhelm an ecosystem's resilience causing it to reorganize. However, resilience is often maintained by the diversity and heterogeneity produced by disturbance. Disturbance both produces and destroys resilience. The key to this apparent paradox is the scaling relationship of disturbance and resilience.

Ecological Scale

I define a scale as a range of spatial and temporal frequencies. This range of frequencies is defined by resolution below which faster and smaller frequencies are noise, and the extent above which slower and larger frequencies are background. Different ecological processes occur at different scales. For example, forest fires occur at different scales in space and time from a deer mouse's foraging behavior. Processes that operate at the same scale interact strongly with each other, but the organization and context of these interactions are determined by the cross-scale organization of an ecosystem. It is this type of cross-scale interaction that typically occurs between disturbance and an ecosystem. Small, frequent disturbance often helps an ecosystem, survive, and recover from large, severe disturbance. An example of this dynamic between disturbance and resilience

recently occurred in the South Florida. During Hurricane Andrew in 1992, mature mangrove trees were killed by wind damage, however many young mangroves survived. Many of these young mangroves were located in gaps caused by lightning. Local lightning disturbances provided the mangrove population with increased resilience to the large-scale disturbance produced by Hurricane Andrew (Smith et al. 1994). It is these cross-scale interactions between resilience and disturbance that I explore in this dissertation.

A Dissertation Outline

This dissertation investigates the dynamics of resilience and disturbance from a combination of theoretical and empirical perspectives. I begin the dissertation by providing a motivation for this investigation of disturbance and resilience.

In the second chapter, I discuss the ecological dynamics of global change. I distinguish between natural and anthropogenic global change, provide a brief history of natural and anthropogenic global change, and place current anthropogenic global change in a historical context. This chapter illustrates how a variety of cross-scale processes have provided the resilience that has allowed the biosphere to recover from past global changes, and that humanity's present combination of global changes is reducing the adaptive capacity of the biosphere. Along with the general concern for the health of the biosphere, this also identifies the importance of understanding the resilience of ecosystems and the dynamics of disturbance.

In the third chapter, I discuss problems with translating data and understanding across scales. Assessing the impact of change on ecosystems requires the use of scaling methods, but the resilience of ecological organization to changes in key processes determines the situations in which scaling methods apply, require adjustment, or break down. I propose that ecological resilience can be used to develop scaling methods that incorporate ecological reorganization.

In chapter four, I move from the theoretical considerations of chapter three to detailed cross-scale investigation of forest dynamics in northwest Florida. Resilience and scaling are used to analyze the consequences of contagious fire and seed dispersal across a meso-scale landscape. These concepts are used to compare alternative models of forest dynamics and assess the consequences of alternative land management strategies.

Chapter five, addresses another investigation of forest dynamics, this time in the boreal forest. The organization of the landscape under several alternative models is tested against empirical data, and the sensitivity of the alternative models to climate change is addressed.

Chapter six compresses and generalizes the disturbance models developed in chapters four and five, to produce a general model of contagious disturbance. I identify the key features of contagious disturbance, the variables that define those features, and outline how different relationships among these variables produce different disturbance dynamics. I use these attributes to define four sub-models of my general model, which represent a variety of abstract types of contagious disturbance. These models provide general insights into the consequences of specific ecological organizations, allowing qualitative predictions to be made about the behavior of a poorly understood disturbance process by fitting it into the classification of rates and their relationship.

Chapter seven returns to investigate resilience and its linkages to disturbance. In this chapter, I present a cross-scale model of resilience that integrates disturbance and ecological processes. The model proposes that ecological resilience is generated by diverse, but overlapping, function within a scale and by apparently redundant processes that operate at different scales, thereby reinforcing function across scales. The distribution of functional diversity within and across scales allows regeneration and renewal to occur following ecological disruption over a wide range of scales.

GLOBAL CHANGE AND ECOLOGICAL RESILIENCE

This chapter illustrates how a variety of cross-scale processes have provided the resilience that has allowed the biosphere to recover from past global changes, and that the diverse nature of present day anthropogenic global changes is reducing the adaptive capacity of the biosphere. This decline in the general adaptive capacity of the biosphere will likely manifest itself far more seriously in specific regions. This loss of adaptive capacity supports my argument that understanding the dynamics of ecological resilience and disturbance should lie at the center of applied ecology.

In this chapter I discuss the history and dynamics of natural and anthropogenic global change, before comparing modern anthropogenic global change to past global changes, and presenting a simple model of how global change is eroding adaptive capacity.

Global Change

Global change is different from ecological change at smaller scales. The dynamics of a local or regional ecosystem may be strongly influenced by fluxes and migrations from neighbouring systems, but there is little interaction of the global biosphere with its external environment (Barlow and Volk 1992). The globe receives energy from the sun, and emits heat to space. It receives heat and minerals from beneath the crust, and returns reorganized materials through the ocean floor. However, these fluxes are tiny compared to the fluxes of material and energy in Earth's biogeochemical cycles (Schlesinger 1991).

The closed nature of the Earth means an accumulation or decline of material at a global scale will not be counteracted by external fluxes. This is not true at a local scale. For example, as a plant removes CO₂ from the air near the plant that CO₂ is rapidly replaced

by CO₂ from the surrounding air. At the global scale, CO₂ emissions and fixation have to match, or the stocks of CO₂ begin to change.

At the global scale, change that occurs is largely due to endogenous dynamics. Evidence suggests that an asteroid may have been precipitated the Cretaceous mass-extinctions, but the other mass-extinctions appear not to have had an external trigger (National Research Council 1995). Similarly, recent glacial cycles are probably driven by changes in the Earth's orbit around the sun. However, the magnitude of the global change caused by relatively minor changes in solar input is due to the amplifying power of Earth's endogenous dynamics (Bartlein and Prentice 1989). These internal dynamics are dominated by the biosphere.

Over the history of the Earth, the expansion and diversification of the biosphere have caused massive changes in Earth's physical, chemical, and biological organization altering the Earth's response to external variation (Schlesinger 1991). Today, the expansion of the Earth's human population and the enormous amplification in the power of human technology that has accompanied it is driving a transformation of global flows of energy, materials and biota that overshadows natural global change (Vitousek et al. 1997). This anthropogenic change is combined and intertwined with the natural dynamics of the Earth system. In one sense this combination is trivial, in that for those impacted by global change the cause of that change does not matter. But, understanding how the Earth works, and designing effective policies to mitigate and adapt to global change requires distinguishing the natural and anthropogenic drivers of global change.

Understanding consequences of the human transformation of the Earth system requires understanding the natural dynamics of the Earth system itself. The study of the dynamics of the Earth system is a prerequisite for disentangling the natural and anthropogenic components of global change. In the following sections I outline these two interacting components of global change. I begin with a discussion of the evolutionary

dynamics of the Earth system, before describing the expansion of humanity within the biosphere.

Earth Systems

The evolution of Earth's biosphere has driven periods of revolutionary global change. The study of history provides a rich set of past world organizations that represent alternative configurations of the Earth system. The exploration of how the Earth system responded to past global change helps provide clues to how the Earth will respond to present day global change. In this section I outline Earth's past global changes to place present day ecosystems and ecological change in perspective. I discuss the Earth's relationship with the sun, its internal geophysical dynamics, and the evolution of the biosphere.

Earth and the Sun

The sun has changed over the history of the Earth. It has gradually become brighter, about 25% brighter over the past 4 billion years, and this change has increased the amount of solar radiation reaching the Earth (Lovelock 1988). Over shorter periods, Earth experiences significant variations in the distribution of solar energy upon its surface and timing of that energy. Along with this gradual increase in luminosity, the Earth's orbit around the sun introduces cyclical variation into the amount of sunlight the Earth receives.

Variation in Earth's orbit and a wobble in the tilt of its axis vary the sunlight the Earth receives (Bartlein and Prentice 1989). There are three cycles occurring at different time scales. The slowest change is in the eccentricity of the Earth's orbit. Over 100,000 years it varies between being near circular and being more elliptical. This change alters the difference between Earth's seasons. Over a period of 41,000 years the tilt of the Earth's axis varies. The degree of tilt alters the Earth's seasonality, and therefore temperature differences between the northern and southern hemispheres. The fast cycle, with a period of 23,000 years, corresponds to change in the seasonality in Earth's orbit of Earth's closest approach to the sun. This change either mitigates or enhances seasonality and differences

between the Northern and Southern Hemisphere. It appears that these orbital variations interact in some way with one another and Earth's biosphere, but the interaction is not clear. Variations in polar ice volume are synchronized with these cycles. Until 800,000 years ago, ice ages corresponded strongly with the frequency of axis wobbles, but after that time, ice ages correspond better with the variation in the shape of Earth's orbit (National Research Council 1995). The reasons for this shift in the process driving ice ages are unclear, but either changes in the Earth's biosphere or global oceanic or atmospheric circulation patterns could alter the relative importance of different forms of variation.

Earth's Internal Dynamics

The long term cooling of the Earth drives continental drift (Westbroek 1992). The difference between the hot molten core of the Earth and its surface produces convective currents within the Earth. These currents gradually move the pieces of Earth's crust apart and against one another, generating continental drift. These forces continually rework Earth's surface, splitting continents apart and crashing continents together (Schlesinger 1991). Continental drift has had a major impact on the history of life, bringing together biota that are novel to one another, as well as encouraging speciation by dividing populations and ecologies (Briggs 1995). Also continental drift has driven climate change, by changing the configuration of ocean basins and the location of mountain ranges has altered global oceanic and atmospheric circulation patterns (Ruddiman 1990). Over long periods, continental drift has altered atmospheric composition by producing gas-emitting volcanoes. This effect was strongest early in the history of the Earth.

The development of the Earth's biosphere has diversified Earth's biogeochemical cycles. Mutual reinforcement among these processes tends to self-organize sets of processes that are relatively stable, because interactions among processes that are unstable tend to extinguish themselves (Lovelock 1988). However, the biosphere has periodically been reorganized as new biogeochemical pathways have been created by interaction of

biotic evolution with changes in Earth's geochemical environment. These revolutions have produced fundamentally different biospheres.

One of the central aims of global change research is to assess to what degree human alteration of the Earth is eroding the ability of the current Earth system to maintain itself despite disruption. By examining past reorganizations of the biosphere, current changes and their future consequences can be placed in context. In the following sections, I summarize the history of different Earth system regimes, and the transitions between them, focusing on the development of the biosphere and evolution of novel biogeochemical cycles.

Origin of Earth and the Biosphere

The Earth was formed about 4.5 billion years ago, as planets condensed into orbit around the sun. During its initial development it was bombarded with cosmic debris, which increased its size, and heated the planet to such an extent that it was liquefied, and denser substances migrated towards the core of the Earth. Over time, collisions reduced the amount of the solar debris and the rate at which the Earth was pummeled by meteorites. At this time, about 3.8 billion years ago, the first traces of life are found (National Research Council 1995).

The composition of the Earth and its position in the solar system define internal and external bounds on Earth's biota. The Earth receives the bulk of its energy from the sun. The Earth itself provides heat from radioactive decay, but its main contribution to life is the materials that comprise the Earth, and the chemical energy that they contain. Between the rock of Earth and the space of the solar system the biosphere developed. In the following sections I sketch a brief history of the biosphere, and then discuss how variations in Earth and Solar dynamics have altered the dynamics of the biosphere.

Early Life – the Archean

The biosphere covers the surface of the Earth, and extends at least several kilometers in the Earth's crust and up into the Earth's atmosphere is supported by energy

from the sun, mineral energy from the Earth (Pedersen 1993). The earliest life was almost certainly dependent upon chemical energy, but photosynthetic bacteria soon evolved directly linking life to incoming solar energy (Volk 1998).

While the early history of life on Earth is difficult to reconstruct, one of the earliest consequences of life was a reduction in atmospheric CO₂, as bacteria sequestered carbon. This decrease in CO₂ liberated oxygen. Rather than increasing atmospheric oxygen levels, this oxygen reacted with oxidizable material in the Earth's oceans, atmosphere, and crust. The early Earth was probably a reducing environment, and certainly there were many oxidizable materials on the early Earth. The oxidization of iron dissolved in seawater, produced iron deposits that provide the earliest evidence for photosynthesis (Schlesinger 1991).

Transition to an Oxygen Atmosphere

Between about 2.2 and 1.9 billion years ago (bya) the oxygen increased from being just a trace gas to composing as much as 3% of the atmosphere (Volk 1998). The cause of this rise in oxygen is unclear. It could have been due to increased rock weathering burning more carbon, a decrease in emissions of reducing gases and CO₂ from volcanoes as the Earth cooled, or an increase in the biomass of aerobic bacteria.

It is suggestive that this period corresponds with an expansion of the biosphere. During this time eukaryotes evolved from prokaryotes. Eukaryotes are more efficient photosynthesizers than prokaryotes. Whether an increase in oxygen facilitated the evolution of eukaryotes, or eukaryotes facilitated the rise in oxygen levels is unclear. However, the proliferation of eukaryotes established a positive feedback, as aerobic bacteria encouraged the growth of more aerobic bacteria.

A combination of these processes may have produced the rise in oxygen, because processes such as rock weathering and biotic oxygen production are not mutually exclusive, rather they are mutually reinforcing. As an increase in bacteria populations,

particularly if they colonized land and rock fractures, would have accelerated rock weathering (Schwartzman and Volk 1989).

There was another pulse in atmospheric oxygen between 1 - 0.6 bya. This oxygen pulse also occurred synchronously with a diversification of life. In this case, the rise of oxygen accompanied the development of metazoan life (Canfield and Teske 1996).

Another suggestive feature common to both these revolutionary reorganizations of the biosphere is that both rises of oxygen were accompanied by declines in CO₂ and severe glaciations (Hoffman et al. 1998).

The paleoecological record suggests that as the biosphere became more diverse, the gradual accumulation of oxygen triggered global ecological crises. However, these crises were likely overcome by the negative feedback effect of biospheric cycles. For example, if an increase in oxygen lowered global atmospheric CO₂, reducing the warming produced by the greenhouse effect, this cooling would reduce the rate of plant growth, allowing CO₂ to increase again established a climate more favorable to life (Lenton 1998).

Land Plants

Following the origin of metazoan life, the next major reorganization of the Earth system was the colonization of land by plants. Plants accelerated weathering by a variety of means. Plants increased the surface area of rock weathered through their root networks. By breaking apart rocks they facilitated the creation of organic soil, which increased the ability of water to weather minerals in the soil. These increases in weathering probably removed atmospheric CO₂ (Berner 1997).

Furthermore, this period coincides with the evolution of lignin by plants. It appears that plants used lignin for several million years before fungi developed the means to break apart lignin (Robinson 1990). During this lag period, large amounts of lignin were buried, removing large amounts of carbon from the atmosphere until fungi evolved the ability to decompose lignin. This process may have allowed oxygen levels to climb to their highest levels ever, perhaps even up to 30% of the atmosphere (Lovelock 1988). Beyond this

oxygen concentration, organic matter becomes extremely combustible, and fire would act to decrease oxygen concentrations.

Expansion of Carbon Cycling

Another key ecological transformation was the evolution of calcium carbonate precipitating plankton. These plankton fundamentally altered Earth's carbon cycle, and perhaps even plate tectonics when they evolved 200 million years ago (mya). By producing calcium carbonate (limestone) from CO₂ and calcium they removed CO₂ from the atmosphere. By moving carbon deposition into the deep sea these plankton, surprisingly, made CO₂ more available to the atmosphere. Large volumes of limestone precipitated by plankton were pushed underneath continental plates. Some of the carbon in this limestone was returned to the surface through volcanoes, recycling carbon through a slow cycle driven by continental drift. Limestone deposition may even accelerate continental drift, and consequently carbon cycling (Lovelock 1988, Westbroek 1992).

Development of the Biosphere

The functional elaboration and diversification of life on Earth over geological time has increased the number of biogeochemical pathways in the biosphere. These pathways often perform similar functions, but do so at different scales. For example, carbon is cycled between the ocean and the atmosphere over minutes, while carbon moves from the seabed to the atmosphere over hundreds of millions of years.

A general pattern in the development of the biosphere is that the gradual accumulation of low entropy, high-embodied energy waste products, such as oxygen or lignin, accumulated to the extent that they provided a utilizable resource. In turn the evolution of new functional groups to take advantage of this concentrated energy lead to the accumulation of new waste products, containing ever more embodied energy. This ratchet of complexity has allowed the elaboration and articulation of Earth's biosphere.

The existence of a diverse set of ecological functions, such as the various steps of biogeochemical cycles, that are replicated at many temporal scales, such as the many separate pathways in the carbon cycle, suggests that the development of the biosphere may have produced an increasing ability to respond to variation or disturbance across wide variety of scales. Whether this is indeed the case, or not, is unclear. Life has been able to maintain itself and the Earth's temperature, in the face of a 25% change in the sun's output (Lenton 1998, Lovelock 1988). The response of the present globe to more subtle changes in the in Earth's distance from and orbit around the sun, and continental drift is more complicated.

Multiple Climate States

Biospheric reorganizations appear to have interacted with the Earth's geophysical dynamics and solar forcing to produce alternative stable states in the Earth system. At the scale of hundreds of millions of years the Earth appears to have alternated between periods in which glaciation was possible, what have been termed 'icehouse' worlds, and those in which it is not, 'greenhouse' worlds.

The most recent transition between these organizations of the world was 34 mya. At that time continental drift caused a change in the world ocean circulation triggering a planetary cooling, shifting the Earth from a 'greenhouse' to an 'icehouse' state. This occurred when continental drift caused Australia to separate from Antarctica, allowing water to circulate uninterrupted around Antarctica at the South Pole. Prior to this event, the Earth's oceans were broken into a series of basins, in which cooler and warmer water mixed. The circulation of cool water around the south pole, cut off polar water from mixing with warmer temperate water, and established a steep temperature gradient between pole and equator which lead to the deep water circulation of cold Antarctic water across the ocean floor (Prothero 1994).

The cooling of Antarctica may have established a positive feedback cycle, because as Antarctica cooled it began to accumulate ice, which in turn increased the albedo of

Antarctica, causing it to absorb less heat from the sun, cooling the continent further, allowing glaciers to develop and spread (Briggs 1995). Another possible cause of global cooling was the uplift of the Tibetan plateau, which probably led to increased weathering, removing CO₂ from the atmosphere (Ruddiman 1990). Regardless of the exact cause or combination of causes, these changes moved the world from a 'greenhouse' to an 'icehouse' state.

During this current icehouse regime, the world has been repeatedly glaciated. It has alternated between, short warmer inter-glacial periods and longer, cooler glacial periods. During the course of this recent 'icehouse' regime, oceans have shrunk, novel plant metabolic pathways formed, and new animal communities emerged (Cerling et al. 1997). It was in this low CO₂, cool, and dry world that humanity's ancestors evolved, and humanity came into being.

Expansion of Humanity

One hundred thousand years ago the ancestors of modern humanity were a population of several hundred thousand large hunter-gathers living upon the African savanna. Today, a population of almost 6 billion people live in all over the world, in highly organized aggregations, in ecosystems that have been largely shaped by human action (Cohen 1995). During this time, an ice age ended, global sea levels have changed - altering the configuration of continents, a wide variety of large mammals, birds and reptiles became extinct, and entire ecosystems have reorganized.

The greater part of humanity's expansion occurred during the past few centuries (Figure 2-1), whether measured in absolute population size, population growth rate, or energy and material use per capita. In the two hundred years from 1600 to 1800 the world's population increased about 1.7 times, while in the two centuries from 1800 to 1995 the world's population increased 6.3 times (Figure 2-2). Similarly, the amount of

non-animal or plant energy used per person/year increased about 28 times from 1800 to 1900, and another four times from 1900 to 1987 (Cohen 1995).

Malthus & Darwin: Limits & Adaptation

All living things are subject to limits to their growth. Malthus observed that populations often grow faster than their ability to acquire new resources, leading to resource shortages (Malthus 1798). These resource limitations bound the increase of a population. This Malthusian relationship suggests that populations should grow until they reach their limits, and then remain or oscillate around that steady state. Darwin's theory of natural selection extended this Malthusian dynamic (Darwin 1859). He noted that not all individuals in a population are identical. If some individuals have traits that enable them to obtain resources better than other individuals, then those individuals are more likely to reproduce than others. Darwin's theory of natural selection, showed how a population could adapt to a set of environmental limits and possibly find ways to escape from that set of limits.

Human societies being able to learn and reorganize their means of production are more able than most species to adapt and innovate to escape from Malthusian pressures. Indeed, the demographic expansion of humanity has progressed hand-in-hand with the expansion of humanities ability to manipulate and construct ecosystems. Locally increased population densities, put more pressure on local ecosystems. This pressure causes ecological degradation and, in some cases, inspires innovative forms of ecological engineering. While many societies become caught in a Malthusian trap some societies managed to innovate to temporarily escape from Malthusian pressures, by reorganizing their local ecologies to increasingly support humans rather than other non-human ecologies, and these innovations usually spread to other groups (Goldstone 1991, Spicer 1996). While these reorganizations have enabled phenomenal growth in humanity, by increasing the amount of ecological production aver by people, they have removed resources and support from non-human ecosystems.

Human Regimes

Many innovations have expanded the resources available to people. To organize my discussion I consider four expansions of anthropogenic ecological domination: the domestication of fire, agriculture, long distance trade, and public health. These ecological innovations were made possible by combinations of technological and social innovations that did not occur simultaneously around the globe, but rather occurred unevenly as innovations spread out from various centers. However, the spread of these ideas by conquest and trade makes these transitions meaningful at the coarse global scale (Spicer 1996), and despite some regions of poverty and disorder, the major proportion of the world's population has passed or is passing through these ecological transformations.

There is a suggestion of these transitions in the population data of Figure 2-1 and Figure 2-2. When the same data is displayed on a log-log graph, the ever accelerating nature of these transitions can be seen (Figure 2-3). On a log-log graph, exponential growth produces a curve that initially climbs steeply, before flattening off. Therefore, any portion of a log-log graph with an increasing or constant slope indicates an accelerating growth rate. On Figure 2-3, there is an acceleration at about 10,000 years ago that coincides with the introduction of agriculture. Similarly, the expansion of global trade 500 years ago, and global public health measures of the past 50 years both boost growth until the fertility declines of the past decade, which is more clearly shown in Figure 2-4. While the quality of the data plotted in Figure 2-3 is low, the figure does suggest that humanity as a whole has been quite successful at evading Malthusian limits. I discuss each of the expansions of human dominated ecosystems in more detail below.

Fire

Fire has large ecological effects, strongly influencing vegetation growth and succession, and consequently animal community dynamics (Bond and van Wilgen 1996). Humans probably domesticated fire about half a million years ago (Goudsblom 1992). Fire may not have been the first, but it was certainly one of the most powerful early

ecological engineering tools that humanity mastered. The effect of this event on human population growth is hidden in the distant past, but it is reasonable to assume that it was large.

People have used fire for hunting, war, and agriculture all over the world. Indeed, one of the most common paleoecological records of human settlement is an increase in charcoal in lake sediments (Goudsblom 1992). Records from Australia (Kershaw 1988), New Zealand (Flannery 1994), and North America (Cronon 1983) all show evidence of increases in fire frequency with the arrival of people. The domestication of fire also aided in food preparation, allowing people to expand the range of food items that they could consume.

Agriculture

Agriculture probably was invented about 10,000 to 12,000 years ago, following the last ice age (Diamond 1998). Agricultural domestication of plants and animals allowed people to develop novel variations of natural ecosystems that channeled their production into resources for people.

Agriculture is unremarkable in a fashion; after all ants have domesticated aphids and fungi. However, people have relentlessly innovated - expanding the range of plants and animals domesticated, and physically restructuring places to channel energy and resources away from non-human ecosystems towards human-dominated ecosystems.

Trade

Agricultural innovation was expanded through trade. The local diffusion and spread of technologies and domesticated plants and animals has occurred for a long time, as is evidenced by the spread of the banana from New Guinea to Africa (Diamond 1998). However, ecological engineering received a large leap forward following the European discovery of the Americas, which integrated the world's population into a single world system (Wallerstein 1974). Between 1650 and 1850s, this system became tightly integrated through trade, and migration. The transport of domesticated plants and animals

among disparate regions greatly increased agricultural yields (Cohen 1995). The impact of the potato and maize upon Europe and the sweet potato and Manioc upon the tropics provide two examples of the greatly increased agricultural yields that followed these agricultural modifications (Crosby 1972, Diamond 1998).

Public health

Humanity's novel ecosystems produced novel problems. By requiring denser human settlement agriculture changed conditions for human ecosystem parasites and diseases (McNeill 1976). Global trade and transport connections also encouraged the development of epidemic diseases. While novel human ecosystems provided support for humanity, they also created new ecological niches for parasites, such as rats and cockroaches, and pathogens, such as tuberculosis and smallpox (Crosby 1986). While medicine improved during the 19th century, it was only in the 20th century that public health programs managed to massively decrease mortality from epidemic diseases such as smallpox, malaria, and tuberculosis. At the same time, sanitation measures re-engineered urban ecosystems reducing mortality from infection. Following the Second World War massive worldwide immunization and sanitation programs public began to have great success (McNeill 1976). These programs can be regarded as ecological engineering. By eliminating disease populations, by immunization, and reorganizing human ecosystems through sanitation and other public health measures public health programs greatly reduced or even eliminated many of humanities parasites. This reduced human mortality, allowing population growth rates to increase to their highest levels (Figure 2-4).

Recently, a fifth transition appears to be occurring. In the past decade fertility rates have declined (Figure 2-4). The phenomena is diverse and not well understood, however it may represent an important advance in the ability of people to regulate their own reproduction, or it may be a temporary side-effect of an increasing average age (Cohen 1995, Lutz et al. 1997).

Despite this recent decline in the fertility rates population growth is expected to continue until the world's population is near 10 billion people, six times the world's population at the beginning of the 20th century. This growth in absolute population size, the human ability to innovate, and the desire for an improved material standard of living is expected to increase the human domination of Earth above its already high levels.

Human Domination

Humans currently dominate the structure and functioning of Earth's ecosystems. The human impact on the Earth has increased at an accelerating rate due to the increase in human population and concomitant increases in per capita use and consumption of natural resources, expanded technological capacity to access resources, and the expansion of human settlement over the globe (Turner et al. 1993). These increases mean that humanity has, and will probably continue, to expropriate an ever-increasing share of the Earth's renewable and nonrenewable resources and increasingly rearrange and reengineer the Earth's physical, chemical, and biological systems.

Anthropogenic global change is usually divided into a number of separate classes that are usually considered in isolation, despite the well recognized links that exist among them. Below I provide a quick outline of the dimensions of several key types of anthropogenic global change, specifically land-use/land-cover change, atmospheric change, ecological appropriation, biodiversity loss, and the modification of biogeochemical cycles. I follow this discussion with my approach to integration.

Land-use/Land Cover Change

Humanity currently uses 2/3 of vegetated land and an estimated 40% of net primary productivity (NPP) of this land (McNeely et al. 1995). The ability of humans to transform landscape is ancient, perhaps beginning with the domestication of fire thousands of years ago. The invention of agriculture, and irrigation amplified the role of humans as ecological engineers.

Land use change involves conversions from one type of land cover to another, as well as changes in management practices. For example, the area of forest converted to agriculture or grassland since pre-agricultural times is estimated to be about 8 million km², with 3/4 of this land cleared after 1680 (Turner et al. 1993). Similarly, about 7 million km² of grassland have been converted to agriculture, and 0.5 million km² has been submerged beneath artificial lakes (Turner et al. 1993).

Land-use/land cover change directly alters the amount and distribution of various ecosystems, and biota. It also alters ecological dynamics such as the dispersal of biota (Harris 1984), the provision of ecological services to neighboring locations (Forman 1995), and the interactions of between vegetation and the atmosphere (Pielke et al. 1993).

Atmospheric Change

Anthropogenic emissions are altering the composition of the atmosphere. Land use change has resulted in net addition of large amounts of CO₂ and methane, along with other gases to the atmosphere (Walker and Steffen 1997). More importantly, the combustion of large volumes of fossil fuel has also increased atmospheric concentrations of CO₂ and nitrogen compounds.

The atmosphere's current CO₂ concentration is about 360 ppm, and increasing (Walker and Steffen 1997). In the centuries before industrialization, the atmosphere maintained a concentration near 280 ppm (Schlesinger 1991). Global average temperature is closely correlated to atmospheric CO₂ levels. The Intergovernmental Panel on Climate Change 1995 assessment (Intergovernmental Panel on Climate Change 1995) concludes that increased concentrations of CO₂, and other greenhouse gases, have probably already altered the world's climate, and that this alteration is likely to become more extreme in forthcoming decades.

Furthermore, the production and emission of CFCs has caused decreases in stratospheric ozone, as well as being a strong greenhouse gas. These decreases in ozone

have increased the amount of ultraviolet radiation reaching the Earth's surface, particularly near the North and South poles.

Ecological Appropriation

Humanity uses a significant proportion of the Earth's total ecological production. Recent estimates put humanity's use of terrestrial ecological production at between 39 % and 50 % and our use of oceanic production at about 8% (Vitousek et al. 1997). This ecological production is unavailable to non-human ecosystems, and is suggestive of both the large stress that humanity is placing on the global biosphere, and of the limits to further growth in the amount of ecological production that humanity appropriates.

Modification of Biogeochemical cycles

Human action has for most of history altered biogeochemical cycles through the modification of the environment, for example by burning a grassland. However, the ability of modern industrial societies to mine and synthesize minerals and chemicals has caused humans to directly alter global chemical cycles.

The synthesis of phosphate and nitrogen fertilizer has doubled the global cycle of these key ecological nutrients (Vitousek 1994), driving a global eutrophication of terrestrial and aquatic ecosystems.

Mining and fossil fuel use has greatly magnified the amount of poisonous heavy metals in the globe's biogeochemical cycles. For example, the amount of lead has increased twenty five times, cadmium seven times and mercury ten times (Turner et al. 1993).

The success of synthetic chemistry has unleashed a massive wave of novel synthetic substances into the global environment that have produced novel biogeochemical processes. These introductions have often had, unexpected negative impacts on people and animals. The most recent danger is the potential consequences of ubiquitous endocrine disrupting chemicals (Colborn et al. 1996).

Loss of Biological Diversity

Humanity's spread across the world over the past tens of thousand years appears to have initiated a mass extinction episode. The spread of people to the New World (Martin 1984), Australia, and New Zealand (Flannery 1994), the Pacific archipelago (Steadman 1995), and other islands (Crosby 1986, Diamond 1992) all instigated regional mass extinctions. Estimates of current extinction rates suggest that the current rate of species loss is 100 to 1000 times greater than the average pre-human rate of species loss (Lawton and May 1995).

Currently several different forces appear to be driving biodiversity loss: habitat loss, harvesting, and biological invasions. Habitat loss is due to land-use/land cover change, which was mentioned above, as well as ecological appropriation of the resources that animals and plants require to survive and reproduce. Secondly, harvesting and hunting of animals is due to ecological appropriation of the animal and plant populations themselves. Thirdly, biota has been purposely and accidentally transported within human transport networks. Transported biota can compete with, prey upon, or modify the physical environment of native biota, frequently producing large ecological impacts (Lodge 1993). Furthermore, biodiversity loss may occur due to previous extinctions. A species creates habitat or provides food for other species, its extinction can lead to the extinction of its dependent species.

Comparing Human and Historic Global Change

The magnitude of modern anthropogenic change appears to be roughly comparable to past revolutionary global changes. The biosphere has been able to adapt to these changes. For example, about 6 to 7 million years ago, the continuing decline in atmospheric CO₂ led to the evolution of C₄ metabolism plants, which are able to survive warm temperatures and moisture stress better than C₃ plants at current atmospheric CO₂

concentrations. However, these adaptations have all occurred on an Earth in which the biosphere has been unconstrained in its response to these changes.

Present day anthropogenic global change is disrupting a disrupted biosphere. The current biosphere is not as free to adapt as in the past. Humanity demands a variety of ecological services, such as food production, from human ecosystems thereby constraining the degree to which these ecosystems can be allowed to adapt to global change. Humanity and our constructed ecosystems have greatly reduced the extent of non-human dominated ecosystems. This reduction may have been as much as 50% (Vitousek et al. 1997), but it appears to be at least 10% (Gorshkov 1995). This elimination of much of the Earth's adaptive capacity will likely reduced the ability of the biosphere to respond to anthropogenic global change.

Past innovations in biogeochemical cycling appear to have often resulted in crises in global biogeochemical regulation. As discussed above, the development of an oxidizing atmosphere and the evolution of land plants, lead to periods in which global regulation of climate broke down, leading to global glaciations.

Present day anthropogenic global change is reorganizing global cycles to a degree comparable to past ecological revolutions. Human alteration and acceleration of biogeochemical cycles, the burning of fossil fuel, and the synthesis of novel chemicals has produced a wide variety of new biogeochemical pathways, many of which are significant proportions of global fluxes (e.g. N, P, Hg) or are new materials with significant effects (e.g. CFCs). The synchrony and extent of these changes increases the possibility that another collapse of Earth's homeostatic processes may occur. The biosphere has managed to survive past collapses at the cost of mass extinctions and ecological reorganization. Probably, humanity could also survive an ecological collapse, but such a collapse would have immense human, economic, and spiritual costs.

A simple conceptual model of the impacts of global change illustrates the risk of the simultaneous degradation and alteration of global ecological processes. The integrated

impact of various global change processes depends upon the degree of interaction among these separate changes. If these processes are independent of one another, then their combined impacts can be obtained by adding the individual impacts together. If global change processes are not independent of one another, but rather positively interact with one another, then their integrated impacts can be obtained by multiplying the impacts together.

I illustrate this model by considering the linkages among the global change processes. Usually, the response or adaptation to a global change process depends upon the flexibility of other components of an ecosystem. For example, more reliable ecosystem services appear to be produced by diverse ecosystems (Holling et al. 1995). Reductions in the diversity of species inhabiting a watershed may reduce the ability of that watershed to reliably provide an ecological service, such as clean water. Similarly, the adaptation of ecosystems to climate change, depends upon the presence of a diverse pool of species that can flourish under different sets of conditions. If biodiversity loss and land-use/land-cover change, eliminate species or their ability to migrate across a landscape, the historical ability of ecosystems to adjust to climate variation will be greatly reduced.

The different risks associated with the independent and interaction models can be clearly illustrated by representing the using a Gaussian probability distribution to characterize the impact of a global change process. For example, consider the interaction of four different processes (Figure 2-5). A comparison of the independent and interactive models of integrative global change reveals two key differences between them (Figure 2-6). First, the uncertainty surrounding the integrated impacts of global change is much less if processes are independent than if they interact with one another. Secondly, severe impacts are much more likely if processes interact with one another. This suggests that the framework used to integrate global change processes strongly influences the prediction of risk. While this model of system responses to change is simple, it illustrates the importance of interaction between processes, and the importance of taking an integrated perspective.

Summary

Anthropogenic global change appears to be of the same magnitude as Earth's previous periods of revolutionary ecological change. However, the biosphere and humanity are probably in a more brittle state during this transition than during past transitions, due to the increasing proportion of the Earth's biosphere that is used by humanity. The likelihood that humanity's domination of the biosphere is reducing the resilience of the Earth to anthropogenic global changes underscores the importance of analyzing the resilience of Earth's biosphere.

The meso-scale is also the scale at which people live and structure the landscape. These meso-scale activities drive much of global change, and it is through changes to these activities that people will experience much of the impact of global change. In the following chapters I analyze how changes in larger scale processes impact the dynamics of the meso-scale, and the interactions that meso-scale processes have with larger and smaller scale processes.

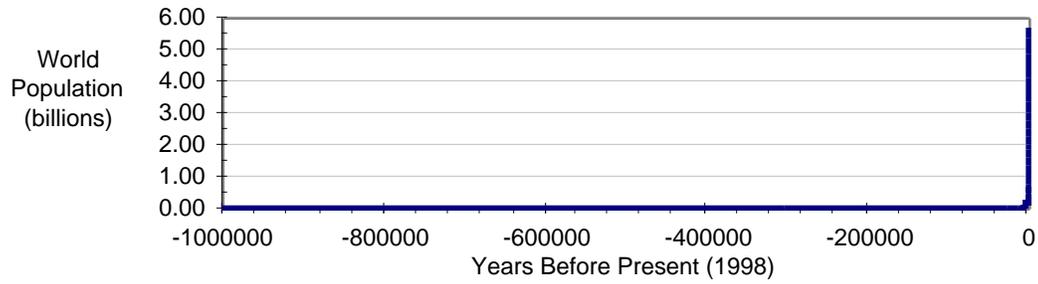


Figure 2-1. The size of the global human population over the past million years. The early data is estimated with much less accuracy than the most recent data, but on the scale of this graph even large relative errors in estimating the past are dwarfed by the magnitude of current human population. Data are from Cohen (1995).

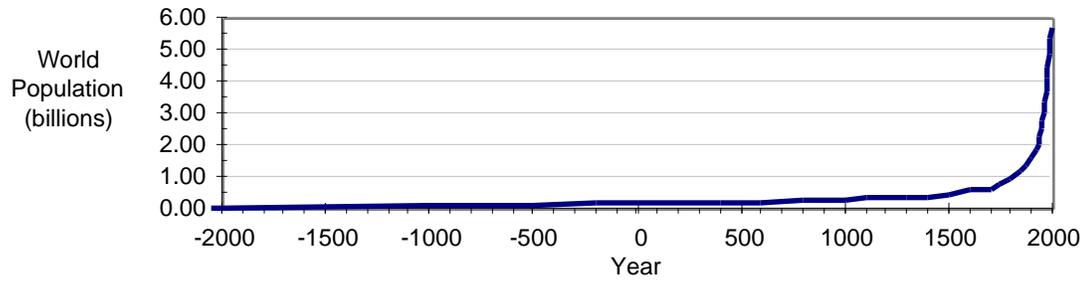


Figure 2-2. The size of the global human population over the last four thousand years. Examining the recent past more closely indicates the most of human population growth has occurred quite recently. Data are from Cohen (1995).

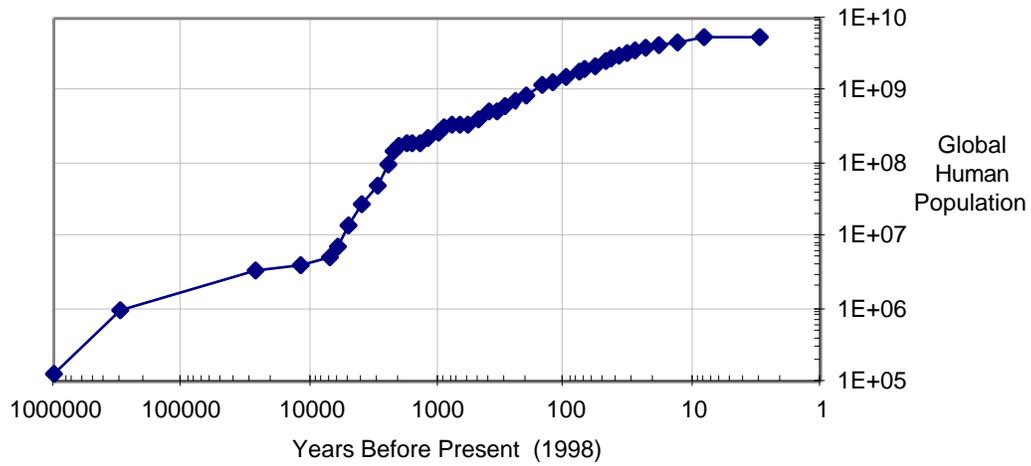


Figure 2-3. Population of the Earth over the one past million years. The data is plotted on a log-log scale, diminishing relatively recent large absolute changes. This presentation shows that the population growth rate has varied greatly over time. On this graph simple exponential growth follows a curve with a decreasing slope. Data are from Cohen (1995).

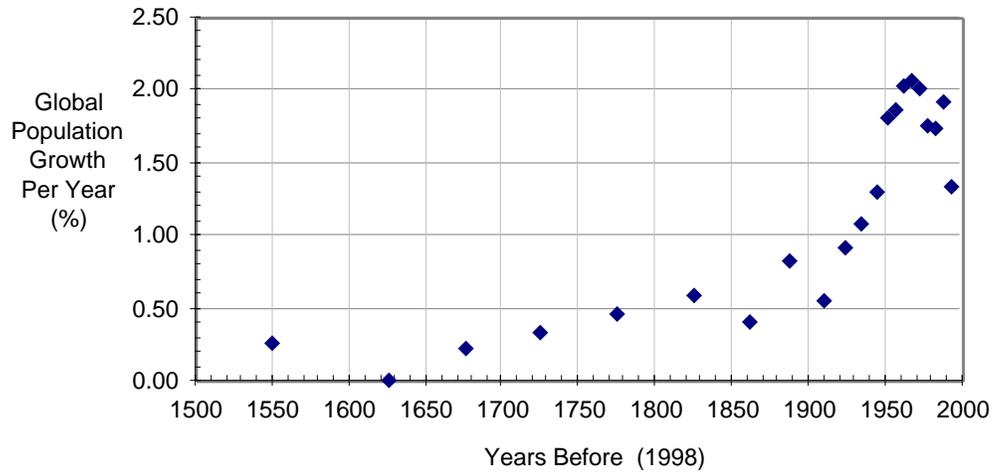


Figure 2-4. Estimated yearly growth rate of humanity over the last five hundred years. The global population growth rate has clearly increased over the past few centuries, and especially over the last fifty years. While recent growth rates are lower than the 1950's or 1960's they are still higher than any time before then. Data are from Cohen (1995).

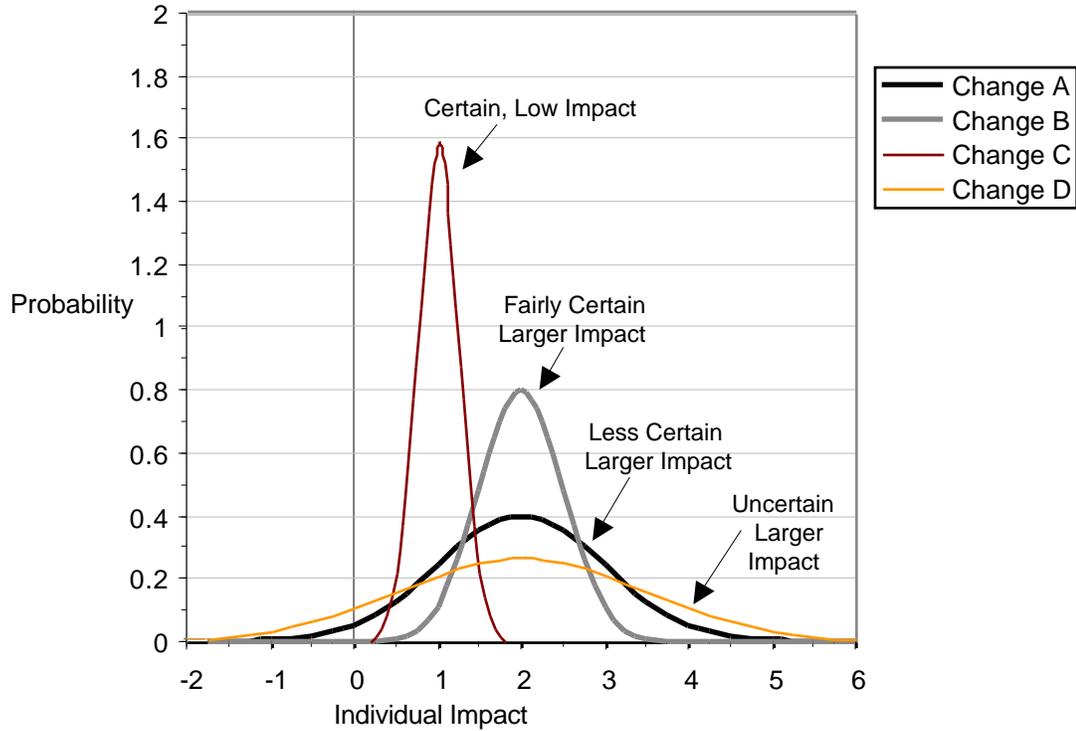


Figure 2-5. Example estimated probability distributions of impacts of four imaginary global change processes. The impact of A is low and quite certain. The impact of B is less certain, but expected to be larger. C is also expected to produce a large impact, but less certainly than B. It could even have a positive impact. Similarly, the impact of D is expected to be large, but it is highly uncertain. Its impact may quite substantial, or it may be insignificant.

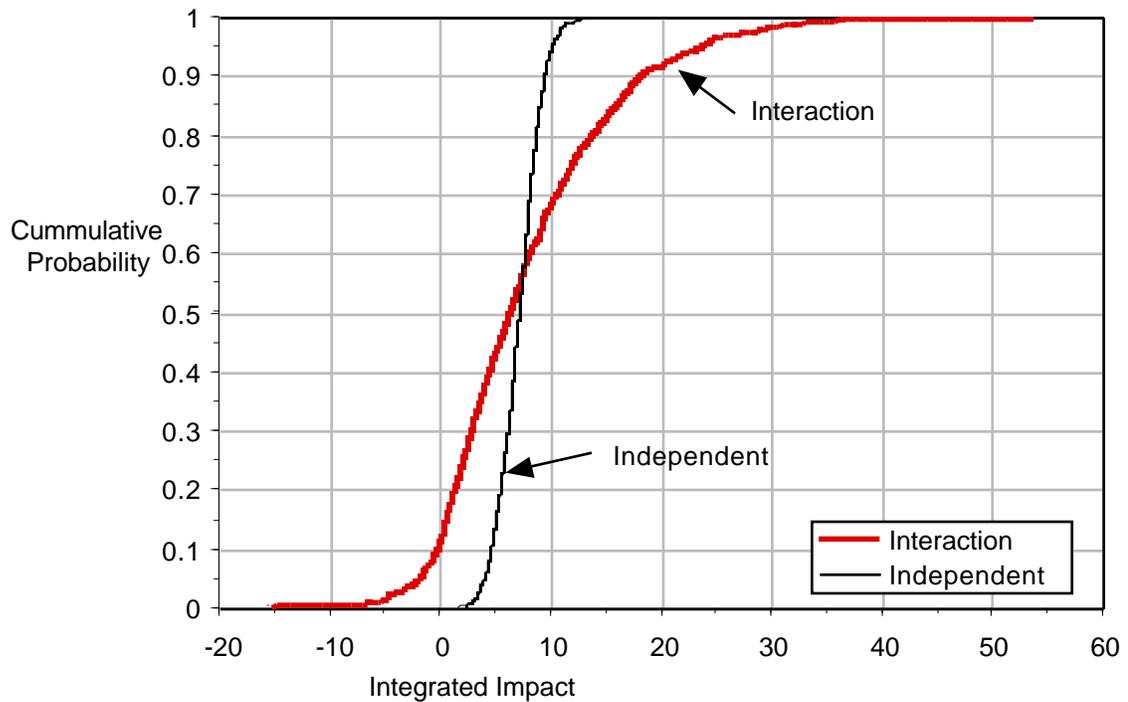


Figure 2-6. The integrated effect of the global change processes A, B, C, and D is quite different depending upon whether they interact following the Interaction or the Independent model. The cumulative probability distribution for the integrated impacts, shows that minimal or extreme impacts are much more likely with process interaction case, than with process independence. If the processes are independent, they have a 95% chance of having a cumulative impact less than 10. However, if the processes are interactive they have an only a 70% chance of having a cumulative impact less than 10, and a 95% chance of having a cumulative impact of less than 24.

SCALING ECOLOGICAL DYNAMICS: SELF-ORGANIZATION, HIERARCHICAL STRUCTURE & RESILIENCE

Introduction

Global change research centers much of its efforts on understanding the global consequences of local actions, and how global changes impact specific, local sites. These efforts require techniques that are able to translate understanding developed at one scale to other scales. Unfortunately, it is usually quite difficult to ‘upscale’ results from small scales to large scales and ‘downscale’ the results of global models to local sites (Ahl and Allen 1996, Levin 1992, Wiens 1989).

Finding useful ways of translating across scales requires understanding the problems that scaling presents, which I outline in the next section. I then discuss cross-scale interactions, focussing on the analysis of hierarchical structure, the identification of hierarchical reorganization, and the search for the potential alternative organizations. Finally, I discuss how ecological resilience and scaling are intertwined using an example from the boreal forest. But first, I discuss the problems of scaling.

Scaling Problems

Global change research continually confronts upscaling and downscaling problems. Upscaling involves applying the results of a local study to a wide region, such as extrapolating the effects of an experiment on CO₂ fertilization of trees in a forest plot to the response of the entire boreal forest to an increase in global CO₂ levels (Körner 1996). Downscaling involves moving in the opposite direction. Downscaling attempts to determine the local consequences of a large scale change on a local site, such as the impact

of global climate change on agricultural production in a field (Parry et al. 1996). Most global change research has used simple scaling methods, such as averaging or interpolation, to translate data across scales.

Unfortunately, these methods often fail to adequately map processes from one scale to another. For example, variation of ecosystem productivity to CO₂ fertilization is not the sum of the variation in the response of individual species, but due to compensation and complementarity among species the response is far less (Körner 1996). These methods fail for four related reasons: non-linearity and environmental heterogeneity, dominance of different processes at different scales, cross-scale connections, and emergent processes.

Non-Linearity and Heterogeneity

First, and perhaps fundamentally, ecological processes are usually non-linear. Local non-linearity combined with the spatial heterogeneity of the world means that the aggregate large-scale behavior of local processes is difficult to predict (Levin 1976). For example, the process of fire interacts with the ecological structure provided by tree species in North Florida sandhill communities. Either oak (*Quercus* spp.) or longleaf pine (*Pinus palustris*) tends to dominate these communities. The interaction of fire with fire-suppressing oaks and fire-encouraging pines produces a non-linear relationship between the time since a site has burned and its combustibility. A lack of fuel tends to suppress fire in oak stands, encouraging the growth of more oaks, while fuel accumulation in stands of pine tend to encourage fire, suppressing oaks and encouraging the growth of pine (Abrahamson and Hartnett 1990, Rebertus et al. 1993).

The ability of fire to spread, and consequently the stability of patches of oak or pine, is determined by the distribution of oaks and pine across the landscape. The combination of spatial heterogeneity and positive feedbacks make the dynamics of forest difficult to predict from the study of a local site, since processes that define a site are determined by the properties of its neighbors.

Different Processes Dominate at Different Scales

Different processes dominate at different scales. This observation can be illustrated by examining vegetative pattern in the North American boreal forest (Figure 3-1). The growth of an individual tree is determined by vegetative processes influenced by factors such as light availability, soil moisture, nutrient availability, and temperature. Studies of tree growth, in small 1 m² plots over several years, have produced a great deal of knowledge of tree growth, and these studies have been synthesized in simulation models. These models predict that shade-intolerant tree species should gradually be replaced by shade-tolerant trees (Bormann and Likens 1981). However, this replacement does not occur in the boreal forest, because large-scale spruce budworm (*Choristoneura fumiferana*) outbreaks periodically defoliate and kill large areas of shade-tolerant balsam fir (Blais 1983). These outbreaks require large areas of susceptible trees to begin, but the presence or absence of susceptible areas cannot be detected by small-scale studies. Therefore, up-scaling local observations requires the accounting for the presence of budworm dynamics at larger scales.

The presence of different dominant processes at different scales means that as a scaling method attempts to span a wider range of scales, it needs to incorporate the effects of an increasing number of processes. Scaling methods can either ignore or incorporate shifts in dominant processes across scales, but both approaches have problems. Ignoring changes in structuring processes can produce an inaccurate scaling method, however more complex scaling methods that incorporate multiple processes may be too complicated or costly to use effectively.

Cross-scale Connections

Processes at different scales do not function independently of one another. Processes operating at small and fast scales are constrained by processes that operate at slow and large scales, but these large and slow processes are constructed and organized by the interactions of many small fast processes (Ahl and Allen 1996). These cross-scale

connections make scaling difficult, because scaling relationships only hold if organization at other scales remains constant. However, change occurs at all scales.

The dynamics of spruce budworm illustrate the importance of cross-scale connections. Large scale budworm outbreaks are connected to local forest dynamics via tree mortality. At the local scale, an individual tree is connected to the large scale by providing a rich food source and refuge from predation that are required for outbreaks to occur (Ludwig et al. 1978). In this case, these cross-scale connections allow the forest to be organized into either a cycle of budworm outbreaks or local low-level budworm infestation (Clark et al. 1979). In the forests of New Brunswick, logging and spraying to suppress the budworm changed the existing state of the forest from large even-aged stands with periodic large outbreaks, to smaller and denser even-aged stands with chronic shifting budworm infestations (Baskerville 1995).

Alternative behaviors, emerging from the same processes, demonstrate how understanding developed at one scale may only be relevant or useful as long as the structures and processes at other scales that are maintaining system organization persist. These cross-scale connections suggest that scaling can only apply over specific ranges of scale and in specific situations. Forest pattern would scale differently in a forest that has periodic budworm outbreaks, than it would in a forest experiencing chronic budworm infestation. By recognizing alternative ecological organizations and assessing what drives the shifts among them, analysts could improve scaling methods. Separate scaling methods could be developed for each alternative organization, and the rules for transitions among alternatives could be used to synthesize these separate scaling methods into an aggregate scaling method that incorporates the behavior of the ensemble of states.

Emergent Processes

Occasionally the interaction of process and pattern at one scale produce emergent organization at a larger, slower scale. For example, the interaction of air and water circulation over tropical oceans can produce a self-reinforcing vortex, which strengthens

itself as it draws in increasing volumes of warm air. The continued growth of this vortex produces a hurricane (Barry and Chorley 1992). Emergent processes form due to non-linearity across heterogeneous space (Nicolis and Prigogine 1977). Many small fast processes repeatedly interact to produce a larger slower structure that constrains the behavior of the small processes in such a way that they mutually reinforce one another. Such emergent processes are self-organized. They are not created by some outside force, but are created from the mutual reinforcement of their component processes. Emergent processes present the strongest challenge to scaling theories, because they demonstrate that in some situations systemic change is not only non-linear, but also structural.

Emergent processes are common in ecology (Perry 1994). They exist in all of the previous examples. For example, the interaction of tree growth, avian predation, and budworm population dynamics can create either budworm outbreaks or chronic budworm infestations. Slight changes in avian predation can shift budworm dynamics from infestation to outbreak behavior (Figure 3-2). The ecological consequences of outbreaks are qualitatively different from dispersed chronic budworm infestation. Budworm outbreaks increase budworm densities over a thousandfold above non-outbreak budworm densities. At these high densities budworm defoliation kills trees over large areas. The death of a large number of trees during a short period of time over large area alters nutrient cycling, tree growth, forest combustibility, and create large even-aged stands that have the potential to trigger future budworm outbreaks (Clark et al. 1979).

The production of emergent pattern and process complicates scaling, for it suggests that the organization that is being analyzed can abruptly reorganize, rendering previously developed scaling relationships invalid as the structures and processes that they incorporate cease to exist. This issue is particularly important in global change research, as global change will change ecological organization and processes in novel ways leading to the production of unexpected ecological processes and structures (Kates and Clark 1996).

Coping with Scaling Problems

Simple scaling, using addition or integration fails when the scaling problems discussed above apply. Attempting to scale processes by adding new processes and variables as the scale range of a model increases will work across small ranges of scale, but will become unmanageably complex across broader ranges of scale. Both of these approaches are static. They are based upon the assumption that the current organization of structure and processes will persist over time. The existence of emergent processes demonstrates that cross-scale organization is dynamic. Translating across these scales in a dynamic manner requires understanding existing cross-scale ecological organization, possible alternative organizations, and pathways by which systems can reorganize (Figure 3-3).

Self-organizing systems appear to be structured by a few key variables (Holling et al. 1996), which suggests that identifying these variables, and constraints under which they interact will allow a dynamic, parsimonious method of translating across scales. In the following sections of this paper, I present a framework for the analysis of cross-scale interactions based upon self-organization, and then apply this framework to the analysis of cross-scale resilience.

Cross-Scale Interactions

Ecological organization emerges from the interaction of structures and processes operating at different scales. Traditionally, the effects of scale on the organization of ecological systems have been analyzed using hierarchy theory. Hierarchy theory focuses upon the consequences of hierarchical organization, but translating information across spatial and temporal scales also requires understanding how hierarchical organization is constructed and how it falls apart.

Hierarchy Theory

Hierarchy theory is an extension of systems theory that attempts to analyze the effects of scale on the organization of complex systems (Simon 1974). Hierarchy theory does not assume that a system is necessarily hierarchically constructed. Rather, it divides the world into hierarchical levels to simplify the analysis of cross-scale interactions (Ahl and Allen 1996, Allen and Starr 1982, O'Neill et al. 1986).

Hierarchy theory regards the world as systems that are comprised of components. It views a system as a set of interacting components (i.e., lower-level entities) that is itself a component of a larger system (i.e., a higher level entity). A hierarchical system is composed of a set of coupled subsystems (O'Neill et al. 1986). Hierarchical organization removes or attenuates interactions between system components. In a non-hierarchical system any components may interact with any other; however in a hierarchical system components are grouped into sub-systems that interact strongly internally, but only weakly with other sub-systems (Simon 1974).

Hierarchy theory analyzes ecological patterns by separating the large from the small, and the fast from the slow. Hierarchy theory has been used to organize analysis at different scales, both spatially and temporally. Ecologists have analyzed how vegetation patterns and the processes organizing pattern change with spatial scale (Krummel et al. 1987, O'Neill et al. 1991). Similarly, the constraints of slower temporal dynamics on faster processes have been analyzed at a variety of scales. For example, fire frequencies in the southwest United States are constrained by El Niño fluctuations (Swetnam and Betancourt 1990). This approach is useful for analyzing existing ecological configurations, but it is not as useful for understanding the formation, dynamics, and reorganization of hierarchies.

Hierarchical Organization

The concept of a hierarchy is a human construct, but natural hierarchical organizations may have arisen because hierarchy offers life a more stable alternative to

'flat', non-hierarchical organization. Because hierarchical construction increases stability, systems with hierarchical organizations should be able to form and persist (Holling 1992a, Simon 1974).

Simon (1974) uses a parable of watchmakers to illustrate the advantages of hierarchy. He describes one watchmaker who uses a hierarchical watch construction, while another does not. When the work of the two watchmakers is periodically disrupted each watchmaker loses his work, but the watchmaker using hierarchical construction, loses only that component. Therefore, even if the costs of hierarchical construction are high and the disturbance rate low, the hierarchical watchmaker is able to produce far more watches than the non-hierarchical watchmaker. This parable illustrates the virtue of modularity as a defense against disturbance. It argues that the ideal complexity of a module depends upon the disturbance rate, and the cost of isolating function within a module. A low disturbance rate encourages complex modules, while a high disturbance rate encourages simple modules.

Ecological organization occurs as processes interact with structure across space and time. For example, the mutual reinforcement between the process of fire and structure provided by longleaf pine will only occur if the fires are started frequently and fires are able to spread across a large area. Otherwise, sites will burn infrequently and fire-encouraging vegetation will be replaced by fire-suppressing vegetation. The mutual reinforcement of fire and vegetation pattern produce spatial patterns of fire, longleaf pine and hardwoods, at a scale larger and longer lasting than any individual fire or mix of vegetation.

Simon's argument can be inverted to understand why and how self-organized hierarchies form in ecosystems. Ecosystems are hierarchically organized, because they are composed of individual organisms and abiotic processes that operate at a variety of scales. The persistence of a particular organization depends upon the degree to which the interactions are mutually reinforcing relative to the degree to which the organization is disrupted. If conditions are favorable, spatial-temporal interaction of structures and

processes produces an emergent pattern at a larger and slower scale than the scale of the processes and structures themselves. These self-organized patterns and processes can, through interaction with other larger and slower processes, organize still larger and slower sets of pattern and process. This type of interaction produces nested hierarchies in nature.

I claim that a nested hierarchy exists in the boreal forest. The forest is composed of stands, which are composed of trees. Patterns at higher scales emerge from interactions at the smaller levels. At the scale of a tree, interactions over tens of meters between trees determine ecological structure. The cumulative impact of a tree and its neighbors, shapes fuel accumulation over a larger area. The larger scale process of fire interacts with this fuel accumulation, to produce stand creating, tree-destroying forest fires. The pattern of patches across the landscape influences larger scale processes, such as moose foraging (Pastor et al. 1993) and weather (Knowles 1993), shape the forest at larger scales. The emergence of new structuring processes at larger scales means that it is inappropriate to consider larger scales simply as aggregations of a large number of small-scale entities.

Hierarchy theory suggests that the rules that organize a hierarchy are the ones that should be used to translate across scales. For example, if higher hierarchical levels average changes in the lower levels, then simple scaling methods, such as interpolation or averaging, are likely to be successful. While, if non-linear processes produce the higher levels then a scaling rule that is appropriate to those specific non-linear interactions can be discovered. For example, the frequency of forest fires of different sizes can be appears to be a function of fire size raised to an exponent (Malamud et al. 1998). This type of power law relationship can be used to scale forest or fire dynamics.

While hierarchy theory can explain why hierarchical organization offers advantages over flat organization, it does not provide much insight into how hierarchical structure forms, changes, or dissolves. Understanding these processes requires examining process dynamics.

Dynamic Hierarchy

The conventional view of hierarchies is static and structural (Pickett et al. 1989, Wu and Loucks 1995), however this approach ignores the processes that build and destroy hierarchical structure. In the past decade, complexity theory has expanded and enriched systems theory, producing a dynamic conception of hierarchy. Holling (1986) has proposed a general model of ecological change that I use to organize my discussion of dynamics in hierarchies.

Holling's adaptive cycle model proposes that the internal dynamics of systems cycle through four phases: rapid growth, conservation, collapse, and re-organization. As unorganized processes interact, some processes reinforce one another, rapidly building structure, or organization. This organization channels and constrains interactions within the system. However, the system becomes dependent upon structure and constraint for its persistence, leaving it vulnerable to either internal fluctuations or external disruption. Eventually, the system collapses leaving disorganizing structures and processes to reorganize a new set of structures. This dynamic can be seen in a forest stand. As a young stand grows it gradually becomes denser, accumulates fuel, and becomes increasingly susceptible to fire. Following a fire, the stand is reorganized as plants resprout from roots or seeds, producing a new forest stand.

The key point of this model is that during the development of a system, its organization changes, and due to these changes there are times when it is either more or less vulnerable to internal and external fluctuations. This point of view acknowledges the importance of top-down constraint on processes, but it also recognizes that during some periods large-scale processes are unstable and are vulnerable to change from below. For example, in a dense old forest damage to an individual tree may allow bark beetles (Coleoptera: Scolytidae) to reach densities at which they can attack and kill nearby healthy trees, initiating an outbreak that can alter forest pattern over a large area (Berryman et al. 1984). Similarly, after clear-cut logging, quick small-scale processes, such as seed

dispersal and competition between seedlings, shape the subsequent development of that site for decades (Bormann and Likens 1981). During other times, slower and larger scale processes are stable and resilient, constraining the lower levels and integrating noisy variation of small, faster processes. It is during the periods of destruction and reorganization that a system is most vulnerable to small, fast processes (Gunderson et al. 1997).

I propose that there are three ways that change propagates through dynamic hierarchies (Figure 3-4). First, change at a higher level alters a lower level due to the constraints that it places upon it. Second, small-scale disturbance can trigger larger scale collapse if the larger system is at a brittle stage in its adaptive cycle. Third, following the collapse of a system, small-scale organization drives the formation of large-scale structure during periods of reorganization. These changes occur within a dynamic hierarchy that is embedded in a larger environment, that is itself composed of other dynamic hierarchies. By considering these hierarchical dynamics a richer set of scaling methods can be developed. For example, a forest that is vulnerable to a bark beetle outbreak will be better represented by different scaling methods than a forest that is not. Identifying the reorganization events that cause an ecosystems scaling to change allows an integrated scaling method to be developed that identifies the conditions in which different scaling relationships are appropriate.

Cross-Scale Change

Ecological organization across scales is the result of the interaction of processes operating at different scales. For organization to persist these interactions must not immediately disrupt one another, rather they should be independent of one another or reinforce one another. But as these processes alter ecological structures, the interactions that are possible change. For example, the accumulation of oak leaves in a forest can suppress the growth of understory vegetation, reducing the possibility of fire. Changes in ecological organization can: alter the scale at which a process functions, eliminate a process

by disrupting the interactions that maintain it, or create new interactions that enable a new process to occur.

The spatial and temporal scale of a fire regime is defined by the cross-scale interaction of fire with relatively slower vegetative processes and faster atmospheric processes (Figure 3-1). The key processes defining a fire regime are the rate of fire ignition, the rate of forest recovery following a fire, and the rate of fire spread. If fire spreads faster than a forest recovers from fire, and forest recovery is faster than the ignition of another fire, then the average fire size is proportional to the rate of recovery divided by the rate of ignition (Drossel 1997). These rates emerge from the interaction of vegetative and atmospheric processes. Changes in these processes that alter these key variables will alter the fire regime. For example, a change in climate that increases the frequency of thunderstorms could increase the rate of fire initiations, which would produce smaller and more frequent fires. Alternatively, a region invaded by pyrogenic grass can recover from fires far quicker, and this would increase the frequency and spatial extent of fire (D'Antonio and Vitousek 1992).

Changes in the scale of fire regime will alter the scale range over which a scaling method works. Incorporating the variables that drive these changes into a scaling method allows scaling methods to become dynamic, because it incorporate changes in scaling relationships into a scaling method. For example, given a scaling law that describes forest fire frequency as a power law of forest fire size (Malamud et al. 1998), simulation modeling could be used to assess the sensitivity of the scaling exponent to changes in fire ignition, forest recovery, and fire spread. This type of analysis could potentially identify when the scaling behavior of an ecosystem would break down.

The emergence, maintenance, and destruction of ecological organization are due to cross-scale interactions. The stability of a given organization over time and space depends upon the nature of these interactions. The strength with which they reinforce one another, their sensitivity to disruption, and the presence of alternate configurations of interactions.

These attributes of ecological organization can be integrated and analyzed from the perspective of cross-scale resilience.

Cross-Scale Resilience

Ecological resilience is a measure of the amount of change or disruption that is required to cause an ecosystem to switch from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures (Holling 1973). As long as an ecological organization maintains its resilience, its organization persists. If the scaling behavior of a given ecological organization can be represented by a scaling method, maintaining resilience also means maintaining the ability to use a scaling method. The limits of an ecosystem's resilience are also the limits to the applicability of a given scaling method. A loss of resilience causes an ecosystem to reorganize, and the scaling behavior of a new ecological organization should be represented by a new scaling method. Resilience emerges from both cross-scale and within-scale interactions (Peterson et al. 1998).

Cross-scale resilience is produced by the replication of process at different scales. The apparent redundancy of similar function replicated at different scales adds resilience to an ecosystem, because disturbances are limited to specific scales, functions that operate at other scales are able to persist. For example, Fragoso (1997) has shown that in Brazil's Maracá Island Ecological Reserve palm seeds are dispersed across a range of scales by a variety of species. Seed dispensers range in size from small rodents, which typically disperse seeds within 5m of parent trees, to tapirs (*Tayassu tajacu*), which disperse seeds up to 2 km. Seed dispersal at multiple scales allows the palm population to persist despite a variety of disturbance processes occurring at different scales, because the trees are distributed across the landscape at different scales. Cross-scale resilience is complemented by within-scale resilience.

Within-scale resilience is produced by compensating overlap of ecological function between similar processes that occur at the same scales. In the previous example a variety of species, including deer, pecaries, primates, and rodents, disperse palm seed short distances (Fragoso 1997). Population fluctuations of a species do not have a large effect on the rate of short distance seed dispersal, because a decline in seed dispersal by one species leaves more seeds available for other species. An increase in seed availability allows other species to increase their seed dispersal compensating for initial decline in dispersal. This compensating complementarity among seed dispersers reduces the impact of population fluctuations on ecosystem function (Frost et al. 1995), increasing its resilience.

By focussing on the cross-scale and within scale sources of an ecological organization's resilience one can assess the vulnerability of a particular scaling relationship to within-scale and cross-scale changes. In the following section I discuss how such an approach has been applied to boreal forest dynamics.

Avian Predation and Spruce Budworm

In the forests of the Canadian province of New Brunswick, outbreaks of spruce budworm periodically defoliate and kill large areas of mature boreal fir forest (Clark et al. 1979, Morris 1963). The specific form that the budworm/forest system organizes into is controlled by a variety of forces including climate, landscape pattern, and avian predation on budworm. Changes in any of these factors can alter the organization and scaling pattern of the forest, but I will focus upon the effects of variation in avian predation.

Avian predation on budworm slows budworm population growth, altering the frequency and extent of budworm outbreaks (Holling 1988). Avian predation can prevent budworm population growth over a wide range of budworm densities. However, at high densities avian predation has a minimal impact on budworm population dynamics, because the per budworm effect of avian predation declines. This decline allows the budworm population as a whole to grow at a faster rate, escaping from avian predation. The range of

budworm densities over which avian predation can control budworm population growth controls the frequency and intensity of budworm outbreaks, and the effectiveness of avian predation is determined by within-scale foraging diversity and cross-scale reinforcement.

Within-scale foraging diversity means that similar sized bird species prefer different prey items. These differences in preferences increase the robustness of predation, because if a particular prey item increases in abundance, it becomes easier to capture, and species that did not previously prey upon it will begin to consume it (Murdoch 1969). These predators switch from their preferred prey because the increasing relative abundance of a resource makes its use less costly. This switching behavior increases the effectiveness of avian budworm predation, because the group of species provides more resilient predation than any single species.

Cross-scale functional reinforcement occurs because different species of birds forage for budworm at different scales. A bird's body size has a strong influence on how it forages, determining the amount of food a bird can consume and the scale at which it searches for food (Peters 1983). At high population densities, budworms are spatially aggregated. The concentration of food that is available in these aggregations allows larger birds to consume budworm. These birds do not eat budworm when it is dispersed, because searching for individual budworm is not worth the effort. Additionally, larger birds forage over wider areas than smaller birds. Consequently, the size of birds that are able to effectively consume budworm and the distance from which they are attracted will increase as the size of local aggregations of budworm increase.

While within-scale and cross-scale diversity do produce effective predation on budworm, budworm populations can escape from control by birds. Local concentrations of budworm can be controlled by bird migration, but budworm increases over a wide area require a huge amount of predation to control. The density of budworm at which avian predation is unable to control budworm populations determines the frequency of budworm outbreaks and their spatial scale. Holling (1988) used Ludwig et al.'s (1978) mathematical

model to calculate that large changes in bird predation, an approximately 50% decline in effectiveness, would be necessary to significantly to shift the scale of budworm outbreaks. I used the same model to illustrate how different levels of avian predation alter the temporal scaling behavior of forest vegetation.

I used Ludwig et al.'s (1978) simple analytical model of budworm outbreaks to simulate budworm-forest dynamics. This is the same model that I used to generate Figure 3-2. This model simulates budworm-forest dynamics through three coupled differential equations that represent slow changes in forest volume, medium term changes in tree foliage, and fast changes in budworm densities.

I used the parameter values of Ludwig et al (1978) as a base case, I altered the maximum amount of predation that was possible in the model. This alteration is equivalent to simulating increases or decreases in avian populations. I generated a millennium of forest dynamics, and then analyzed the variance in forest age using a range of temporal windows. I normalized these variance relationships to be proportional to the maximum variance in each simulation run. Changes in the normalized variance reveal the relative amount of variance present at a scale (Figure 3-5).

The greater the rate of decrease in relative variance at a scale, the greater the proportion of variance present at that scale. Vertical arrows indicate the time scale at which the greatest amount of variance has been lost. These scales correspond to the periodicity of budworm outbreaks at different levels of predation. Reducing predation decreases the scale over which variation occurs. Increasing the amount of predation increases the scale of budworm outbreaks. When predation is increased more than 17% above the base level predation becomes strong enough to prevent outbreaks from occurring, causing forest dynamics to follow a fundamentally different scaling relationship.

The analysis of the sensitivity of scaling relationships to changes in the processes that support a specific ecological is useful in showing how changes in underlying processes shift scaling relationships, and cause them to fall apart. Figure 3-5, shows that the

difference between no predation and 50 % of the base predation is very slight, but that at a 20% increase over the base predation would cause the existing scaling relationship to collapse. This collapse in the scaling relationship corresponds to the difference between the chronic budworm infestation and budworm outbreak that are shown in Figure 3-2.

Such a change occurred in the forests of New Brunswick when pesticide spraying, which by killing budworm is similar to an increase in predation, eliminated budworm outbreaks causing a chronic budworm infestation (Baskerville 1995).

Scaling and Ecological Reorganization

Scaling relationships are essentially models that are used to predict the behavior of a system over space and time, given a few measurements. These models are constructed based upon the analysis of the existing cross-scale dynamics of a system. However, a given set of scaling relationships is unlikely to persist in a world experiencing global change. Global changes in climate, land-use/land-cover, and biodiversity will all alter ecological organization and scaling.

Analyzing the cross-scale dynamics of existing ecological organization allows the assessment of the degree to which change alters scaling relationships, or causes them to collapse entirely. As was illustrated in budworm predation example, models can be used to assess the resilience of ecological organizations. Additionally, if alternative ecological organizations are known, and the causes of switches between these configurations can be determined then multiple relatively simple scaling rules can be used in large models, without explicitly incorporating the dynamics that drive changes in scaling into a scaling method itself.

Conclusions

The dynamics of ecological organization are an essential component of global change research. Global change is the convolution of a huge variety anthropogenic changes in Earth's biosphere, geosphere and atmosphere that all, to some degree, alter

ecosystem functioning. Assessing the impact of change on ecosystems requires the use of scaling methods, but these scaling methods may not apply in an altered world. The resilience of ecological organization to changes in key processes determines the situations in which scaling methods apply, require adjustment, and break down. These analyses can be used to developing scaling methods that dynamically compensate for shifts in ecological organization.

Translating either data or understanding across scales is often difficult, because the interaction of ecological processes self-organize dynamic hierarchical structure. Ecological change can alter the resilience of an ecosystem, cause ecological reorganization, and eliminate alternative ecological organizations.

Ecological change that alters the resilience of an ecosystem may shift its scaling relationship, reducing or expanding the scale range over which a relationship applies, as shown by the analysis of changes in avian predation on budworm. Reduction in predation leads to more frequent outbreaks, reducing the scale of budworm outbreaks. This changes the scaling of forest pattern. Similarly, the loss of large-scale seed dispersal would reduce that scale of forest patterning.

Change may push an ecosystem beyond the limits of its resilience, causing it to reorganize. Ecosystems as diverse as coral reefs (Done 1992), shallow lakes (Scheffer 1998), and woodlands (Dublin et al. 1990) have been clearly shown to switch between alternative ecological organizations. Such ecological reorganization alters an ecosystem's scaling, as new ecological processes operate over different scales.

Furthermore, the addition or subtraction of processes from an ecosystem may eliminate alternative ecological organizations. This appears to have occurred during the Pleistocene when the extinction of mega-herbivores eliminated the disturbance processes that maintained specific ecological organizations (Owen-Smith 1989, Zimov et al. 1995). The loss of a form of ecological organization is extremely difficult to reverse, particularly if that organization was generated by a species that has become extinct (Flannery 1994).

I have argued that by focusing upon the cross-scale processes that create, maintain, and destroy ecological organization scaling relationships can include important ecological dynamics. By analyzing the cross-scale organization of ecosystems, methods for translating across scales can be developed. These scaling methods can be improved by considering the dynamics of cross-scale organization. By perturbing dynamic ecological models, the effects of change on scaling methods can be calculated, and the limits of a system's resilience predicted.

Ecological change that alters the resilience of an ecosystem may shift its scaling relationship; reducing or expanding the scale range over which a relationship applies.

Humanity lives and manages the landscape at the meso-scale. As well as changing the distribution and organization of ecosystems, these activities have also altered the scaling of ecological processes. For example, fire suppression and landscape fragmentation have altered the scaling behavior of fire. In the following chapters I analyze how these types of larger scale processes impact the dynamics of meso-scale processes, and how, in turn, these transformed meso-scale processes influence larger scales.

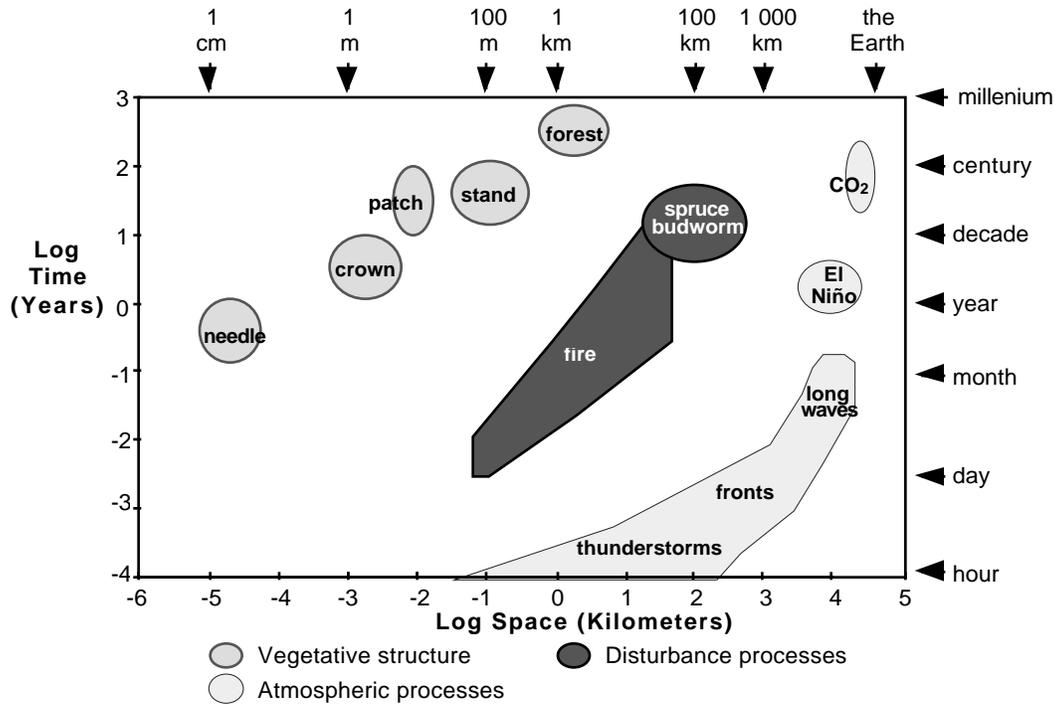


Figure 3-1. Time and space scales of boreal forest structures (Holling 1992a) are compared with disturbance and atmospheric processes which structure the forest. These processes include spruce budworm (*Choristoneura fumiferana*) outbreaks, fire, atmospheric processes, El Niño, and the rapid CO₂ increase in modern times (Clark 1985).

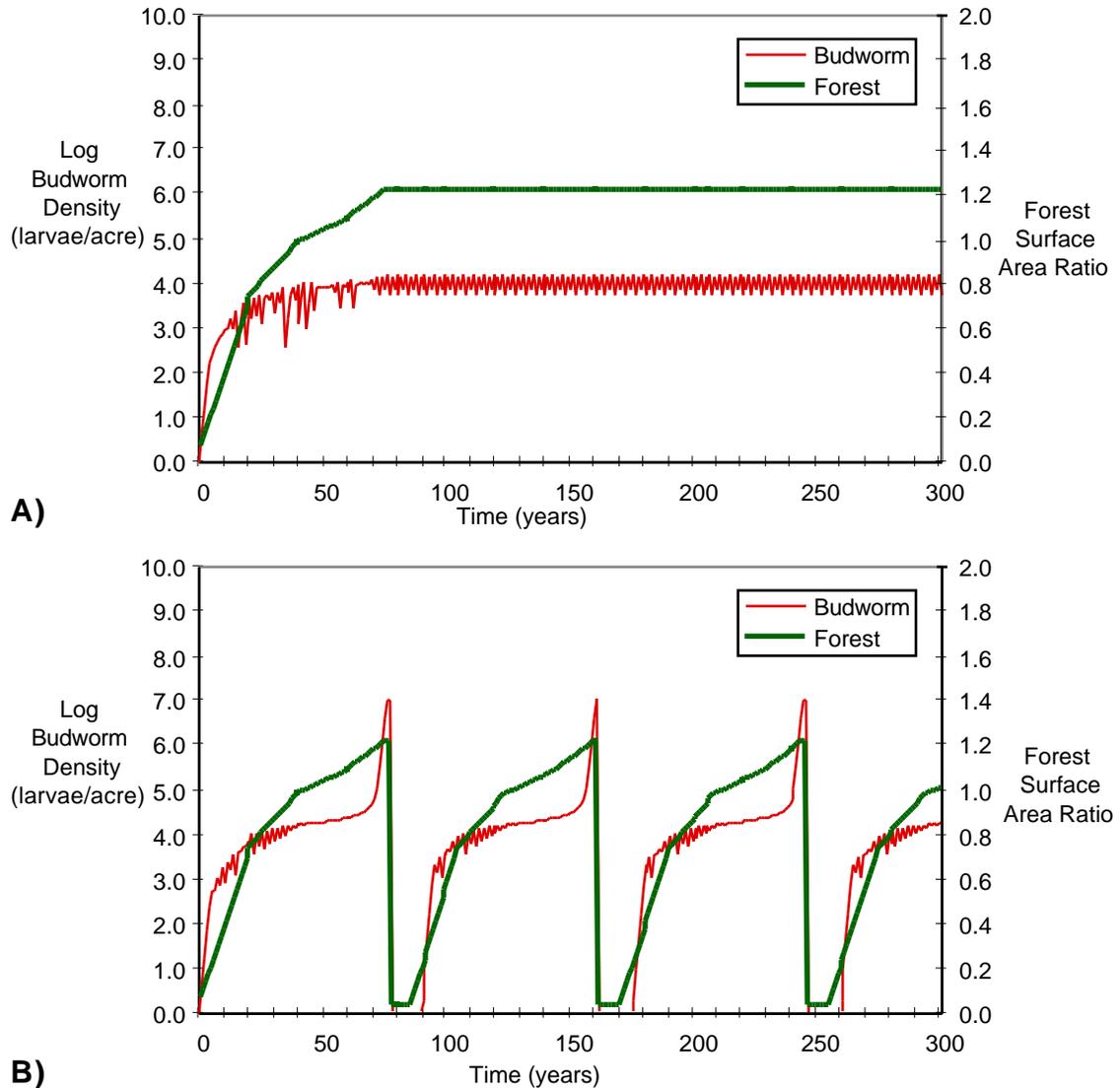


Figure 3-2. Two plots illustrating alternate relationships between spruce budworm and boreal forest volume, generated from Ludwig et al.'s (1978) simple analytical model of budworm outbreaks. Graphs A and B use Ludwig et al.'s base parameters, except the maximum avian predation rate is 25% higher than the base in graph A. A) Non-outbreak spruce budworm, infecting a forest at relatively high densities. Budworm populations are controlled by higher than observed levels of avian predation. The forest suffers some loss of productivity from budworm, but little mortality. B) When avian predation is reduced to observed levels, budworm outbreaks occur. These outbreaks increase budworm densities a thousandfold over the non-outbreak budworm densities. At these high densities budworm defoliation kills trees. The outbreaks entrain forest structure, producing a disequilibrium forest that has a periodicity of about seventy years.

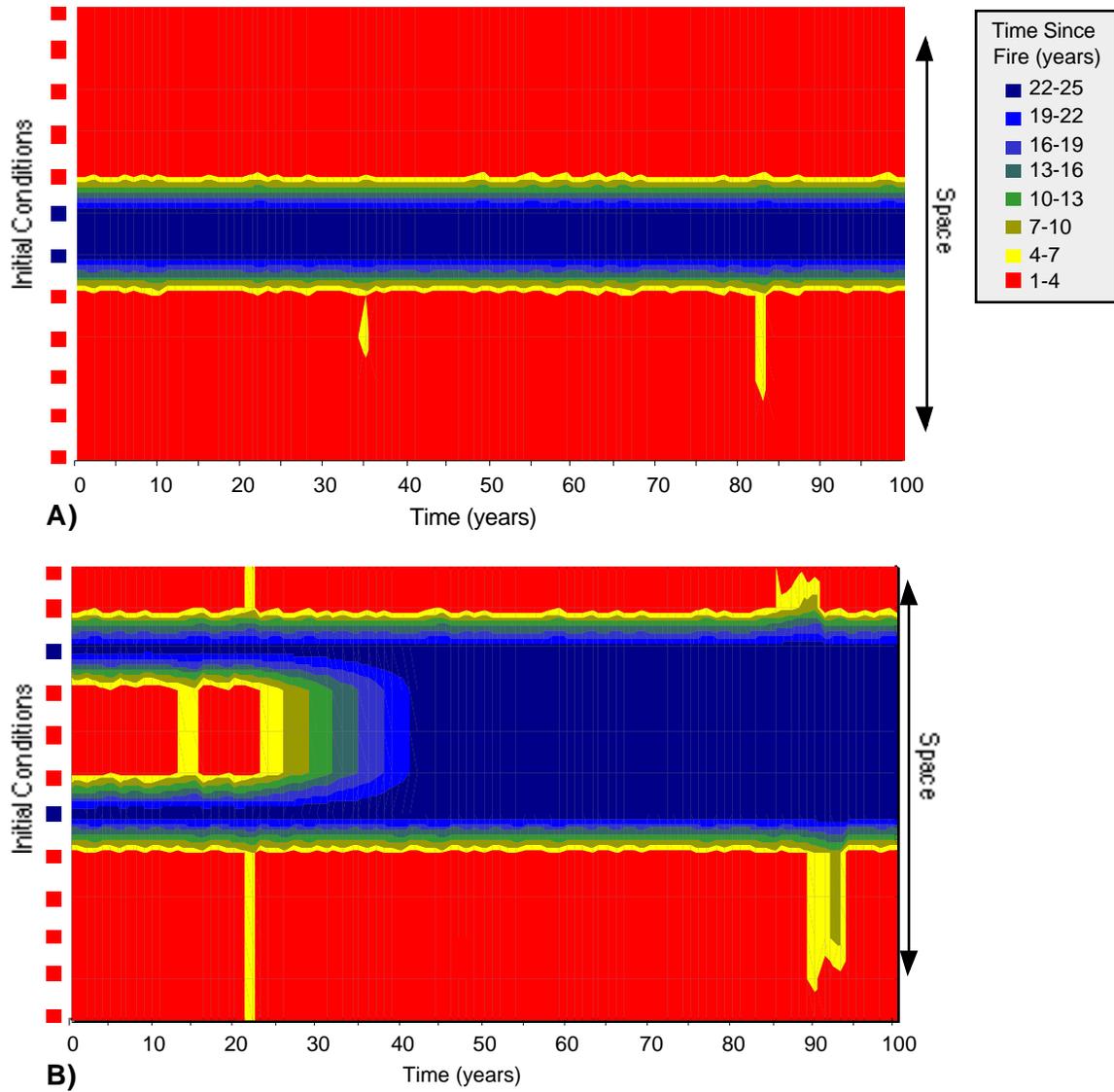


Figure 3-3. Simulation of two longleaf pine forest with the same initial composition of forest types, but different spatial distributions of those types. The model used is a one dimensional spatial model of fire and forest dynamics (Peterson In Press). A) Two old sites are adjacent to one another. The sites remain old, while the other sites remain young. B) Two old sites are separated by several young sites. Fire is prevented from burning these sites, and they become old. The other young sites remain young. After 100 years of simulation, both the mix of site types and their spatial pattern are quite different. If the behavior of these models had been extrapolated from either the initial conditions of sites, or the initial mix of sites, those extrapolations would have been inadequate, unless the spatial relationships among sites are also considered.

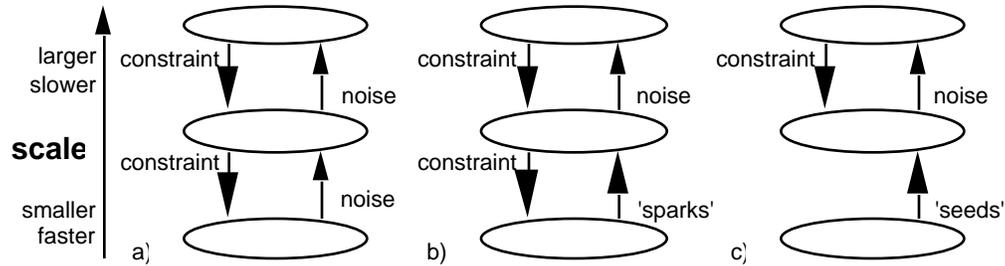


Figure 3-4. An idealized map of the relationships between a hierarchical level and the levels directly above and below it, as the nature of the central level is dominated by different types of processes. a) A system during 'normal' times. Each level is strongly constrained by the level above it. 'Noise' from the faster levels below each level has a minimal effect upon higher levels. The system is resilient. b) A 'brittle' system strongly constrains the level beneath it, but also extremely vulnerable to any change in the level beneath it. This brittleness allows a small disturbance to rapidly propagate through the entire system. c) A reorganizing system only weakly constrains its subsystems, making it prone to organize around any 'seeds' of order that emerge from change in the lower levels.

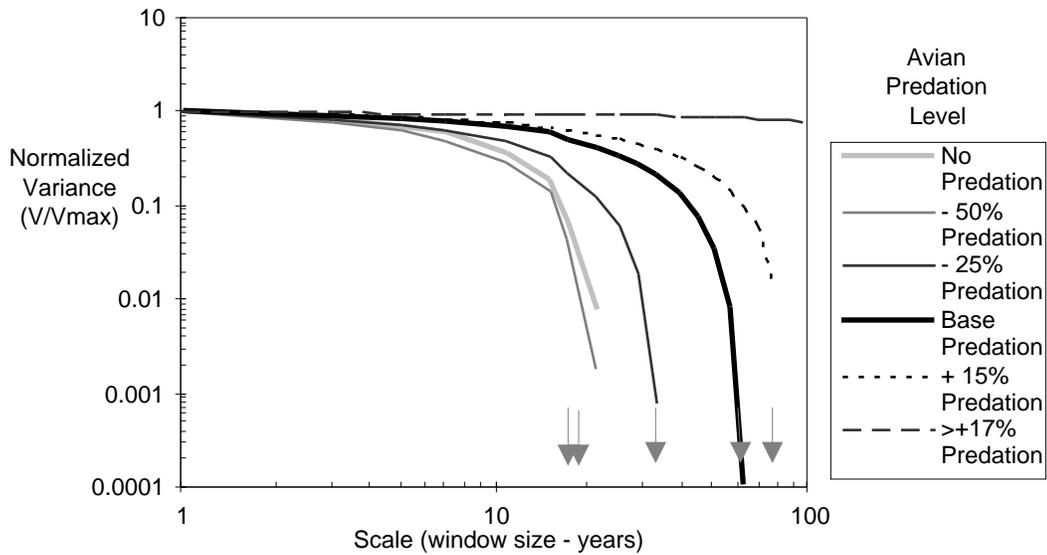


Figure 3-5. Changes in the intensity of predation alter the scaling of forest pattern in a simple model of budworm outbreaks. Ludwig et al.'s (1978) simple analytical model of budworm outbreaks was used to calculate variance in forest age over a range of temporal window size. These variances were normalized based upon the maximum variance at each level of predation. Using the parameter values of Ludwig et al (1978) as a base case, I altered the amount of avian predation that was possible in the model. Reducing the predation rate decreases the scale over which variation occurs, by decreasing the frequency of budworm outbreaks. Increasing the maximum amount of predation, increases the scale of budworm outbreaks, until outbreaks can no longer occur. Predation levels greater than 15% above the base case are sufficient to prevent outbreaks, causing the forest pattern follows a fundamentally different scaling relationship. The vertical arrows indicate the time scale over which almost all the variance has been lost for the 'Base Predation' case and reduced predation cases. These time scales correspond to the periodicity of outbreaks, which are respectively: 17 years, 24 years, 35 years, 65 years, 89 years, and no outbreak.

FIRE, SEED DISPERSAL AND MULTIPLE STABLE STATES IN LONGLEAF PINE FOREST

Introduction

This chapter focuses upon understanding the cross-scale dynamics of human dominated longleaf pine (*Pinus palustris*) ecosystem in northwest Florida. It applies the general discussion of resilience, ecological scaling, and large-scale global dynamics to a specific, complicated managed ecosystem.

I use the concept of ecological resilience to construct a set of alternative models of longleaf pine sandhill forests that are used to explore the ecological behavior of the managed forest of Eglin Air Force Base in northwest Florida. In this introduction, I discuss my approach towards ecosystem management and then describe the longleaf pine forests of Eglin Air Force Base. The remainder of this chapter is divided into four sections. First, I present the set of simple alternative models, or caricatures, that I use to explore the structure, dynamics, and management of northwest Florida longleaf pine forest. Second, I describe and use a non-spatial model to explore the temporal dynamics of longleaf pine forest. Third, I describe and use a spatially explicit model to explore the spatial-temporal dynamics of longleaf pine under a number of management regimes. I conclude by discussing the ecological and management lessons learned from this exploration. This includes identifying the important areas of uncertainty that remain and suggesting appropriate management actions.

Ecological Management

Human transformation of the earth has largely occurred at the meso-scale. These transformations have altered the abundance and distribution of biota. More subtly, human action has altered the functioning of ecological processes, encouraging some, suppressing others, and creating others. These changes in ecological processes often have gradual, but cumulative effects that present a significant challenge to humanity's ability to effectively manage ecosystems. These changes produce ecosystems that are organized in novel ways. Learning how to structure human relationships with poorly understood, changing ecosystems is one of the central challenges of modern ecology.

Applied ecologists are caught in a trap. Ecological change requires that they act, but ecological change means that they have limited knowledge of how they should act. Applied ecology, or ecosystem management, is based upon an abstraction of nature. From the vast complexity of nature, managers abstract a set of system attributes that they feel capture the structure and dynamics of the system of interest, and then use that set of relationships to guide their decision making. Usually this decision process is based upon some form of ecological theory, even if it is unarticulated. Often scientists work with managers with the aim of improving the ecological model used by managers. However, often there are a variety of competing ecological models that can not be rejected based upon existing knowledge of the ecosystem being managed. One approach to this dilemma, which is advocated by adaptive management (Holling 1978, Walters 1986), is to base management upon a set of alternative ecological models rather than attempt to discover which model performs the best according to a set of criteria.

Exploring a broad set of alternative models helps researchers ask better questions about how ecosystems work. This allows managers and ecologists to engage in an iterative process of synthesis, reflection, and experimentation that helps them move towards a richer understanding of ecosystem dynamics. Perhaps more importantly, the continual use and evaluation of a diverse set of models reminds ecological managers to attend to the

uncertainty that exists over how the system operates, encouraging management that tests rather than follows models.

Developing such models is difficult, but the general ecological concepts of multiple stable states, resilience and scaling, as discussed above, can provide a framework for model construction. Useful models of complex situations compress a great deal of understanding into simple, yet rich models that exhibit the minimum complexity to describe important system dynamics. Such models cannot be developed immediately. Often they can only be developed after many different complicated interactions are explored and tested. Such a process usually narrows the set of interactions that have significant effects on ecological dynamics. This process allows complex models to be compressed into minimal models. I used these concepts to develop multiple ecological models to explore management alternatives for forest restoration in Northwest Florida.

Longleaf Pine Forest on Eglin Air Force Base

From the end of the Pleistocene until recently, the majority of the coastal plain of the southeastern U.S.A. was covered by longleaf pine (*Pinus palustris*) forest. During the past two centuries, human activities such as logging, agriculture and fire suppression have reduced the area covered by longleaf pine from about 250,000 km² to less than 12 500 km² (Schwartz 1994). The largest remaining area of contiguous old-growth longleaf pine forest is located in the northwest Florida, within the 1 870 km² Eglin Air Force Base.

Either longleaf pine or various oak species (*Quercus spp.*) can dominate forest sites located on the sandy soils of northern Florida (Abrahamson and Hartnett 1990). The frequency of ground fires usually determines which vegetation type dominates at a specific location (Heyward 1939). Mature stands of longleaf pine often produce open savanna ecosystems that possess an understory rich in grasses, and herbs. Longleaf pine shed needles that, in combination with the understory vegetation, provide a combustible medium for fire. While longleaf pine stands encourage fire spread, oak stands tend to inhibit fire

spread. Mature oaks form dense stands that reduce the amount of light that reaches the ground, producing a sparse understory. Oaks shed leaves that form a compressed, low oxygen litter layer that suppresses the accumulation of understory vegetation and other potentially combustible detritus.

Fire plays a key role in determining what types of tree seedlings survive to become trees. Longleaf pine, in all but its young sapling state, survives fire. It also drops many fine needles which ignite. Young oaks, however, are killed by fire. The absence of fire from oak stands or longleaf pine stands allows the growth of young oaks. However, regular fires suppress oak growth allowing longleaf pine to thrive (Rebertus et al. 1989).

The difference between fire's relationship with longleaf pine and oaks drives forest dynamics in northwest Florida. Longleaf pine through the combination of fire resistant and the production of fine fuels drive a forest site towards a frequently burned longleaf pine savanna. While oaks through the combination of fire inhibition and rapid growth in the absence of fire drive forest sites towards infrequently burned oak scrub-forest.

While the tension between oak and longleaf pine dominance occurs over much of the southern coastal plane, a third tree species, sand pine (*Pinus clausa*), further complicates ecological dynamics on Eglin Air Force Base. Sand pine historically occurred along the coast, but in past decades has spread into areas formerly occupied by longleaf pine (Provencher et al. 1998). The Choctawhatchee variety of sand pine that inhabits northwest Florida is ecologically distinct from other sand pine. While interior Florida sand pine are serotinous, requiring fires to open their cones before seeds can regenerate, the Choctawhatchee variety is not (Parker and Hamrick 1996). Sand pine is not as fire tolerant as longleaf pine, but sand pine reaches sexual maturity much faster than longleaf pine. These differences mean that sites that are not regularly burned can be invaded by neighboring sand pine within several years.

On Eglin Air Force Base, longleaf pine savanna has been replaced by pine plantations and invaded by oaks and the Choctawhatchee variety of sand pine. Presently,

the land managers at Eglin Air Force Base are attempted to restore the now rare longleaf pine savanna ecosystem (Jackson Guard: Eglin Air Force Base 1993).

Restoring the forest requires understanding its ecology and its history. Ecological understanding is needed to develop useful management plans, while an understanding of the past is required to understand what processes and states should be encouraged or discouraged. While there is a large body of knowledge concentrated on longleaf pine forest (Glitzenstein et al. 1995, Platt et al. 1988), this knowledge has often been developed at the scale of forest stands over several years. However, ecosystem management operates at the scale of thousands of square kilometers and decades. This scale mismatch requires translating understanding and uncertainty across scales. The development of simulation models provides a means of integrating ecological and management knowledge. By constructing alternative models, different models of cross-scale dynamics can be formulated, explored, and tested. It was this approach that I applied to Eglin Air Force Base.

Ecological Caricatures and Management Alternatives

Management alternatives are developed based upon models of how the forest functions. From meetings and discussions with land managers and ecologists I developed a set of simple caricatures of Eglin's forest types and dynamics. These caricatures were developed to articulate the concepts that implicitly underlie most actual and proposed management strategies. These caricatures assume specific types of landscape change. Testing these caricatures may eliminate a several of them, along with the management strategies that they imply. Furthermore, testing the caricatures reveals the key differences among them, and the situations in which these differences matter to management. Identifying these points allows a more refined set of alternative hypotheses to be posed and tested through management actions.

Caricatures of Ecological Dynamics

I identified five caricatures of the changes that have occurred in Eglin's forests. Two focus on the temporal dynamics of the forest, while three present alternative models of spatial and temporal interactions. Each caricature and a management strategy associated with it are defined below.

Out of Tune Forest: Fire frequency determines whether vegetation is maintained or changed. The frequency of fire in Eglin has decreased, leading to an increased presence of hardwood tree species and sand pine in the forest.

Suggested Management: Restoring longleaf pine requires returning the forest's fire frequency to its historical level. This task requires discovering the 'right fire frequency.' Apply this frequency of fires to the landscape and the forest will be restored.

Transformed Forest: The invasion of hardwoods and sand pine has fundamentally changed the forest. Fire behaves differently and has different impacts in this transformed forest.

Suggested Management: Restoring longleaf pine savanna requires intensive fires to transform the forest. Once the forest is restored it can be maintained with less frequent fires. This requires policy that varies the fire frequency applied to an area based upon the vegetation of that area.

Edaphic Forest: Soils and topography limit vegetation to specific locations on the landscape. Changes in vegetation occur only within a limited set of alternatives depending upon local site characteristics.

Suggested Management: Some sites will be difficult or impossible to change.

Managers should focus their efforts on the areas that can be improved should areas and ignore the areas cannot be altered.

Divided Forest: Development has broken the landscape into many pieces, altering the spread of fire across the landscape, which has decreased the frequency

of fire experienced by sites. This has led to the loss of longleaf pine and the invasion of hardwoods and sand pine

Suggested Management: The scale of fire must be expanded from beyond fragments to cover the entire landscape.

Invaded Forest: Sand pine has invaded the forest, altering its dynamics.

Suggested Management: Fire frequency must be sufficient to prevent sand pine spread. The areas that are occupied by sand pine will expand over time unless the spread of sand pine is controlled. Managers should focus upon rapidly removing areas of sand pine that have the potential to invade substantial areas.

The first two caricatures focus upon the interaction of fire and vegetative processes through time. The next three caricatures focus upon how changes in landscape pattern shape fire and seed dispersal, which are the processes that strongly influence the pattern of the landscape itself. These caricatures are not mutually exclusive. Changes in the forest are likely due to a combination of these processes, but management actions will be quite different based upon which of these caricatures best captures the forces shaping Eglin's landscape. A modeling process was used to test and explore the differences among these caricatures.

Modeling Approach

Ecological modeling serves a variety of goals. Primarily, a model is a synthetic hypothesis. It combines many diverse and heterogeneous results, observations, and theories into a unified framework that proposes a model of how an ecological system works.

The process of developing a model can be useful in and of itself. By assembling the concepts surrounding an issue in a system, and attempting to synthesize them is an opportunity for learning about the system. It provides participants to learn about areas

outside their area of expertise, can reveal hidden connections, and establish important gaps in existing understanding (Walters 1986).

Once a model is constructed, it is a tool for reflection. When its builders examine it they may not like what they see, but what they see is what they chose to put there, because a model embodies their prejudices, and ignorance as well as their knowledge. Models allows individuals and groups to see if they believe what they thought they believed, by clearly and explicitly laying out the things and processes that people consider to be important to the function of a system.

The process of reflection often results in the development of alternative models as processes that were thought to be important are shown to be peripheral, and marginalized processes are shown to be important. Changes in the processes considered by a model usually requires changes in the variables that are included within a model. Often a model evolves over several years, from discussions that alternate with attempts at synthesis, that are followed by periods of reflection, criticism, speculation and model reformulation. Frequently, this process can produces a set of models, or a modeling framework that is acceptable to the people involved in the modeling processes.

For Eglin Air Force Base, I produced a set of models that embodied the ecological caricatures above. These models represented what workshop participants felt were key ecological structures, processes, and management actions. At this point the model's basic structure, but not the rules describing how vegetation changes, were accepted as being reasonable by the various workshop participants. The model provides a formal document of consensus opinion of how, in broad terms, of how and why sandhill forest in north Florida changes. I used this modeling framework to conduct two sets of simulation experiments to identify what aspects of forest dynamics have important consequences for landscape management. The first set of experiments used a non-spatial model to explore forest dynamics under a wide variety of environmental regimes. The second set of

experiments used a spatially explicit model to explore spatial-temporal forest dynamics under a narrower set of forest management scenarios.

Succession and Fire – Temporal Dynamics

Modeling Vegetation Dynamics

The central abstraction in the model is its representation of forest in Eglin as a mix of the three dominant tree species. I assumed that an area of forest could be represented as a mix of longleaf pine (LL), sand pine (SP) and hardwood species (HW). This allows the character of a forest patch to be characterized by its relative proportion of these three tree types. This mix of tree types can be plotted as a position within a triangle, because of the assumption that the proportions of the three types comprise the total canopy (i.e. $LL + SP + HW = 1.0$). Changes at a site in the forest can therefore be thought of as tracing a trajectory through the triangular state space representing the various potential canopy types (Figure 4-1).

Vegetation types

The various possible combinations of longleaf pine, sand pine and oaks that are possible in Figure 4-1, were reduced to a set of discrete states. These states were based upon translating existing management classifications into the triangular state-space representation of forest composition. The infinite number of possible mixes of tree types was reduced to eight distinct vegetation states, each representing a discrete type of forest. These classes are briefly described below, and illustrated in Figure 4-2.

Longleaf pine (LL) : Longleaf pine with recruitment, hardwood understory, and continuous herb cover.

Longleaf pine and hardwoods (LLHW) : Longleaf pine canopy without recruitment, hardwood midstory, and discontinuous herb cover.

Longleaf pine and immature Sand pine (LLSP) : Longleaf pine canopy without recruitment, sexually immature sand pine present, and some hardwoods.

Hardwood/Longleaf pine (HWLL): Hardwood and longleaf pine canopy with no longleaf recruitment, sparse herb cover.

Sand pine/Longleaf pine (SPLL) : Sand pine and longleaf pine canopy with no longleaf recruitment, hardwood mid-story, sparse herb cover.

Hardwood (HW) : Hardwood canopy, with sand pine possibly present.

Sand pine and Hardwoods (SPHW): Mixed co-dominant sand pine and hardwood.

Sand pine (SP): Sand pine canopy, with hardwood midstory.

These vegetative states can be visualized as representing areas within the triangle defined by the combination of longleaf pine, sand pine and hardwoods (Figure 4-3).

Vegetation dynamics

Fire and vegetation succession determine the transitions among these states. The model represents fifteen different transitions among the eight states (Table 4-1). These rules were derived from a series of workshops and discussions with people from: The Nature Conservancy, the land managers at Jackson Guard on Eglin Air Force Base, other longleaf pine managers, and ecologists. The general structure of these transition rules, for example that unburned longleaf pine sites will be invaded by sand pine and hardwoods, is well understood and has been reviewed in many publications (Heyward 1939, Platt et al. 1988, Rebertus et al. 1993). However, the specific fire frequencies that are necessary to shift a site from one state to another are much less well known. What is certain is that these frequencies vary with soil, topography and climate conditions. Therefore, the rules that have been proposed to model Eglin Air Force Base will likely be subtly different from the transition rules that would describe even neighboring stands of longleaf pine in different soil conditions. For example, Blackwater River State Park located just north of Eglin Air Force Base has less sandy soils than Eglin making it more difficult for fires to kill hardwoods, among other differences.

Table 4-1. Vegetation transition rules used in the Eglin Longleaf pine model. Transitions among vegetation states are based upon a sites time since fire (TSF) and the presence of seeds from either or both pine species.

From --> To	LL	LLHW	LLSP	HWLL	SPLL	HW	HWSP	SP
LL		TSF>12 years	TSF>5 years & sand pine seeds					
LLHW	TSF<5 years for last three fires			TSF>35 years				
LLSP	TSF<10 years				TSF>12 years			
HWLL		TSF<5 years for last three fires			TSF>30 years & sand pine seeds	TSF >250 years		
SPLL			TSF<5 years for last three fires					TSF >250 years
HW				TSF<2 years & longleaf pine seeds			TSF<2 years & sand pine seeds	
HWSP						TSF >250 years		
SP					TSF<2 years & longleaf pine seeds			

The transitions among LL, LLHW, LLSP and the processes of sand pine and hardwood invasion are relatively well understood. The transition rules describing the conversion of HW, SP, HWSP, SPLL, and HWLL to sites with greater amounts of LL are the least certain parts of the model. These transitions need to be further explored by field experimentation. The transitions in the model are based upon the experience of land managers at Eglin. There burning has been more successful at eliminating hardwoods than

in many other areas of Florida, however the amount of burning to decrease the hardwoods in a HWLL site to the extent that it can be considered a LLHW is uncertain. In view of this uncertainty, the model uses the same transition rule for both sand pine and hardwood based upon the idea that in the absence of evidence to the contrary these transitions will be assumed to be equally likely. Below, I explain the derivation of these rules.

Longleaf Pine

Longleaf pine (LL) will remain longleaf pine if it is frequently burnt. Without frequent fire the longleaf pine will be invaded by hardwoods or sand pine, if sand pine seeds reach the site. Hardwoods are assumed to be always present at low densities at Eglin, however after twelve years without fire they reach a size that is sufficient to survive future fires (Rebertus et al. 1993). Managers in Eglin have observed that sand pine can quickly invade neighboring sites. If these sites are not burned within 5 years of sand pine establishment, the sand pine reach sexual maturity and begin producing cones (Parker and Hamrick 1996). However, if these sand pines are burned within twelve years of establishment they can be killed, or at least have their growth slowed.

Longleaf Pine and Hardwoods

Forest in the longleaf-hardwood (LLHW) state requires three fires within five years to be restored to a longleaf pine savanna state (LL). One or two fires, within a 3-5 year interval, are not sufficient to eliminate hardwood trees from longleaf stands (Robbins and Myers 1992). More fires are required, but how many and at what frequency was uncertain and debated. For this model, three fires within less than 5 years of one another was settled upon as a reasonable threshold.

Longleaf Pine and Sand Pine

The mixed longleaf-sand pine (LLSP) state is composed of sexually mature, but young sand pine trees. If this site is burned before the sand pine reach sufficient size the sand pine will be killed and the site will return to being a longleaf forest (LL). However, if the sand pine remain unburned for ten years, they will reach sufficient size to be more

difficult to kill with fire, and the site converts to the sand pine–longleaf (SPLL) state (Provencher et al. 1998).

Hardwoods and Longleaf Pine

The hardwood-longleaf (HWLL) state can only be burned with difficulty. The model assumes that some hardwoods can be killed with repeated fires. This assumption is supported by field experience at Eglin Air Force Base (Provencher et al. 1998), however the periodicity of fires that is necessary is not at all certain. Given this uncertainty, I decided to require three fires within less than 5 years of one another to convert the site to a mixed longleaf-hardwood state (LLHW). This transition rule is extrapolated from the transition rule from LLHW to LL states. It is assumed that since sizeable hardwoods are being killed in the LLHW to LL transition, a similar fire frequency is required to kill some of the hardwood in a HWLL state. This transition is reasonable, and consistent with field experience at Eglin Air Force Base, but unsupported by any experimental studies. However, such studies are on-going at Eglin Air Force Base.

Within an unburned hardwood-longleaf (HWLL) site, longleaf pine cannot successfully regenerate. The longleaf pine in these sites will eventually die, shifting the site to the hardwood (HW) state. Longleaf pine can live over four centuries, but most trees do not (Platt et al. 1988). Over time, older trees are killed by lightning and other events. The model uses the estimates that 250 years without fire are required to eliminate longleaf from a hardwood-longleaf site.

Forest in the hardwood-longleaf state can be invaded by sand pine. If sand pine seeds are available, and the site remains unburned for more than thirty years, these sand pine accumulate and transform the forest to a hardwood-sand pine (HWSP) state. This rate is based on observed changes in the Eglin landscape over the past fifty years (Provencher et al. 1998).

Sand Pine and Longleaf Pine

Forest in the sand pine – longleaf (SPLL) state is difficult to burn. Fire is assumed to be able to kill sand pine and convert a SPLL site to LLSP, but little is known about the specifics of such a process (Provencher et al. 1998). I assumed that sand pine can be killed by the same fire frequency that the model requires to reduce hardwood densities, which is at least three fires with a frequency of less than five years. It is possible that even more frequent fires, over a longer time are needed. Without fire, longleaf pine will persist along with the sand pine, but will not regenerate. Without longleaf regeneration a site will convert to pure sand pine. Longleaf mortality is assumed to be have completed the transformation from a SPLL to a SP state after 250 years without fire.

Hardwoods

Forest dominated by hardwoods (HW) can be invaded by longleaf or sand pine, but only during specific short periods. Immediately after a fire, longleaf or sand pine can invade a site if their seeds are present. Longleaf pine is assumed to be only able to invade if the longleaf pine is producing a mast crop of seeds that year (Platt et al. 1988).

Hardwood Sand Pine

Hardwood-sand pine sites are stable, but without fire sand pine will not be able to survive in the understory, and as with the hardwood-longleaf sites, after 250 years without fire a hardwood sand pine site will return to a pure hardwood stand. This transition is unimportant to the model, because it will almost never have the time to occur during a model run.

Sand Pine

Sand pine sites can be invaded by longleaf pine immediately after a fire, if longleaf seeds are available. However unless fires continue to frequently occur, the site will remain dominated by sand pine with a few longleaf.

Fire and vegetation

The transitions rules described above are driven by the frequency of fire. Fire frequency is itself influence by the time since last fire and the vegetation that is being burned. This section describes how fire dynamics were represented in the model.

Ground fires in the forest of north Florida consume fine fuels, and kill the above ground portion of understory and midstory vegetation, but they usually do not burn the canopy trees of the forest. The top-killed understory vegetation is usually able to regenerate very quickly. Within a year, or less in the case of spring fires, understory vegetation is able regrow to such an extent that the accumulated fuel can once again propagate fire. After a site has gone several years without fire, its combustibility begins to decrease (Platt et al. 1988, Robbins and Myers 1992).

There are significant differences in the combustibility of different forest states, however almost all forest states are most combustible in the years immediately following a fire. Sites containing a greater proportion of longleaf pine are more combustible than sites that contain less longleaf (Rebertus et al. 1989, Robbins and Myers 1992). Sand pine and oak dominated sites also differ in their combustibility. Assuming a constant amount of longleaf, sites with a significant sand pine component are less combustible than sites that have significant hardwood species present (Provencher et al. 1998).

Vegetation State Combustibility

To quantify the relative combustibility of different vegetation types at different times since fire, Eglin's fire managers were asked for their assessment of the relative combustibility of different types of vegetation. While there are eight vegetation types, several of these states were thought to have similar functional relationships between the time since fire and vegetation combustibility (Figure 4-4).

Two sets of vegetation states were assumed to have probabilities of combustion that were independent of the time since last fire. Sites with a significant longleaf component, LL, LLHW, and LLSP, were assumed to have a constant high probability of combustion:

$$P_{\text{comb,LL}} = 0.25.$$

While hardwood sites were assumed to have a constant low probability of combustion:

$$P_{\text{comb,HW}} = 0.035.$$

Two other sets of vegetation states were assumed to have probabilities of combustion that decreased with the time since last fire. Hardwood-longleaf sites were assumed to burn well if recently burned, but as time since fire increase their combustibility decays. This decline in the probability of combustion of a site was represented as a negative exponential function of time since fire, which eventually reaches the same low probability of burning as a pure hardwood stand. Specifically, the equation used is:

$$P_{\text{comb,HWLL}}(\text{TSF}) = P_0 * e^{(-r*\text{TSF})} + P_{\text{comb,HW}}$$

Where $P_0=0.25$ and $r_{\text{HW}}=0.035$.

SPLL, HWSP, and SP, are assumed to be easier to burn following a fire than HWLL vegetation, but their combustibility decrease, at an increasing rate following after several years. This relationship was represented by a negative logistic relationship. Specifically, the equation used is:

$$P_{\text{comb,SP}}(\text{TSF}) = (1 - 1 / (1/P_0 + ((K+P_0)/(K*P_0)) * e^{(-r*\text{TSF})})) / 3$$

Where $K=0.9$, $P_0=0.25$, and $r_{\text{SP}}=.125$

Fire Season

These probabilities of fire combustion change at the time scale of years. There is a substantial body of fire management literature on the seasonal effects on burning (Robbins and Myers 1992). Seasonality of fire is not included in the Eglin longleaf model. There are two reasons for this omission. The first is that there is a minimal effect of burning season on longleaf pine (Glitzenstein et al. 1995). Secondly, the model is focussing upon decadal-scale landscape dynamics rather than short-term consequences of a single fire. This focus reduces the importance of seasonal variation in burn, since over the long-term variation should approach a long-term average.

Integrated model

An integrated model of vegetation dynamics was constructed (Figure 4-5). This model represents the forest with two sets of variables. The first represents the vegetation of the forest as one of the eight states (Figure 4-3). The second represents the fire history of the forest by storing the time since last fire, and the frequency of previous fires. These two variables describe the state of the forest. Every year, the vegetation transition rules are applied to the forest (Table 4-4), and the forest vegetation may change state. This forest is subjected to a fire regime that periodically attempts to ignite the forest. The success of these ignition events is determined by the probability of combustion functions (Figure 4-4). This non-spatial model was used to test the *Out of Tune Forest*, *Transformed Forest*, and *Invaded Forest* caricatures by exploring the dynamics of vegetation under a broad set of fire regimes.

Succession and fire regime

Fire frequency determines what changes occur in the landscapes of north Florida. Alternative visions of this relationship are embodied in the *Out of Tune Forest* and *Transformed Forest* caricatures. The simulation model can be used to distinguish between these caricatures. The key difference between these two caricatures is in the homogeneity of a forest's response to fire. The *Out of Tune Forest* caricature proposes that specific forest types correspond to specific fire frequencies, while the *Transformed Forest* caricature proposes that fire suppression causes fundamental changes in the organization and combustibility of a forest. These changes produce a hysteretic effect, because shifting a forest from an unburned forest to a burned forest requires more fire than maintaining a forest as a burned forest.

These caricatures were tested by experimentally assessing the impact of a wide variety of fire frequencies on a variety of vegetation types. Each vegetation type was burned at a range of fire frequencies, and its behavior observed over 100 years. Fire frequency was controlled using the yearly probability of a site's ignition. The inverse of

the probability of ignition is a site's expected fire frequency. For example, the probabilities 0.01 and 1 correspond to average fire frequencies of 100 years and 1 year respectively. Using a probability of ignition allows the time between fires at a site to vary, but still correspond to an average fire frequency. These probabilities were varied from 0 to 1, in 0.01 increments. The state of a site after 100 years of burning was recorded. Five hundred replicates of each vegetation type were exposed to each fire regime. From these replicates the likelihood of a vegetation class of maintaining its existing vegetation, or shifting to another vegetation type can be calculated.

These calculations were conducted for the vegetation types LL, LLHW, LLSP, HWLL, SPLL, HW, and SP. The vegetation type HWSP was ignored, because it is not present in the existing landscape, it occurs infrequently in the simulation model, and it does not change in periods less than 250 years rendering its dynamics uninteresting over the period of 100 years. Each of these sites was simulated with and without the dispersal of longleaf or sand pine seeds into the site. These cases explore the impact of neighbouring sites on a site's dynamics. These results clearly show that for all fire frequencies a few vegetation states are much more likely than others (Figures 4-6, 4-7, and 4-8).

These results reveal that some states are more likely than others across all fire regimes, that the likelihood of vegetation states is strongly influenced by the presence of external seed sources, and that the initial vegetation state influences model dynamics. These results invalidate the *Out of Tune Forest* caricature, and support the *Transformed Forest* caricature.

Likelihood of States

The model output shows that LL is the most likely state when fires are frequent, but that any of HWLL, SPLL, SP or HW is likely to occur when fire is infrequent. Which of these states occurs depends upon what a site's initial conditions are, and whether external seed sources are present. If a site is initially in LL, LLHW, or HWLL and there is no dispersal of sand pine the site is most likely to end up in either LL, if fires are frequent, or

HWLL, if fires are infrequent. There is a much lower likelihood of the site being in the intermediate state of LLHW. Similarly, if the site is initially in LLSP or SPLL, or if there is sand pine seed dispersal into LL, LLHW, or HWLL sites, then the site will likely end up in LL, at high fire frequencies and SPLL, at low fire frequencies. Although, the situation is more complex at intermediate fire frequencies on LLHW and HWLL sites that are being invaded by sand pine.

Without seed dispersal HW and SP are completely stable states, regardless of the fire frequency they will maintain themselves. However, their behavior becomes more complicated when there is seed dispersal. Longleaf dispersal without sand pine is not particularly important for any states except for SP and HW, because all the other states already contain longleaf pine. However, in the case of HW it can be invaded by LL if a longleaf seed source, but no sand pine seeds are present. However, longleaf is only weakly able to invade HW, due to the low probability of a mast year coinciding with a burn of a hardwood site. Sand pine can also be invaded by longleaf at high fire frequencies. When both sand pine and longleaf seed sources are present, then longleaf is not able to invade hardwood sites, being pre-empted by sand pine, but it still manages to invade sand pine sites.

There are several ecological consequences of these transitions. Firstly, the important transitions are from the initial states of LL, LLHW, LLSP, HWLL, and SPLL as the other states (HW, SP, and HWSP) occur over minor areas of the landscape. In these five states, three states are the most likely to occur. With frequent fires, LL dominates, while infrequent fires cause HWLL or SPLL to dominate, with SPLL being dominant when sand pine seeds are available.

Forest hysteresis

Despite the fact that the same small set of states dominates the model's ecological dynamics there are quite different dynamics depending upon the initial state of the model. That is, different states respond differently to the same fire frequency. These differences

are clearly shown in Figure 4-9 and Figure 4-10. These figures plot the fire frequencies in which a state has a greater than 50% chance of maintaining the same proportion of longleaf pine. For example, if a site containing LL without seed dispersal is burned at a fire frequency less than one fire every four and a half years, it will not be maintained as LL. Similarly, if a HWLL site is not exposed to fires more frequently than once every six years it will remain HWLL. Figure 4-10, reveals how adding longleaf and sand pine seed dispersal alters the sites ecological dynamics, for example increasing the frequency of fire needed to maintain LL and decreasing the frequency of fire needed to maintain SP and HWLL. These graphs show that a similar fire regime has quite different effects upon different vegetation types, and that there is no fire frequency that will maintain all vegetation types. These results support the *Transformed Forest* caricature of Eglin Air Force Base's ecological dynamics.

Seed dispersal

Comparing these seed dispersal and non-seed dispersal cases (Figures 4-6 to 4-10) reveals that the strong influence that the presence of seed sources has on the response of vegetation to fire. These results indicate that applying a specific fire frequency across a landscape will produce variable results even in the same vegetation type, based upon the input of other site's seeds into that site. This finding supports the *Invaded Forest* caricature, by illustrating that the location of other forest types has a strong impact on ecological dynamics. This support suggests that the spatial dynamics across the landscape influence temporal dynamics, and need to be incorporated into management planning. To do this, a spatially explicit version of the Eglin succession model was constructed.

Succession and Fire – Spatial Dynamics

Spatial processes fundamentally influence the modeled ecological dynamics of Eglin Air Force Base. Understanding the interactions of these processes over time required the

construction of a spatially explicit model that allows the spatial heterogeneity of the landscape to influence fire and seed dispersal.

As discussed above, there are three spatial caricatures of Eglin Air Force Base that this model had to address the *Edaphic Forest*, *Divided Forest*, and *Invaded Forest* caricatures. To explore these caricatures the model had to include topographic variability, fragmentation and seed dispersal along with the central processes of fire and fire management.

Model Organization

A forest landscape is represented as a matrix of sites. Each of these sites undergoes the same successional dynamics as represented in the temporal model, but fire and seed dispersal are explicitly modeled. Additionally, considering the landscape requires the addition of some new landscape types to the model. I will now address each of these components of the spatial model in more detail.

Matrix

The spatial model divides the landscape into a matrix of sites, each of which is 60 m on edge (Figure 4-11). This resolution was chosen for two reasons. Firstly, it is a reasonable scale to develop management alternatives, displaying heterogeneity that is important to management while not providing overwhelming detail (Jackson Guard: Eglin Air Force Base 1993). Secondly, tree size appears have most of its variation at scales less than 28 m (Platt and Rathburn 1993), making 60m an ecologically reasonable scale to represent a portion of forest.

The forest is modeled using a set of overlying matrices that interact with one another (Figure 4-12). The model stores information of vegetation, and fire history as does the succession model, but spatial explicitness also requires a map of seed availability and topography. Seed availability is generated by seed dispersal from existing sites, a process that will be explained below. The topography layer is simply used to provide a template of

ecologically active and ecologically inert sites. This layer allows the presence of roads or developed areas to block the spread of seeds and fires.

New model states

Considering the entire landscape requires a consideration of states other than those that occur in Florida's sandhill communities, because if other states are intermixed with the sandhill vegetation they can alter that vegetation indirectly by influencing the spread of seeds and fire.

Two topographically limited states were added to the model to represent wet forest sites. The sites are both wet forest, but one contains sand pine (WETSP) and the other does not (WET). These forests are wetter than usual sandhill habitat occurring in creek beds. Sand pine is assumed to be able to invade wet forests in the same fashion that it invades hardwoods. The ability of fire to remove sand pine from this forest type is uncertain, but Eglin's land managers think that it lies somewhere between the difficulty of removing sand pine from LLSP and SPLL sites. The rules used in the model are shown in Table 4-2.

Table 4-2. Vegetation transition rules used for the wet forest sites in the .

From --> To	WET	WETSP
WET		TSF>2 years & sand pine seeds
WETSP	Two fires within last ten years	

Both WETSP and WET sites impede the spread of fire. WET sites are slightly easier to burn than WETSP sites. WET sites are assumed to combust similarly to HWLL sites, and WETSP sites are assumed to combust similarly to SPLL sites (Figure 4-4). WET sites do not disperse any seeds, while WETSP sites produce sand pine seeds.

Controlled burns of hardwood-longleaf pine sites (HWLL) are difficult to manage, because the forest is difficult to ignite. Conditions that allow burning can result in locally intense fires that kill existing old longleaf (Robbins and Myers 1992). To explore the effects of this process and help assess the degree of longleaf pine mortality due to particular control burning strategies, a new state consisting of a relatively open stand of hardwoods that includes a significant herb layer was added to the model. Without fire the hardwoods on the site will grow larger and come to dominate the site, shifting into the HW state. Longleaf seeds combined with frequent fires will allow longleaf to reestablish and convert the site back to HWLL. At an intermediate fire frequency or in the absence of longleaf seeds the site will remain HHW. These transition rules are shown in Table 4-3.

Table 4-3. Modifications of vegetation transition rules to include the herbaceous-hardwood vegetation state in the Eglin Longleaf pine model. These additions were added to the transition rules illustrated in Table 4-1

From -->To	LL	LLHW	LLSP	HWLL	SPLL	HW	HWSP	SP	HHW
HWLL		TSF<5 years for last three fires			TSF> 30 years & sand pine seeds	TSF>2 50 years			1% chance of transition during a prescribed burn
HW				TSF<2 years & longleaf pine seeds			TSF<2 years & sand pine seeds		
HHW				TSF<6 years for last three fires & longleaf pine seeds		TSF>1 5 years			

Herbaceous hardwood sites do not burn as well as longleaf sites, but they also are not as difficult to burn as pure hardwood sites. The open structure of these stands allows a

combustible understory to develop. In the model, HHW sites are assumed to combust similarly to HWLL sites (Figure 4-4).

The temporal vegetation model (Figure 4-3), is expanded by the addition of HHW, and the wetland states, WET and WETSP. These states and the transitions among them produce a spatial vegetation model (Figure 4-13).

Topography

The topographic layer added to the model was extremely simple. It simply defined areas where vegetation dynamics could occur and areas that were outside the model. This layer was used to define the boundaries of the simulation area, which in this case were the boundaries of Eglin Air Force Base, and of the central watersheds of Eglin. It was also used to define ecological boundaries within Eglin. Roads and developed areas block the flow of fire and seeds across the landscape. The topographic layer maps these boundaries among all the disparate layers of the model. The more subtle effects of regional topography were implicitly included in the model through the wet forest states (WET, and WETSP) that were discussed above.

Model Spatial Processes

The spatial dynamics of fire spread and seed dispersal are explicitly incorporated in the Eglin Landscape Model. I will describe how each of these processes was represented in turn.

Seed dispersal

Seed dispersal is fairly simply represented with the landscape. While sand pine, longleaf pine and hardwoods all disperse seeds only the dispersal of longleaf and sand pine are explicitly modeled. Hardwood is assumed to be always present within a site, due to resprouting as well as prolific seed production. Both sand pine and longleaf pine disperse their seeds over short distances. The resolution of the model is 60m, and since most cones

disperse under 60m - 70% under 20m (Boyer and Peterson 1983, Burns 1978), the model only includes seed dispersal to the four nearest cells neighboring a site (Figure 4-14).

Longleaf pine seed production varies from year to year. Infrequently, about once a decade, longleaf pine produces a large number of cones (Platt et al. 1988). The model, somewhat conservatively, assumes that these mast events occur once a decade. In other years no longleaf seed dispersal occurs. Sand pine does experience such fluctuations in seed production. Unlike southern sand pine, the cones of the Choctawhatchee variety of sand pine that are native to northwest Florida, do not require fire to open (Provencher et al. 1998), and therefore sand pine seed dispersal occurs continuously.

Fire regimes

Wildfires and prescribed fire were both modeled in this landscape model, but not necessarily at the same time. Wildfires produce their own spatial pattern through interaction with vegetation, while land managers impose the pattern of prescribed burns. Wildfires are ignited by lightning across the landscape, and then spread. The area a fire burns is the product of chance and the existing landscape. Prescribed fire, or prescribed burns, are different, because land managers chose an area of the landscape to burn, and then attempt to burn it. However in prescribed burns fire may not spread into all parts of the designated burn area, especially in areas that are difficult to ignite in large burns.

Wildfire

Wildfire was modeled as a process that propagates itself across a landscape. Every year a number of sites are struck by lightning, and ignited. The lightning based fire initiation rate is about one fire started/ 10 km² (Henkel 1995, Platt et al. 1988), which is equivalent to about 17 fire initiations in the central three watersheds of Eglin Air Force Base every year. A burning site can spread fire to its neighbors. This process is probabilistic and is dependent upon the vegetation type and time since last fire of the fire's neighbouring sites (Figure 4-15). Sites that fire spreads into can then ignite their neighbors. This process continues until the existing burning sites fail to ignite any new sites. An example

of this process is provided in Figure 4-16. As fire spreads across the landscape it does not burn homogeneously. Remnant patches of unburnt vegetation remain with a fire, and fire spread is impeded by older, less combustible vegetation. The spread of fire can be halted by roads, or difficult to burn vegetation. An animation of wildfires in a simulation is shown in Figure 4-17.

Prescribed Burns

Prescribed burns, rather than wildfires, dominate the Eglin landscape. Prescribed burns occur when land managers go out and burn an area of the base. Weather, ignition pattern, the skill of the burn team and other factors affect the results of any prescribed fire, however these variations are outside the focus of this model.

Prescribed burns can be ignited both from the air and the ground. Aerial ignitions, in which fire is dropped from helicopters, allow larger areas to be burned. Depending upon the spacing of ignition sources and the distribution of fuel fire may burn these large areas unevenly. Ground ignitions are started by using drip torches to establish a fire front that is allowed to burn over a plot and into another fire. Ground ignitions can provide more control over fire spread, and may burn more evenly than aerial ignition. However, it is difficult to start and control large fires from the ground.

The simulated large aerial burns and smaller ground burns. The aerial burns are set to cover 24,000 acres (9 km²), while the ground burns cover 6,000 acres (2 1/4 km²). The probability of a site burning depends upon its vegetation type and time since last fire as it does in a wildfire. However, in burn blocks it is assumed that each site has multiple chances to be ignited. Aerial burns are assumed to provide three chances and ground burns are assumed to provide four chances. These rates correspond to a fire front, and an encircling fire respectively. These probabilities produce burn blocks that burn with completeness similar to burn blocks in actual prescribed burns. When burning a hardwood invaded longleaf site a ground burn will actually ignite about 75% of the area, while an

aerial burn will ignite about 60% of the area. Choosing which blocks to burn in which year requires a management strategy, and this strategy can be varied within the simulation.

Landscape Resilience

The ability of a state to persist despite disruption is termed resilience (Holling 1973). Ecological resilience is a measure of the amount of change or disruption that is required to transform an ecosystem from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures.

The concept of resilience can be illustrated by modeling an ecological 'state' as the position of a ball on a landscape (Figure 4-18). Gravity pulls the ball downwards towards pits in the surface. These pits are stable states. The deeper a pit the more stable it is, because increasingly strong disturbances are required to move an ecological state away from the bottom of the pit. The steepness of the sides of a stability pit corresponds to the strength of negative feedback processes maintaining an ecosystem near its stable state. These are the forces that transform the ecosystem, back towards a stable state following a disturbance. The width of a pit is the range of change that a state can experience before transforming to another state. The width of the stability pit corresponds to the ecological resilience of a state (Figure 4-18).

The concept of resilience can be adapted from the analysis of a system of continuously varying variables to a system that experiences transitions among discrete states. In the ball and landscape illustration above, the state of the system was represented by a single variable. The use of multiple variables is possible, but the analysis and visualization of the results becomes increasingly complicated. In the discrete case the use of more than two states is similarly complicated, unless the states are arranged along an axis and transitions do not jump across intervening states. By dividing the multiple possible states in two states, the resilience of discrete states can be simply and clearly assessed by analyzing the likelihood of transitions between states.

In the spatial Eglin model these states are defined on basis of their longleaf density as ‘poor’ (P) and ‘good’ (G). Two states produce four likelihood ratios, because each state can either remain in its state or switch to the other state. Because a state can either remain in that state or shift to the other state, these likelihoods can be written as:

$$P_{toG} + P_{toP} = 1.0 \text{ and}$$

$$G_{toG} + G_{toP} = 1.0.$$

The probability of a state remaining within that state (i.e., P_{toP} and G_{toG}) corresponds to the resilience of that state, as this probability represents the chance that the state will persist given a particular environmental regime. It is important to note that the probabilities of changing from poor to good, and from good to poor are not necessarily equal.

This model can be applied to data by gathering multiple observations of a system and calculating the likelihoods of the four types of transition. For example, the transition likelihoods given in a table can be converted into a resilience ball and landscape model by assigning the likelihood of remaining in a state to the width of a state, and the likelihood of leaving the state as its potential energy. The states are then connected by barrier to state change that is equal in height to the probability of state change:

$$\text{Prob. Of State Change} = 1.0 - \text{the likelihood of remaining within the state.}$$

An example table and diagram are shown in Figure 4-19.

This approach of assessing resilience is observationally based. It does not attempt to analyze the underlying dynamics of a system. Rather it takes observed state-transitions and applies the concept of resilience to them. If this process is inappropriate this method will reveal that the state(s) have no resilience by producing a flat line. This observational approach does not easily allow results that are collected from a system under one environmental regime to be applied to the system under another environmental regime. However, by focusing on transitions between defined states, this method does provide a

method of analyzing the integrated response of a system to a given environmental regime that is based upon management criteria.

The state-transition resilience approach can be applied to landscapes. The spatial distribution of the likelihood of state transitions can be assessed by classifying an initial landscape into two states, and then repeatedly applying a environmental regime to that landscape and recording the post-treatment landscape states.

This approach was applied to the Eglin Air Force Base landscape by classifying Eglin's vegetation-based land management goals. At Eglin managers wish to expand the area in longleaf pine savanna. I used this goal to classify states as either being 'poor' or 'good' longleaf sites. I classified LL, LLSP, LLHW, and WET as good longleaf sites. All the other sites were considered poor LL. By running the simulation model many times, the likelihood of a given site on the landscape changing states can be assessed and plotted on the landscape. This measure not only allows one to assess the stability of a given landscape formation, but also measure the type of change. This approach was used to compare the response of the Eglin landscape to multiple fire management strategies.

Model Testing

The Eglin Landscape Model was tested in a number of fashions. Quantitative tests of the model were impossible, due to a lack of comparable data. However, because this purpose of this model is not to predict the future landscape dynamics of Eglin, but rather to explore the consequences of different sets of assumptions, this lack of quantitative comparison is not a serious failing. The model's dynamics were tested against its ability to reproduce historical landscape dynamics, and its behavior was tested against the expectations of Eglin's land managers. There were two main tests of the model's credibility: its ability to reproduce and maintain the historical Eglin landscape, and its ability to reproduce hardwood and sand pine invasion into longleaf sites. These tests were conducted using the concept of landscape resilience, which I will briefly outline, before discussing the tests themselves.

Historical test

The landscape of northwest Florida was in the recent past dominated by longleaf pine savanna (Schwartz 1994). The Nature Conservancy used a variety of historical and ecological sources to attempt to reconstruct the landscape of Eglin Air Force Base (Kindell et al. 1997, Provencher et al. 1998). This reconstruction did not have sufficient detail for the Eglin Landscape Model, so a number of further assumptions on the distribution of sand pine and hardwoods dominance had to be made before a historical landscape could be produced for the model. This historical landscape, which I extrapolated from The Nature Conservancy's work, is shown in Figure 4-20.

Historical Proposition: If the model was accurately mimicking the natural processes of north Florida, wildfire should be able to maintain this landscape in a shifting steady state fairly close to this reconstructed historical condition.

This proposition was tested by running the model for one hundred years starting from the initial conditions of the estimated historical landscape (Figure 4-20). This model used the estimated historical fire initiation rate, and the vegetation transition rules described above. Ten model runs were used to assess the resilience of the landscape to the historical wildfire regime.

The landscape resilience of the historical landscape to wildfire is shown in Figure 4-21. Most of the landscape area is maintained as either good longleaf or poor longleaf. The areas of degradation, by sand pine spread, are relatively minimal and since the initial distribution of sand pine was itself largely unknown, some variation is to be expected. Therefore, the model successfully maintained the estimated historical landscape.

Fire suppression test

A second test of the model's functioning is its ability to recreate the invasion of longleaf by hardwoods and sand pine following landscape fragmentation and fire suppression. We used the following proposition:

Suppression Proposition: Fragmenting the landscape and suppressing fire for a similar time in the simulation model should produce a situation qualitatively similar to the existing landscape.

Fire suppression began about fifty years ago. Therefore, the current road network fragmented the historical landscape, and fire was suppressed to one fifth of its original level. The model was allowed to run for fifty years, at which time the simulated landscape was compared to the Eglin Air Force Base's present landscape. An animation of vegetation changes during 100 years of fire suppression is shown in the Figure 4-22.

The model landscape successfully reproduces the invasion of sand pine out of creeks, and the limited amount of longleaf pine on the landscape. The vegetation of Eglin Air Force Base has been fragmented by an undocumented, complex set of logging, tree planting, and road cutting that makes quantitative comparison between the simulation and the existing Eglin landscape unreasonable, because these processes are not included in the model. To test the ability of the model to reproduce larger scale changes in the Eglin landscape, the landscape dynamics predicted by the model were shown to and discussed with Eglin's land managers. They felt that the landscape produced by this method accurately captured the speed of hardwood and sand pine invasion of longleaf pine. While this test is not a strong one, it is still a test, because the model could have failed to produce reasonable dynamics. Passing this test does not validate the model, rather it improves the model's credibility. However, the vegetation pattern produced after fifty years of fire suppression was considered to be enough a reasonable representation of the current landscape, that this simulated landscape could be used to represent the current landscape for the comparison of alternative management scenarios. To distinguish this simulated landscape from the actual landscape, I refer to it as the 'current' landscape (Figure 4-23).

Testing summary

This model was developed not to predict the future of Eglin Air Force Base, but rather to serve as a tool to integrate and test existing ecological knowledge. Part of its

utility has been to identify important gaps in that understanding. The Eglin Landscape Model embodies the consensus ecological understanding of Eglin's managers. By observing the dynamics of the model and comparing these dynamics to their tacit feeling for how the landscape functions, managers are presented with an opportunity for learning. Conflict between expectations and model dynamics means that either the model needs to be revised, or that the managers understanding of the landscape needs to be changed. In either case, learning occurs.

The Eglin Landscape Model passed through a series of workshops, in which it was used, discussed and revised. This process lead to a model in which the land managers had some confidence, due to their feeling that the modeling accurately captured their understanding of the forest, and it produced realistic forest dynamics. This confidence allow the model to be used as a tool to investigate alternative land management strategies.

Spatial Dynamics - Management Options

Ecosystem management has been ongoing since the early 1990's. Burning the forest using prescribed fire has been one of the main components of this activity. This burning is motivated by both ecological and safety concerns. Ecologically, prescribed burns are conducted to attempt to increase the area of longleaf pine forest. Additionally, they inhibit fuel accumulation reducing the risk of uncontrollable wildfire.

The main purpose of modeling the Eglin landscape was to explore and challenge the ideas underlying management. In this sprit, the model was used to determine the potential consequences of continuing the current of wildfire suppression without also conducting prescribed burns. This test was conducted by applying the policy of fire suppression to the 'current' landscape (Figure 4-23). Under the policy of fire suppression the 'current' landscape is quite unstable. The landscape continues to lose areas of longleaf pine, and experience sand pine invasion.

Calculating the landscape resilience of fire suppression on the 'current' landscape reveals that a continued policy of fire suppression would lead to the degradation of large areas of the base, and the maintenance of longleaf in only a few small areas (Figure 4-24). Given the management goals of expanding the area in longleaf, this response is not acceptable. For this reason land managers have been applying prescribed fire to the landscape and logging areas of sand pine and hardwood that they wish to restore.

Management Vegetation Classification

Alternate management policies were evaluated, and prescribed burns implemented, based upon a simplification of vegetation into three classes. These classes divided the vegetation types into three states. Because, an increase in the area of longleaf pine is a major management goal at Eglin Air Force Base, these three classes rank vegetation as either being 'best', 'good' or 'poor' based upon the amount of longleaf pine a vegetation state contains (Figure 4-25).

Together the 'good' and the 'poor' class encompass all the land that can be potentially occupied by longleaf pine. The 'best' class is a subset of the 'good' class. The 'best' sites are longleaf pine savanna (LL). All the sites in which longleaf pine is a dominant component (LL, LLHW, and LLSP) are 'good' sites. All the other sites that could include longleaf are considered 'poor sites' (HWLL, SPL, HW, HWP, SP and HHW). The vegetation types WET and WETSP are excluded from these divisions as they do not contain and cannot change to contain longleaf pine.

Land managers would like to convert the 'poor' sites into 'good' sites, and improve the 'good' sites into 'best' sites. However, in meeting these goals they also would like to ensure that they at least maintain the existing area of 'good' sites.

Managing Prescribed Burns

Prescribed burns are difficult to organize. They require trained fire managers, and prescriptions require specific weather conditions. Eglin managers estimate that ecological and social conditions are appropriate for burning about 80 days a year. Optimistically, they

suggest that they could conduct two burns per day during about half of these burn days. These estimates produce a high estimate of 120 prescribed burns a year.

As discussed above, prescribed burns can be ignited from either the ground or the air. Managers estimate that prescribed burns would be evenly split between aerial and ground ignition each year. These estimates provide an upper bound of 60 ground and 60 aerial fires per year. The landscape area being used in the simulation model corresponds to a third of Eglin, which means that the maximum number of prescribed burns in the modelled area is 20 aerial burns and 20 ground burns per year.

These estimates of the number of prescribed burns that could be applied a year are optimistic and do not account for extreme weather, military missions or crises in management such as budget problems or understaffing. Therefore it is useful to observe what effect lower rates of prescribed burning would have on the Eglin landscape. Additionally, applying prescribed burns is expensive. If fewer fires could restore the landscape effectively, spending money on over-burning the landscape would not be sensible. To explore a range of prescribed burn levels, I ran the model with 20, 15, 10, and 5 pairs of aerial and ground fires a year.

Burning Strategy

Using fire to manage a landscape requires a strategy for deciding when and where to burn. Part of the purpose of developing a simulation model is help develop such strategies. Using the model to evaluate land management strategies offers a simple way to test ideas about management – ideas that combine both social and ecological models – and to locate important uncertainties and unintended consequences.

Based upon discussions with land managers I developed four sets of land management strategies. As with most of this model, these strategies were not meant to be realistic, but rather simple caricatures of different management approaches. Three of these approaches use prescribed fire to manage the landscape. These approaches are named

‘maintenance’, ‘conversion’ and ‘rotation’. The fourth approach uses wildfire, and is named ‘fire’.

The ‘fire’ management strategy is used as a base case, against which to compare the other strategies. The ‘fire’ strategies do not use prescribed fire, therefore they cannot be applied at the same frequencies as the prescribed fire strategies. Rather, wildfire is conducted at two levels – the historical rate of wildfire initiation and the current suppressed rate of forest fires.

The simplest management strategy that uses prescribed fire is ‘rotation.’ This strategy divides the landscape into burn blocks. Each block is burned with the same frequency. This frequency is determined by the number of blocks burned per year divided by the total number of burn blocks.

Both the ‘maintenance’ and ‘conversion’ strategies alter the fire frequency of a burn block in response to how the block’s vegetation compares to the remainder of the landscape. Both these strategies vary the fire frequency of burn blocks depending upon the vegetation within a block. These strategies counts the amount of ‘best’, ‘good’, and ‘poor’ sites in a burn block and then use a formula to rank the blocks. The ‘conversion’ and ‘maintenance’ use different formulas. Each year burn blocks are burned in the order their ranking, until the available burns for the year are complete. Sites that have been burned within the last three years are not reburned. The ‘conversion’ strategy aims to convert poor sites to good sites, while also maintaining good sites. The ‘maintenace’ strategy trys to maintain the good sites.

The rule used for the ‘conversion’ strategy is:

$$\text{Score} = \text{Good} + \text{Poor} * 2/3 + \text{Best} * 3/5$$

The rule used for the ‘maintenance’ strategy is:

$$\text{Score} = \text{Good} - \text{Best}/3$$

These alternative management strategies were used to probe the dynamics of the managed Eglin landscape. The purpose of these probes is to test the caricatures discussed

at the beginning of this chapter. While these simulation exercises cannot be expected to predict the details of specific management regime, they can identify which caricatures appear to better represent the functioning of the sandhill communities of north Florida, and where there are important gaps in ecological understanding.

Four different management strategies were tested: ‘maintenance’, ‘conversion’, ‘rotation’ and ‘wildfire.’ These strategies were each tested at several different fire frequencies. Prescribed burns were tested at levels of 20, 15, 10, and 5 pairs of large and small burns per year. While the ‘wildfire’ strategy was tested at ‘historical’ and ‘suppressed’ levels. In combination a total of fourteen different management regimes were tested. The combinations of fire frequency and management strategies tested are shown in Table 4-5.

Table 4-5. Alternative management regimes combining yearly burn amount and fire management strategy.

Fire Types		Fire Strategy			
Prescribed Burns Aerial and Ground	Wildfire Initiations	Rotation	Maintenance	Conversion	Wildfire
20,20		X	X	X	
15,15		X	X	X	
10,10		X	X	X	
5,5		X	X	X	
	Historical				X
	Suppressed				X

The success of these management alternatives was evaluated based upon the changes they produced in the landscape over fifty years. The pattern of change produced by each management strategy has a complex temporal dynamic (Figure 4-26). These experiments, however, focus upon the spatial aspect of northwest Florida forest. To simplify the analysis of changes in the spatial distribution of vegetation a fixed time period of fifty years was used for analysis. The ‘future’ landscape at the end of these fifty years was compared with the ‘present’ landscape, and changes calculated.

Fifty years was chosen, because it long enough to detect the long term consequences of a fire regime on the landscape, but short enough to be relevant to management planning decisions. While management plans are often made at less than decadal time scales, forest management must evaluate these decade-length plans in terms of their effects on longer dynamics.

The management alternatives were evaluated based upon the change in area covered by the different longleaf classes (best, good and poor), and the actual changes in the distribution of good and poor vegetation classes upon the landscape, using the landscape resilience approach described earlier in this chapter.

Management Results

By applying the same strategies with different numbers of prescribed burns per year, the simulations were able to extrapolate the number of prescribed burns required by each strategy to maintain the area of good vegetation. Maintaining the area of good vegetation, which is the same as not increasing the area of poor vegetation, is a fundamental minimal goal of Eglin's land managers (Jackson Guard: Eglin Air Force Base 1993). Calculating this threshold provides managers with an idea of the absolute minimum number of control burns that need to be applied on average each year. These results are shown in Figure 4-27.

The threshold fire frequency at which the total area of good and poor vegetation is maintained is indicated by the point at which the 'poor' and 'good' sites cross the x-axis in Figure 4-27. The 'rotation' strategy does not perform well (16 fires/year). The 'conversion' strategy is able to maintain the area of 'good' vegetation at the lowest number of burns per year (8.5/year). The 'maintenance' strategy performs similarly, maintaining the area of 'good' vegetation at (9 /year). The prescribed fire strategies perform better than wildfire. Wildfire is unable to maintain the existing area of good sites, even though wildfire does manage to increase the area of 'best' sites.

These results also indicate that ‘maintenance’ and ‘conversion’ strategies behave similarly. ‘Rotation’ is the worst strategy for producing ‘best’ sites. While ‘rotation’ can maintain a landscape, it does not burn sites frequently enough to keep them in ‘best’ state. This is clearly shown by the higher proportion of ‘best’ than ‘good’ in all the other strategies.

The effects of different management strategies on the different vegetation classes are shown in Figure 4-28. These show that ‘best’ almost always increases under any strategy. It only decreases in cover under suppressed wildfire, and ‘rotation’ at 10 and 5 burn pairs/year. However, the same strategies also produce declines in ‘good’, even though ‘best’ is a component of ‘good’. This indicates that the area of ‘best’ (LL) is increasing while the area of non-best ‘good’ (HWLL and SPL) are decreasing.

These figures also show that ‘maintenance’ strategy is best at producing ‘best’ sites, and is slightly better than ‘conversion’ at producing ‘good’ sites. However, at low numbers of prescribed burns per year, ‘maintenance’ is less successful at maintaining the area of ‘good’ sites than ‘conversion’.

The resilience maps of the ‘rotation’, ‘maintenance’, ‘conversion’, and ‘fire’ strategies are shown in Figures 4-29, 4-30, 4-31, and 4-32 respectively. These maps of landscape resilience show the landscape resilience of each landscape to 50 years of each management regime, at the 20, 15, 10 and 5 levels of prescribed burning, along with the wildfire and suppressed fire scenarios in the wildfire management scenario.

Results of the ‘maintenance’ strategy, shown in Figure 4-29, shows that the areas of the landscape that are not burned include no degraded sites. The strategy did not burn these sites as they consist almost completely of poor sites. Not burning these sites did not result in any ‘conversion’ of good to poor. Throughout the landscape many yellow sites indicate the ‘conversion’ of poor to good sites, while scattered red sites are the result of sand pine invasion. At lower frequencies, red occurs in some of the unburned blocks

indicating that good sites are degraded within these areas. This process shows how burn blocks with increasing areas of 'good' sites are abandoned to conserve better sites.

The 'conversion' strategy, shown in Figure 4-30, is similar to the 'maintenance' strategy. Similar areas of the landscape are altered, but the 'conversion' strategy has slightly less area of maintained 'good' sites, and a slightly larger area of 'degraded' good sites.

The 'rotation' strategy, shown in Figure 4-31, exhibits quite a different pattern from the 'conversion' or 'maintenance' strategies. It shows that much less area is improved, shown by the yellow sites, than in 'maintenance' and 'conversion'. And the areas that are maintained are less likely to be maintained. This is indicated by the presence of less pure green sites, and more green sites that are shaded red. The spatial pattern is also quite different; there are not abrupt transitions between burned and unburned sites, as the entire landscape is burned at the same frequency.

The fire strategy is also quite different. Since fire maintains areas as easy to burn, the improved and degraded areas are more closely aggregated (Figure 4-32). Areas of maintained and improved 'good' sites are next to maintained and degraded 'poor' sites. However, the total area maintained or improved to 'good' status is much less than in most of the prescribed burn strategies.

One important process that was not captured by the classification of landscapes into 'best', 'good,' and 'poor' classes was sand pine invasion, because the 'poor' class does not differentiate between hardwood and sandpine invasion. This process is clearly seen when the change in the area covered by different vegetation types is analyzed (Figure 4-33, Figure 4-34, and Figure 4-35).

Sand pine spread is only prescribed in five strategies. All three of the 20,20 prescribed burn strategies succeed in controlling sand pine spread, but the 'rotation' 15,15 strategy fails to control sand pine spread, and all of the strategies less than 15,15 fail to control sand pine spread as do both the wildfire strategies. Additionally, while the

'conversion' and the 'maintenance' strategies at 15,15 prescribed burns a year manage to control the spread of sand pine, but they only marginally decrease the area cover by sand pine.

Discussion

Differences among strategies

There are major differences among most of the management strategies, but minor differences between the two adaptive strategies. Both adaptive strategies, 'maintenance' and 'conversion', burn 'good' sites more frequently than 'poor' sites. Because burning improves the state of sites, this process tends to produce sites that are more likely to be burned in the future, reinforcing the tendency of the landscape to divide itself into combustible longleaf pine sites, and less combustible hardwood and sand pine sites. The number of fire set per year determines the mix of 'good' longleaf pine and 'poor' hardwood/sand pine sites that occur upon the landscape.

The 'wildfire' strategy produces a landscape dynamic similar to the 'maintenance' and 'conversion' strategies. However, the limited ability of wildfire to spread across areas of less flammable vegetation limits total areas that fire can burn, and consequently alter. A similar mix of good longleaf pine sites and 'poor' hardwood and sand pine sites occurs, but in quite a different spatial arrangement. The patches of 'good' sites are much more circular than the rectangular geometry imposed by the prescribed burns in the 'maintenance' and 'conversion' strategies. Additionally, in the wildfire strategy patches of longleaf must be a minimum size to be ignited frequently enough to remain longleaf. The smaller the patch the higher the probability that it will not be ignited frequently enough to remain longleaf, and it will begin to be invaded by hardwoods and sand pine. This result means that patches are not as stable as they are in the adaptive strategies, and they contain much more of a mix of different vegetation states due to more heterogeneous burns than in the adaptive strategies. It should be noted that according to this model, this degree of heterogeneity is a consequence of wildfire occurring in a degraded landscape. Wildfire in

longleaf pine dominated landscape results in much more complete burns of the landscape as shown in calculations of the resilience of the ‘historical’ landscape managed using wildfire (Figure 4-20).

The ‘rotation’ strategy is different from all the other strategies, because it applies fire with equal frequency to all the different vegetation types on the landscape. This results in the gradual degradation of the entire landscape, rather than the division of the landscape into two states. There is much more heterogeneity within burn blocks, while there is less heterogeneity at the scale of the landscape. Decreasing the number of fires applied each year decreases the area of poor sites converted into good sites and then increases the area of good sites converted into poor sites. However, rather than being localized in specific places, this degradation is dispersed across the landscape (Figure 4-31). Secondly, the amount of area altered by management is the lowest under the ‘rotation’ strategy. Both in area improved and in area degraded there are smaller changes than in any of the other strategies. It is also the least successful at producing longleaf pine savanna (Figure 4-33).

The difference between an adaptive strategy and a ‘rotation’ strategy can be seen clearly by comparing animated movies of vegetation change over time. The same yearly number of fires, 10 large fires and 10 small fires, were applied to the ‘current’ landscape using the ‘maintenance’ and ‘rotation’ strategies. Figure 4-36, shows the ‘maintenance’ strategy dividing the landscape into ‘good’ and ‘poor’ blocks. Figure 4-37, shows the ‘rotation’ strategy allowing the landscape to gradually be invaded by hardwood and sand pine.

Differences among vegetation classes

A surprising result was that the proportion of ‘best’ sites increased in almost all the management treatments, even when the area of ‘good’ sites decreased (Figure 4-28). This result was surprising because managers felt that the amount of ‘good’ sites should increase before the amount of ‘best’ sites increased. However, this was not the case, due to the

landscape's heterogeneity. Because fire is applied in relatively large blocks, a prescribed burn cannot be targeted to one specific type of vegetation. Internal block heterogeneity means a fire set to convert 'poor' vegetation to 'good' vegetation will also convert existing 'good' vegetation to 'best' vegetation.

Sand pine invasion

Increases in the area covered by longleaf pine occur in almost all the scenarios, even while areas invaded by hardwood also increased (Figure 4-35). It is the spread of sand pine that is the process that degrades longleaf pine vegetation. The area vulnerable to sand pine depends upon the area occupied by sand pine, and the size of the area that sand pine neighbors. Consequently, when sand pine is spreading the area that can be invaded by sand pine also increases over time. This suggests that removing relatively small areas of sand pine before these stands have the chance to disperse seed into susceptible sites can have a significant effect on ecological dynamics, especially when tree removal is combined with prescribed fire. This echoes the finding, from the analysis of the temporal dynamics of the Eglin model, that the presence of seed dispersal decreased the fire frequency required to maintain longleaf pine savanna (Figure 4-9 and Figure 4-10).

Herbaceous hardwood

Herbaceous hardwood sites are produced by hot prescribed fires that kill longleaf in sites that are dominated by hardwoods (HWLL). Herbaceous hardwood is not very important in any of the simulation scenarios. While the rate of HHW production is uncertain, the value used for HHW production was conservative, suggesting that well-managed prescribed fire will improve sites for longleaf much more frequently than they kill existing longleaf, even over multiple decades. For example, using the 'maintenance' strategy at 20 large and 20 small prescribed burns a year increases the coverage of HHW by 1km², while increasing the area of longleaf savanna by 241 km². While suggesting that significant areas of old growth longleaf pine may be lost by prescribed burning, the area of longleaf pine savanna areas established by the same fire regime is far greater. This result

suggests that prescribed burning should continue to be applied to old growth stands, but that efforts to reduce old-growth mortality are also worthwhile.

Caricatures

The spatial model reinforces and refines the conclusions of the temporal model. The *Out of Tune Forest* caricature is untenable, because the landscape responds differently to the same frequency of fire depending upon its current state. While the mixing of wetland and sandhill sites supports the *Edaphic Forest* caricature, it is not particularly useful at helping explain landscape dynamics. The wetland sites are important because they fragment the landscape and provide sand pine seeds to the sandhill community. Both these processes support the *Divided Forest* and the *Invaded Forest* caricatures. These caricatures are more useful than the *Edaphic Forest* caricature, because they identify ecological processes that are important controls on landscape dynamics.

The alternative management scenarios combine with the model's ecological dynamics to produce an integrated management/ecological model. These alternate models are quite simple, especially in their representations of management, but they capture two key structural changes that management can produce in ecological dynamics.

As discussed above, the alternative management strategies, with the exception of 'rotation,' all amplified the existing hysteretic tendencies of the landscape, and drove areas of the landscape toward either longleaf pine savanna, sand pine or hardwood dominance of the vegetation. The 'rotation' strategy, by ignoring the vegetation pattern in its application of fire diminished this hysteretic tendency and produced a landscape composed of a mix of intermediate states.

There was also a fundamental split between the prescribed burn management strategies and the wildfire strategy. The spread of wildfire across the landscape depends upon burning sites igniting their neighbors. This spatial contagion results causes fragmentation of vegetation to have a major effect on fire spread. However, prescribed

burns are applied over continuous areas somewhat independently of the vegetation in that area. This greatly reduces the effect of fragmentation on the landscape's ecological dynamics. However, landscape fragmentation can still effect where prescribed burns occur. For example, when the 'maintenance' strategy is applied at 20 large and 20 small prescribed burns a year, the only sites that are not burned are those directly adjacent to unburnable areas (Figure 4-29). This pattern does not occur because fire cannot spread across those areas, but rather it occurs types is analyzed (Figure 4-33ffected , a burn that costs as much to conduct as a burn by a non-fragmented area. However, even when this subtle effect of fragmentation s considered.

These changes, make the *Transformed Forest* caricature more relevant to management and the *Divided Forest* caricature less relevant. More subtly, they indicate how management policy can shift the relevant importance of different ecological processes, enhancing or reducing the usefulness of a particular caricature. This serves as a reminder of the shifting nature of ecological systems, and of the requirement to continually challenge and test the caricature management is based upon.

Next steps – experiments

The model discussed in this chapter is full of uncertainties, but some of these uncertainties are larger and more important than others. Management that tests and improves the accuracy of these uncertain relationships would provide a clearer picture of how the forest of northwest Florida actually functions, and that understanding could be used to help develop better management practices. There are three particular sets of relationships that are important, yet uncertain: the relationship between fire and longleaf pine restoration, fire mortality of longleaf pines, and seed dispersal distances and rates. I will discuss each of these in turn.

Restoration

The ability of fire to restore longleaf pine savanna that has been invaded by hardwood is central to the Eglin model. Yet the ability of fire to remove hardwood from

these sites is largely unknown, as there has not been enough actual experience at Eglin. The model's transition from HWLL to LLHW is the most uncertain. Testing this relationship would improve understanding of the ecological dynamics of northwest Florida, and could be used to improve the Eglin model.

The ability of fire to restore sand pine invaded longleaf is also uncertain. A better understanding of the situations in which SPLL changes to LLSP, while not as central to the model as the hardwood transition, it is important to understand as these dynamics have an important influence on model dynamics.

Longleaf Mortality

The current model suggests that longleaf mortality due to prescribed burns is a relatively minor problem. This would be the case even if the rate of mortality were several times higher than the value used in the model (see Table 4-3). However, if the rate of mortality was an order of magnitude higher than the value used in the model, longleaf mortality could become significant. Improving estimates of this mortality rate should be relatively easily done by surveying and monitoring the condition of longleaf pine trees in prescribed burns. If these manipulations are done experimentally, it may be possible to assess what aspects of a specific prescribed burn produce longleaf pine mortality, and then develop burning methods that minimize this mortality.

Seed Dispersal

Variation in seed dispersal distances has a strong effect on ecological dynamics (Cody and Overton 1996). While the seed dispersal distances for sand and longleaf pine have been studied, it is important to see how well these measurements reflect seedling establishment on Eglin Air Force Base. Are there any patterns of regional variation? What is the periodicity and variation in longleaf pine masting? Variation in seed dispersal, either reducing or enhancing the effect of dispersal, would change the ecological dynamics of the Eglin landscape. The model may over-estimate sand pine seed dispersal and under-estimate longleaf pine dispersal. In this case it may be easier to restore the landscape than the model

suggests. The ability of longleaf and sand pine to disperse seeds and establish seedlings should be tested at Eglin Air Force Base. However, in terms of restoring the existing Eglin landscape, variation in sand pine seed dispersal is probably the most important issue as longleaf pine dispersal is only important in reestablishing longleaf in a very small area. An increasing understanding of sand pine dispersal would increase the ability to predict the spread of sand pine across the landscape, and as noted above, sand pine spread occurs in most of the simulated management strategies.

Next steps – management

The temporal and spatial models discussed and explored in this chapter do not predict the future landscape of Eglin Air Force Base, but they can identify ecological relationships that are inconsistent with one another or data. These models can also identify what types of ecological caricatures appear to credibly describe a given system. These caricatures can then be used to direct future tests and management of that ecosystem.

The Eglin model offered several recommendations to the ecological managers of Eglin Air Force Base. First, that the forest had changed sufficiently that a restoration program is necessary. Second, that management should consider landscape heterogeneity. Third, sand pine removal could accelerate restoration, and fourth, that managers should try to increase the size and frequency of prescribed burns.

Limits to Restoration

The model shows that allowing wildfires to burn Eglin Air Force Base would not be sufficient to restore its forest. Such a policy would not burn the entire landscape frequently enough to restore the landscape, despite the fact that historically the wildfire managed to maintain longleaf pine savannas. This change exists, because a history of fire suppression and landscape fragmentation allowed sand pine and hardwoods to spread across the landscape, decreasing the ability of wildfire to propagate across the landscape, and reducing the average size of fires.

Management Should Be Embedded in the Landscape

In the simulation scenarios management strategies that failed to consider the heterogeneity of vegetation across the landscape were less successful at maintaining the landscape than strategies that did consider this heterogeneity. This suggests that management practices should pay attention to variation in the landscape and adapt to that variation. For example, it might be necessary to burn an area adjacent to a large area of sand pine more frequently than a similar area that is not adjacent to sand pine.

Sand Pine Removal

Landscape management should also consider the ability of sand pine to spread. Areas of sand pine next to infrequently burned areas are likely to be colonized. Because, the spread of sand pine becomes easier the larger the areas it covers, it makes sense to try to remove sand pine from areas from which it could spread as soon as possible.

Burn Size

Given that the cost of burning is largely independent of the size of the area burned, landscape management should try to burn areas as large as possible. If this were possible it would increase the area burned each year. The simulation models suggest that even optimistic projections of the number of burns conducted per year may not be enough to restore the landscape. Increasing the area of each burn would reduce this problem. If landscape fragmentation, whether due to vegetation or management actions, impedes burning large areas, management should attempt to remove these sources of fragmentation. Increased use of aerial ignition should make it easier to burn larger areas in individual burns.

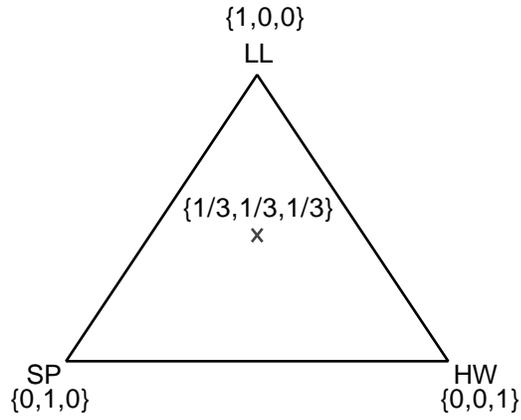


Figure 4-1. The relative proportion of longleaf pine, sand pine and hardwoods present in the canopy can be used to represent the vegetation of a forest site, assuming that these species comprise the total cover of the site.

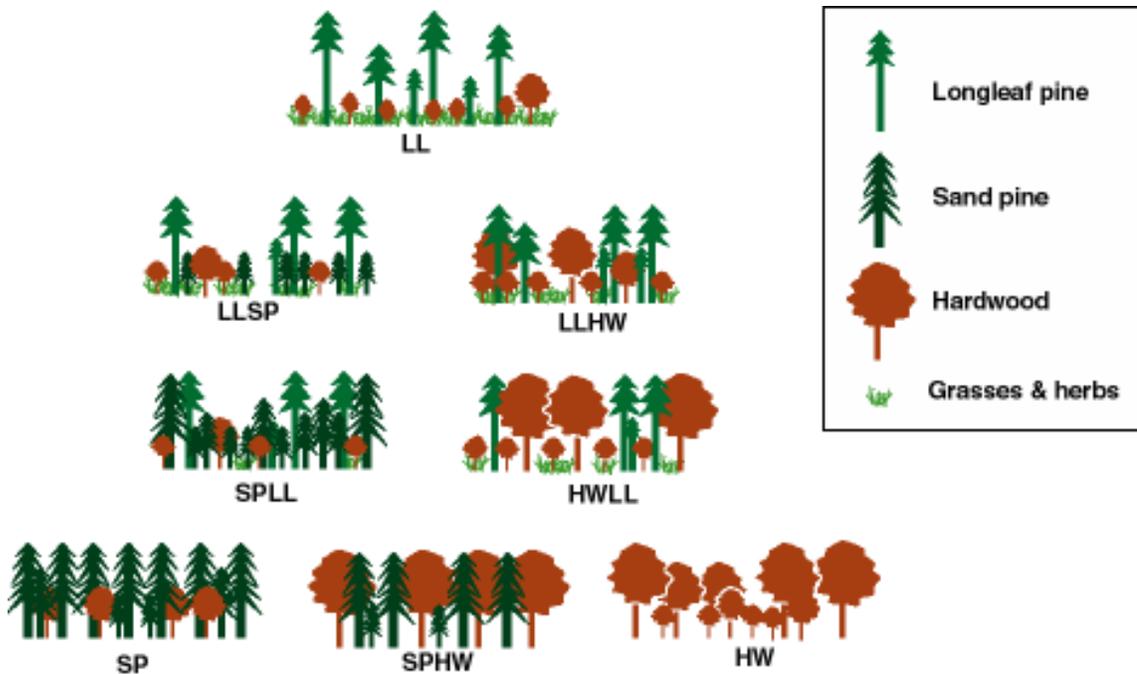


Figure 4-2. A schematic illustration of the various forest states represented in the model. LL - Longleaf pine: longleaf pine with recruitment, hardwood understory, and continuous herb cover. LLHW - Longleaf pine and hardwoods: longleaf pine canopy without recruitment, hardwood midstory, and discontinuous herb cover. LLSP - Longleaf pine and immature sand pine: longleaf pine canopy without recruitment, sexually immature sand pine and hardwoods present. HWLL - Hardwood/Longleaf pine: hardwood and longleaf pine canopy with no longleaf recruitment, sparse herb cover. SPLL - Sand pine/Longleaf pine: sand pine and longleaf pine canopy with no longleaf recruitment, hardwood midstory, sparse herb cover. HW - Hardwood: hardwood canopy, with sand pine possibly present. HWSP - Hardwoods and sand pine: mixed co-dominant sand pine and hardwood. SP - Sand pine: mature sand pine stand, with hardwood understory.

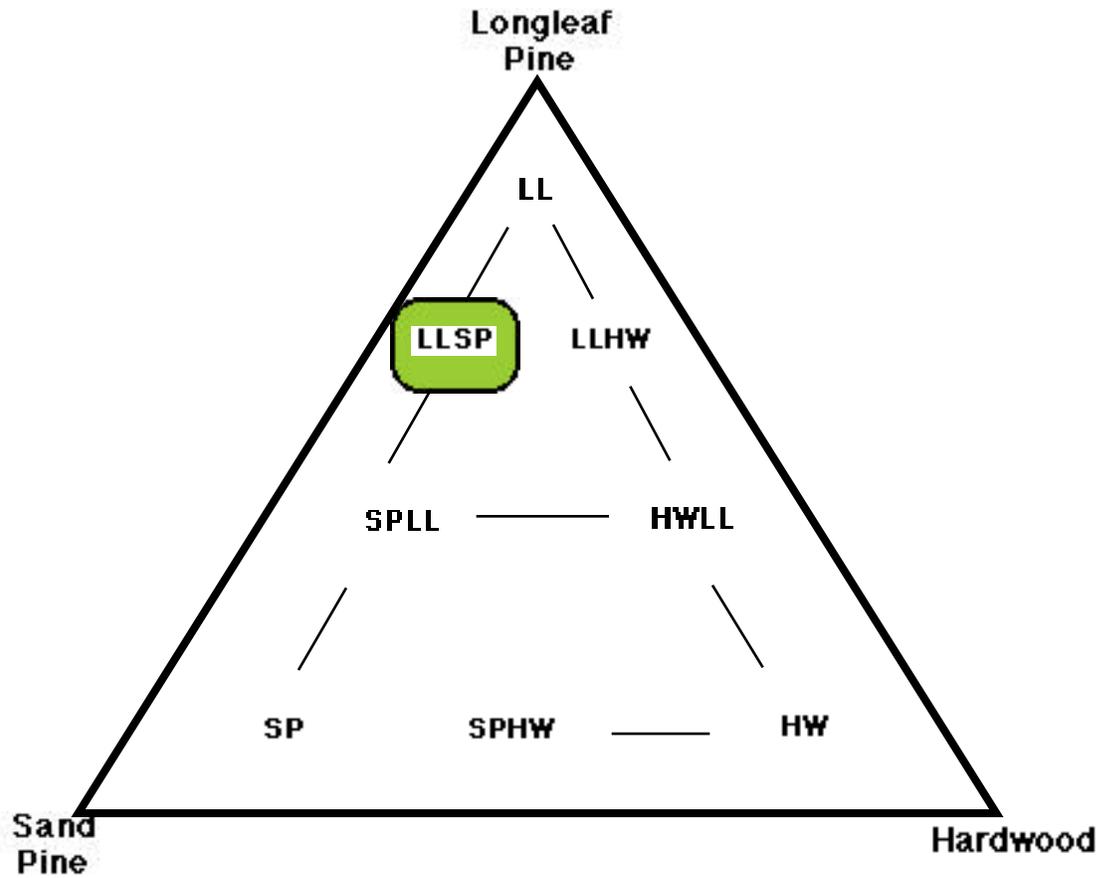


Figure 4-3. A set of vegetation states can be defined within the longleaf pine-sand pine-hardwood triangle. The transitions among these sites define a forest dynamics model.

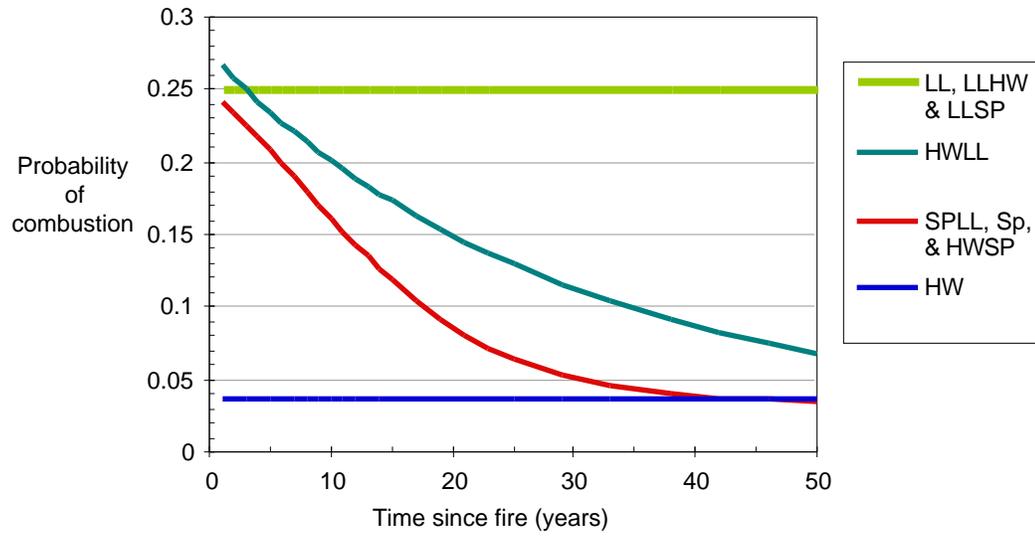


Figure 4-4. The relationship between combustibility of a vegetation type and the time since it has last been burned. Its important to note that if sites are not burnt, or are frequently burnt they will change their vegetation state.

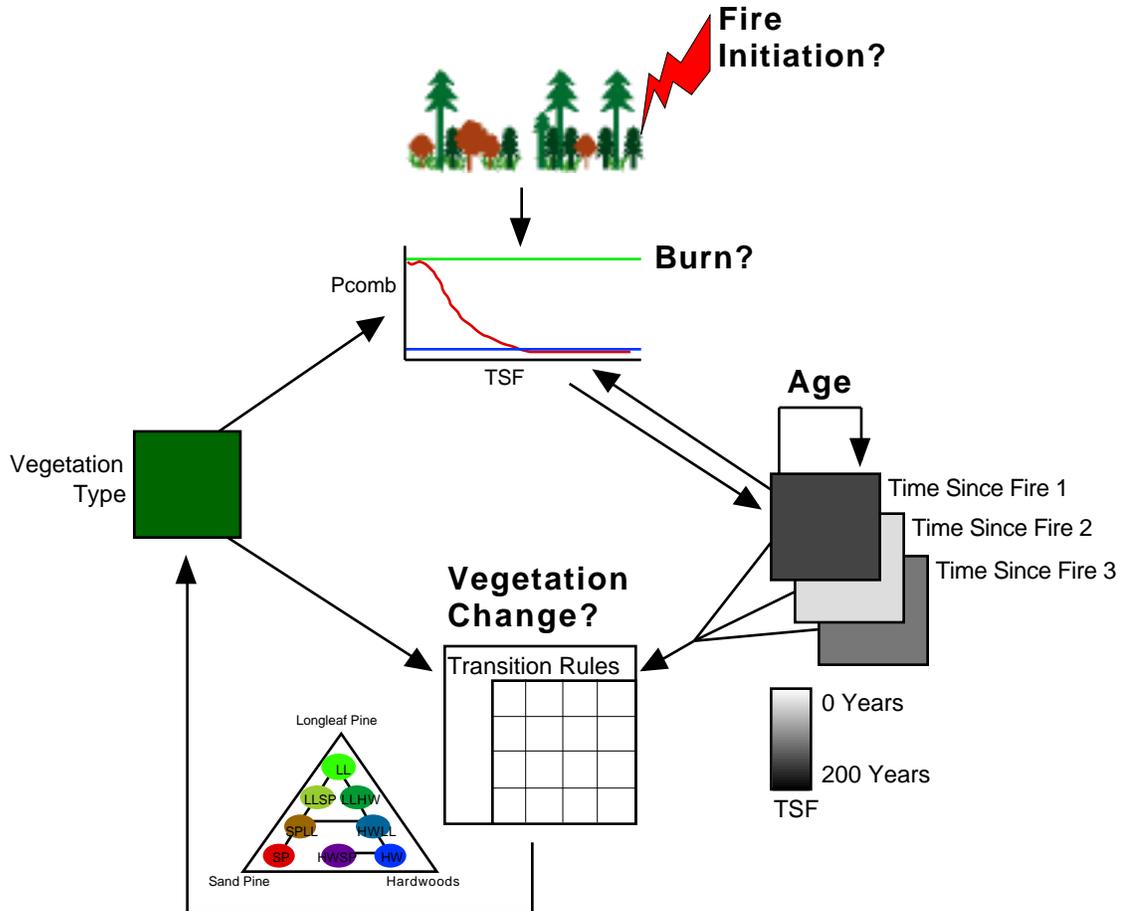


Figure 4-5. The site simulation model. Every year a site ages, it may be ignited, and it may change vegetative state. When a site is ignited it will burn with a probability depending upon the site's vegetation and the time since its last fire. The vegetation state changes following a set of transition rules, which specify transitions among states based upon the current state and previous fire history.

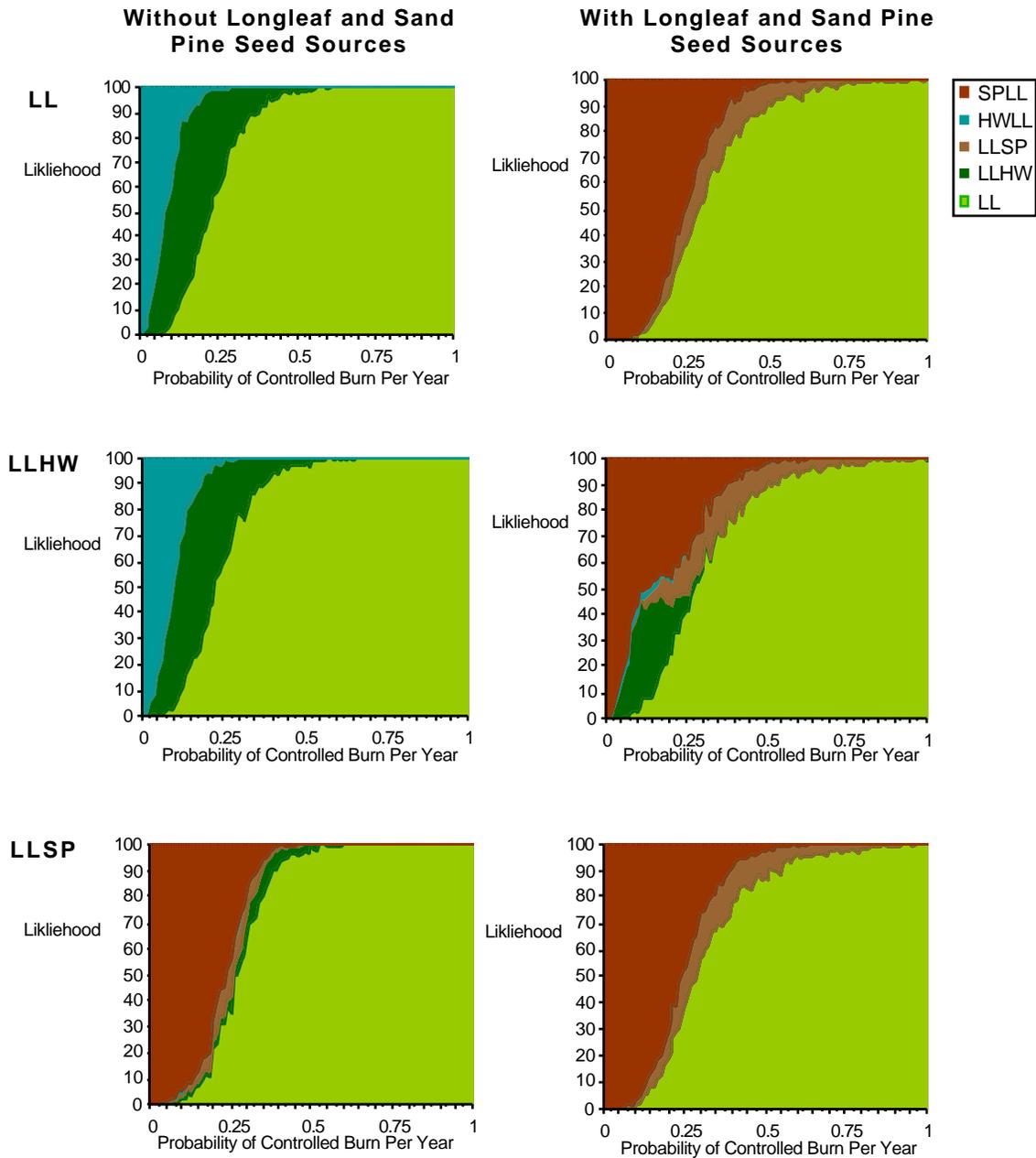


Figure 4-6. Likelihood of vegetation states after 100 years from various longleaf pine dominated initial conditions. Each graph represents the outcome of five hundred simulations at fire initiation probabilities ranging from 0 to 1.0 at 0.01 increments. The probability of ignition is the inverse of fire frequency.

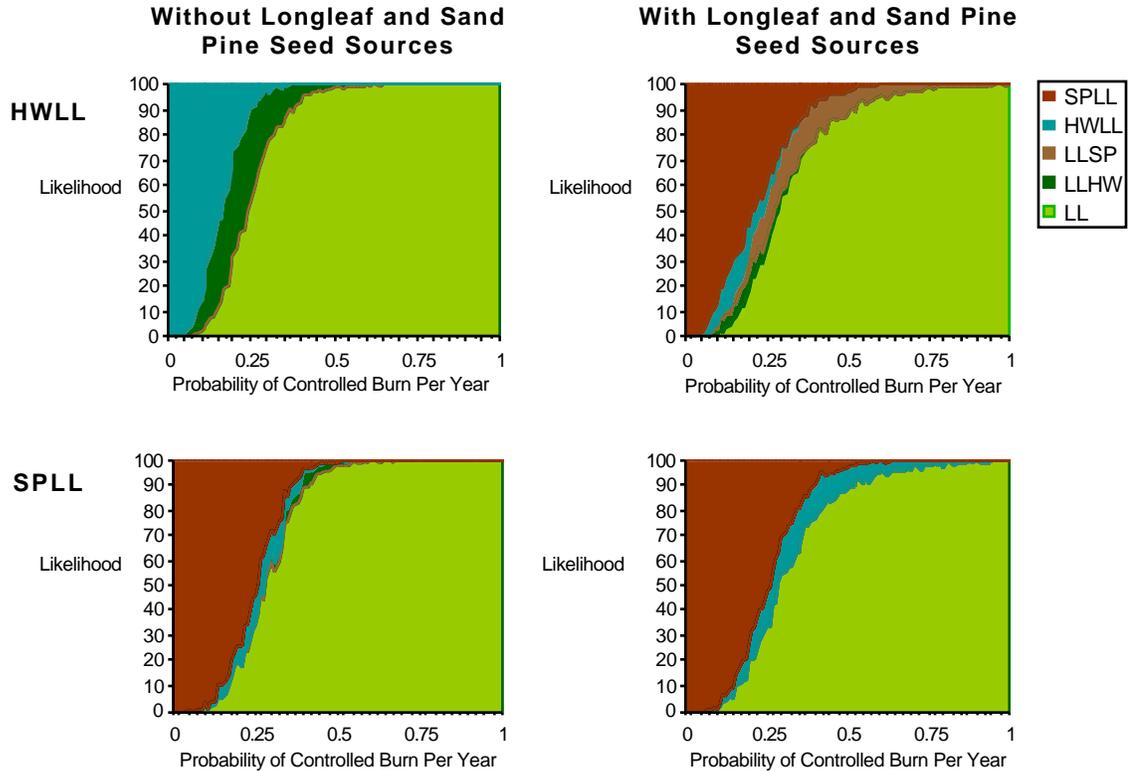


Figure 4-7. Likelihood of vegetation states after 100 years from hardwood longleaf pine site and sand pine – longleaf pine site initial conditions. Each graph represents the outcome of five hundred simulations at fire initiation probabilities ranging from 0 to 1.0 at 0.01 increments. The probability of ignition is the inverse of fire frequency.

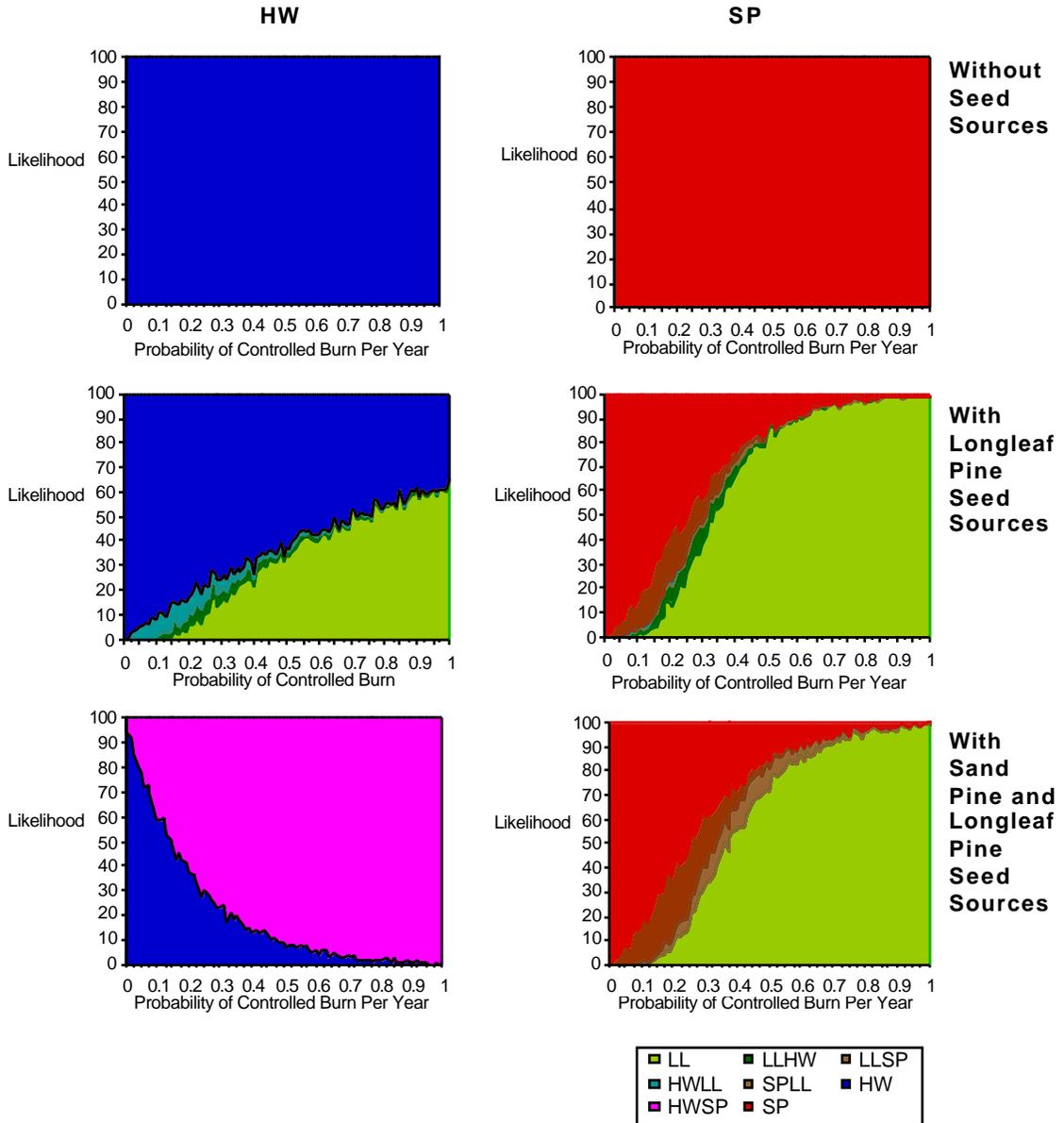


Figure 4-8. Likelihood of vegetation states after 100 years from hardwood and sand pine initial conditions, with and without sand pine and longleaf pine seed dispersal. Each graph represents the outcome of five hundred simulations at fire initiation probabilities ranging from 0 to 1.0 at 0.01 increments. The probability of ignition is the inverse of fire frequency.

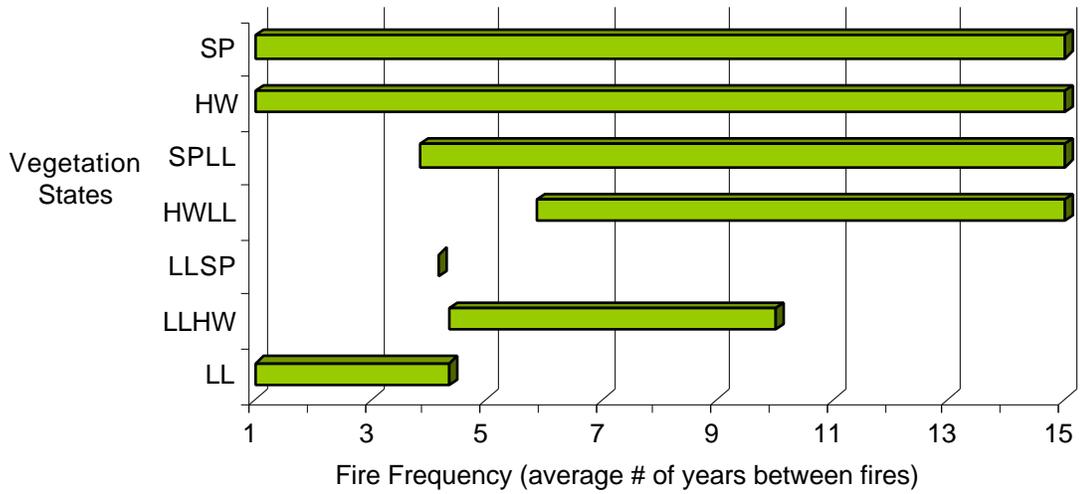


Figure 4-9. Conditions under which an initial vegetative state has a greater than 50% chance of persisting after 100 years for vegetative dynamics with a prescribed burn without seed dispersal.

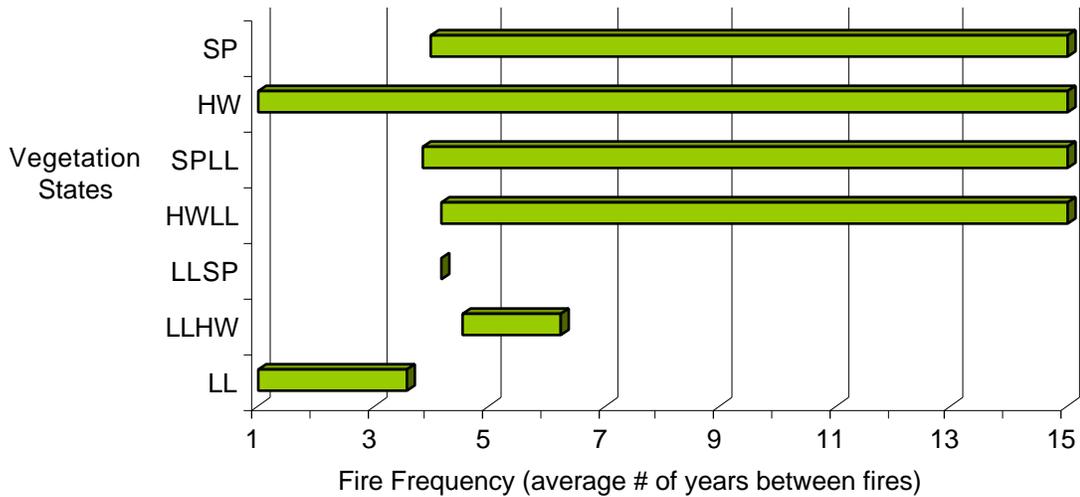


Figure 4-10. Conditions under which an initial vegetative state has a greater than 50% chance of persisting after 100 years for vegetative dynamics with a prescribed burn with longleaf and sand pine seed dispersal.

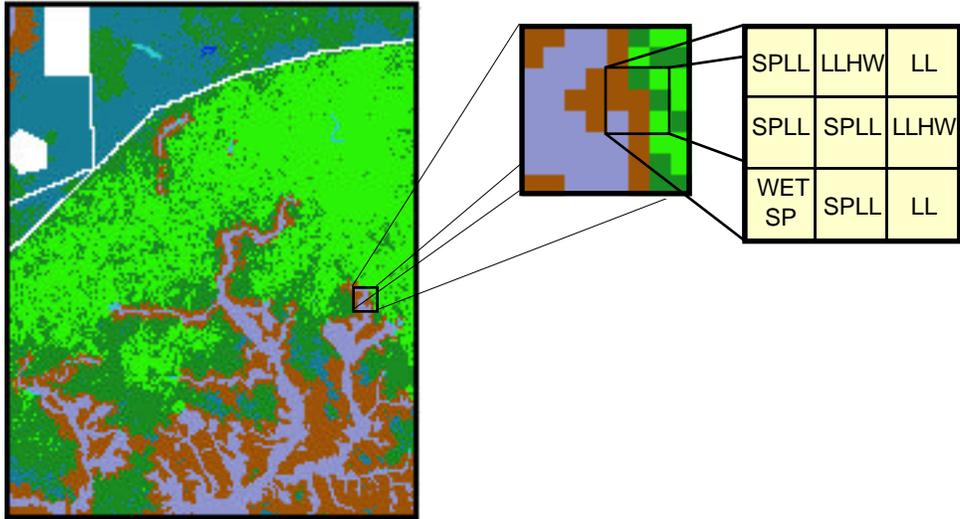


Figure 4-11. A model forest landscape is composed of a matrix of sites of different forest types. Fire and seeds spread across the landscape. Sites change their type over time depending upon fire frequency and seeds dispersal. Each matrix cell represents a site 60 m by 60 m.

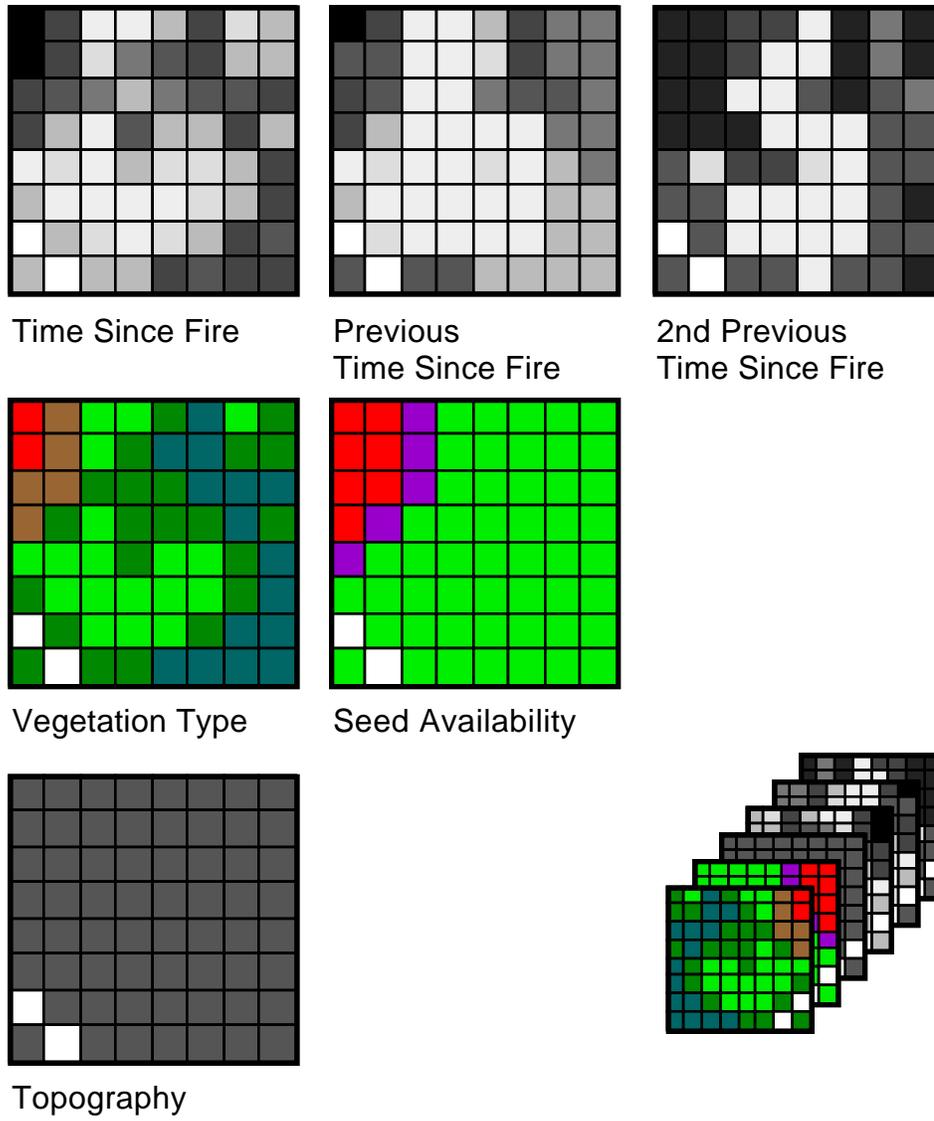


Figure 4-12. The model is composed of six interacting maps that record the landscape's fire history, vegetation, seed availability and topography. These maps are layered on top of one another, in order that vegetation influences fire spread and seed dispersal.

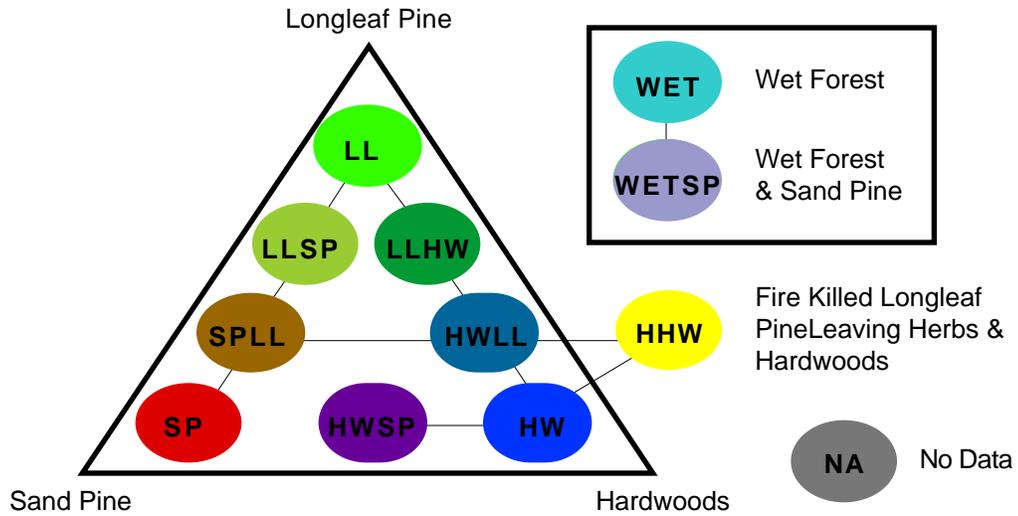


Figure 4-13. The expanded version of the state transition model used in the landscape simulation. The new states include herbaceous hardwoods (HHW), and the topographically constrained wet sites – wet forest, and wet forest including sand pine. An additional state labelled no data is used to indicate locations, such as roads, that are not included in the vegetation model and areas of no data.

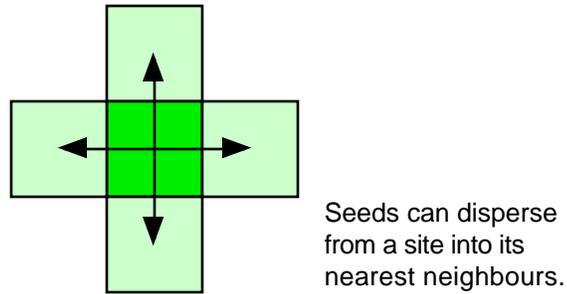


Figure 4-14. Pine seeds can disperse from a site into that site's nearest neighbors, which corresponds to a distance of 60m. Sand pine is able to disperse from SP and SPL sites, but not from LLSP sites. LLSP are occupied by sand pine's that have to reached their reproductive age. Longleaf pine can disperse from LL, LLSP, LLHW, HWLL, and SPL sites. However, longleaf pine is assumed to only disperse enough seeds to colonize a new site during mast years, which occur once a decade.

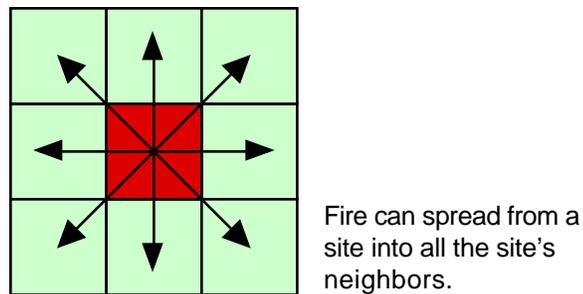


Figure 4-15. Fire can spread from a site into all of that site's neighbors. Fire spread is probabilistic. The probability of fire invading a site depends upon that site's attributes.

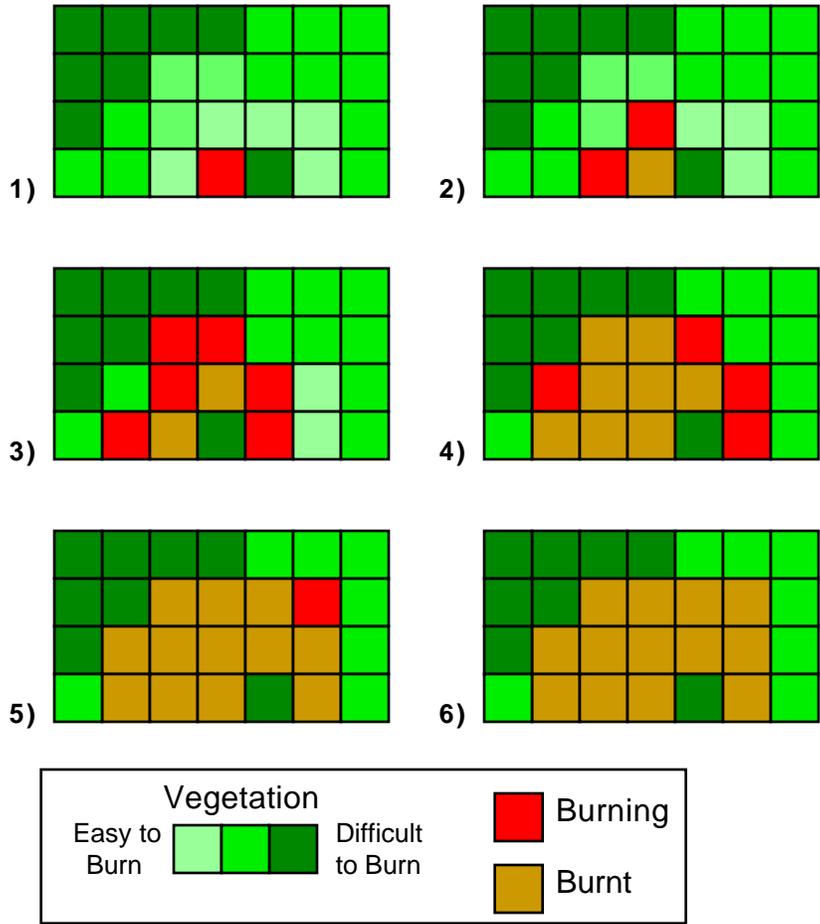


Figure 4-16. An example of fire spread. Fire spreads from burning sites to unburned sites, until there are no remaining burning sites. By altering the spread of fire across a landscape, a site can influence its neighbouring sites. Sites that propagate fire well, such as LL, increase the likelihood that their neighbors will burn, while sites that inhibit fire spread, such as HW, decrease the likelihood that their neighbors will burn.

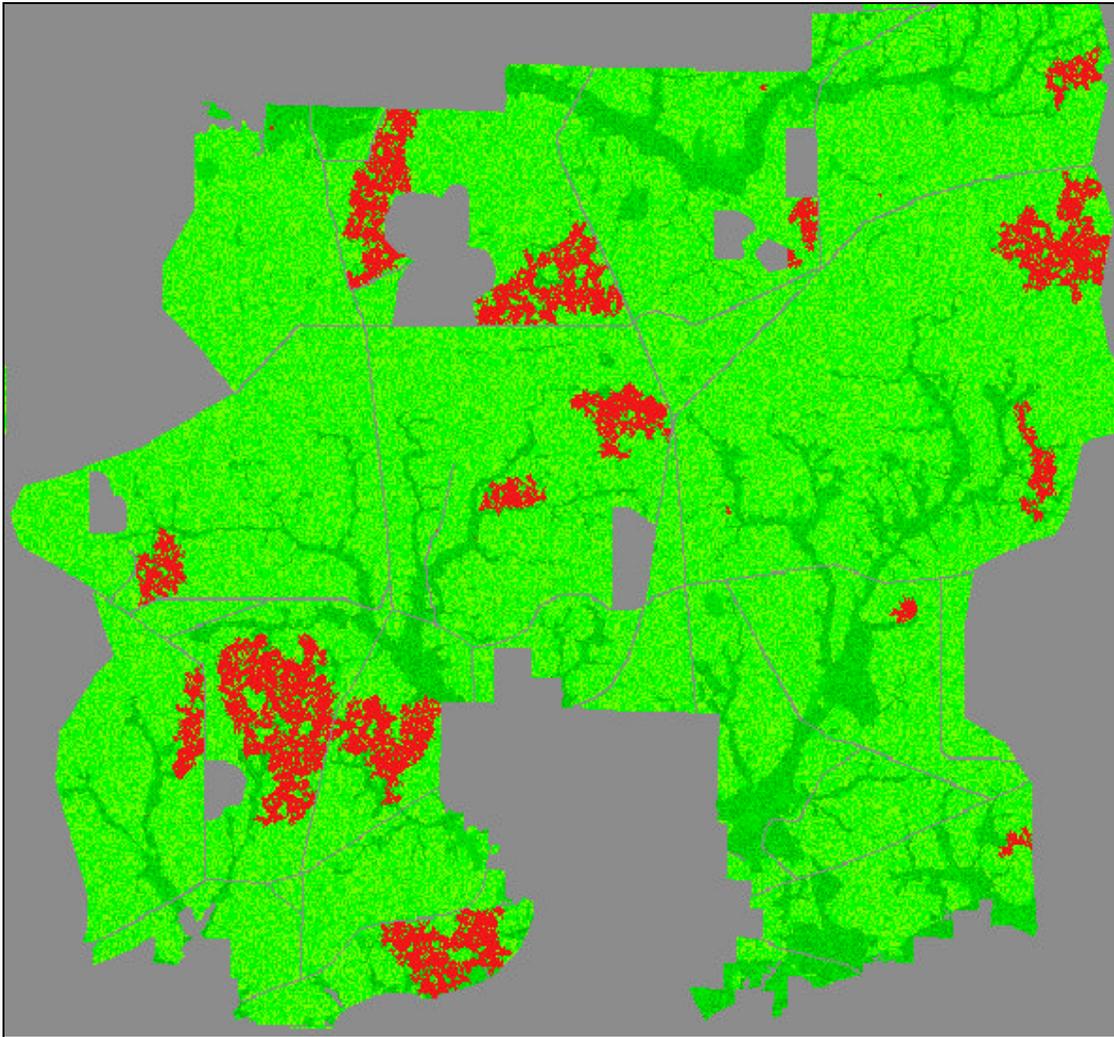


Figure 4-17. Animation of fire in the fragmented historical landscape. As fire spreads across the landscape it does not burn homogeneously. Remanent patches of unburnt vegetation remain with a fire, and fire spread is impeded by older, less combustible vegetation. Fire is stopped by roads (coloured grey), and the stream networks (dark green). This movie shows 20 years of fire. The green sites are vegetated sites. The darker the green of the site the longer its time since last fire.

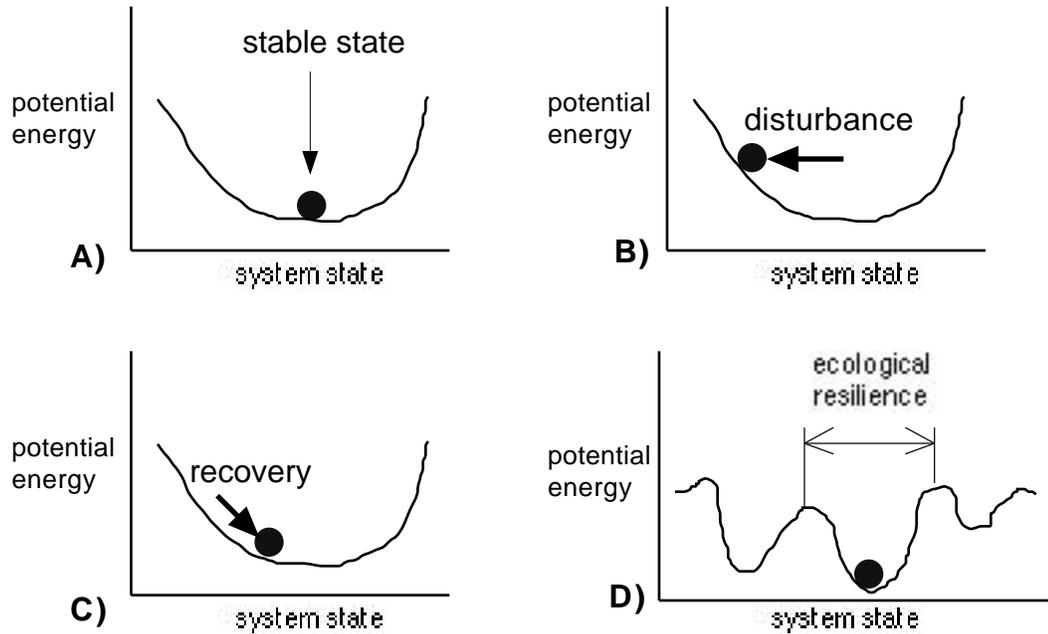


Figure 4-18. The concept of resilience can be illustrated by modeling the ‘state’ of an ecosystem as the position of a ball on a landscape. A) Gravity pulls the ball downwards, and therefore pits in the surface of the landscape are stable states. B) The deeper a pit the more stable it is, because increasingly strong disturbances are required to move an ecological state away from the bottom of the pit. C) The steepness of the sides of a stability pit corresponds to the strength of negative feedback processes maintaining an ecosystem near its stable state. D) The width of a pit indicates the amount of change that a state can experience before it transforms to another state. The width of the pit corresponds to ecological resilience.

State Transition Likelihoods

		To	
		poor	good
From	poor	0.6	0.2
	good	0.4	0.8

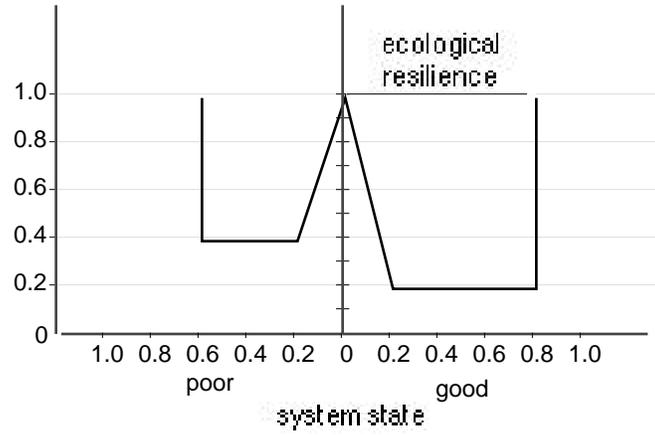


Figure 4-19. State transition resilience. Transition probabilities can be used to produce a resilience landscape that illustrates the probability of remaining within a state or moving to an alternate state.

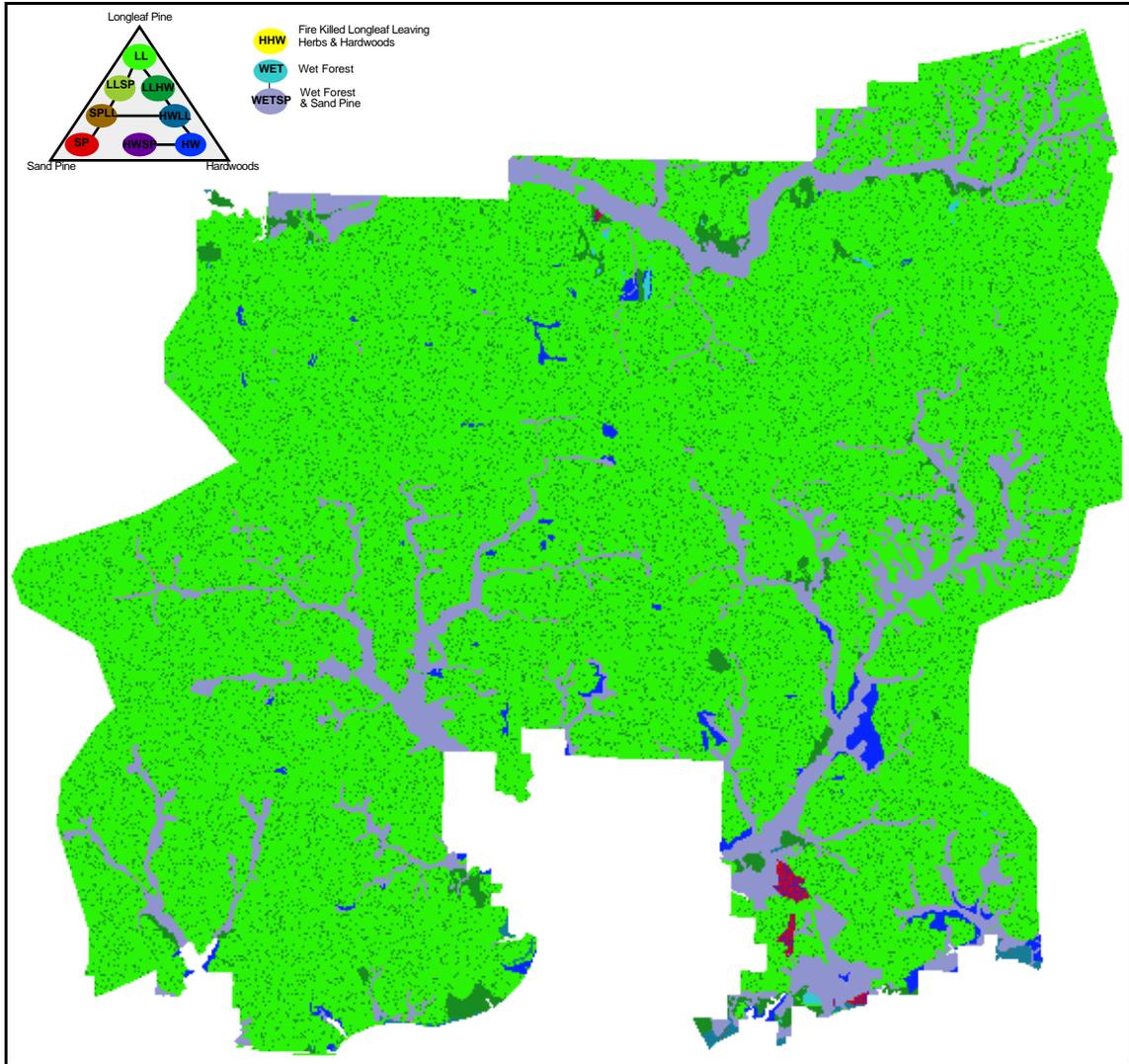


Figure 4-20. A map of the hypothesized historical distribution of vegetation over the central three watersheds of Eglin Air Force. This area spans is 33 km across and 35.4 km high. The area of vegetation cover about 751 km². This area is simulated using about 208,000 60 m by 60m sites.

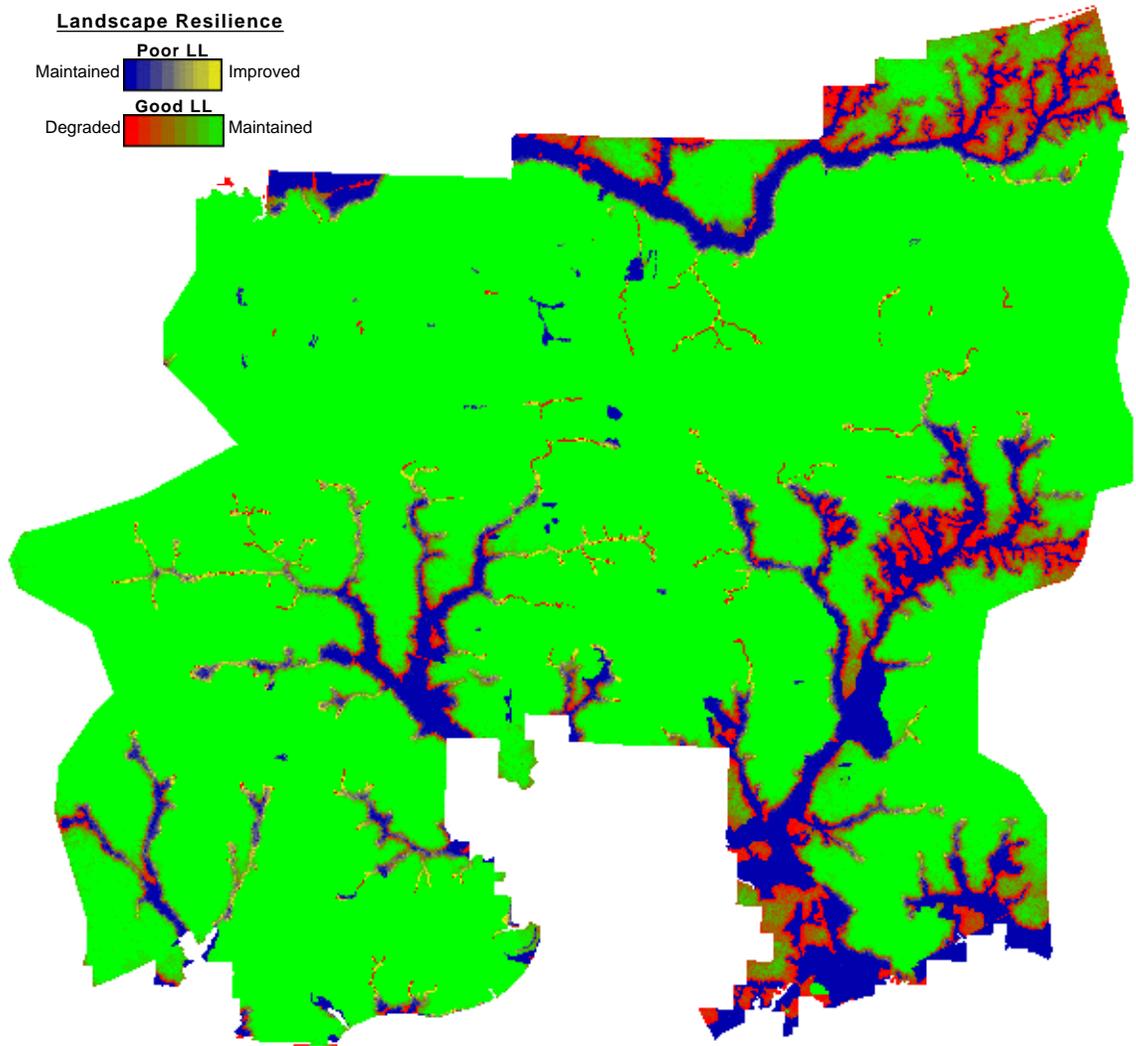


Figure 4-21. Map of spatial resilience of historical landscape under wildfire shows resilience landscape with some sand pine invasion, well within the historical limits of the landscape.

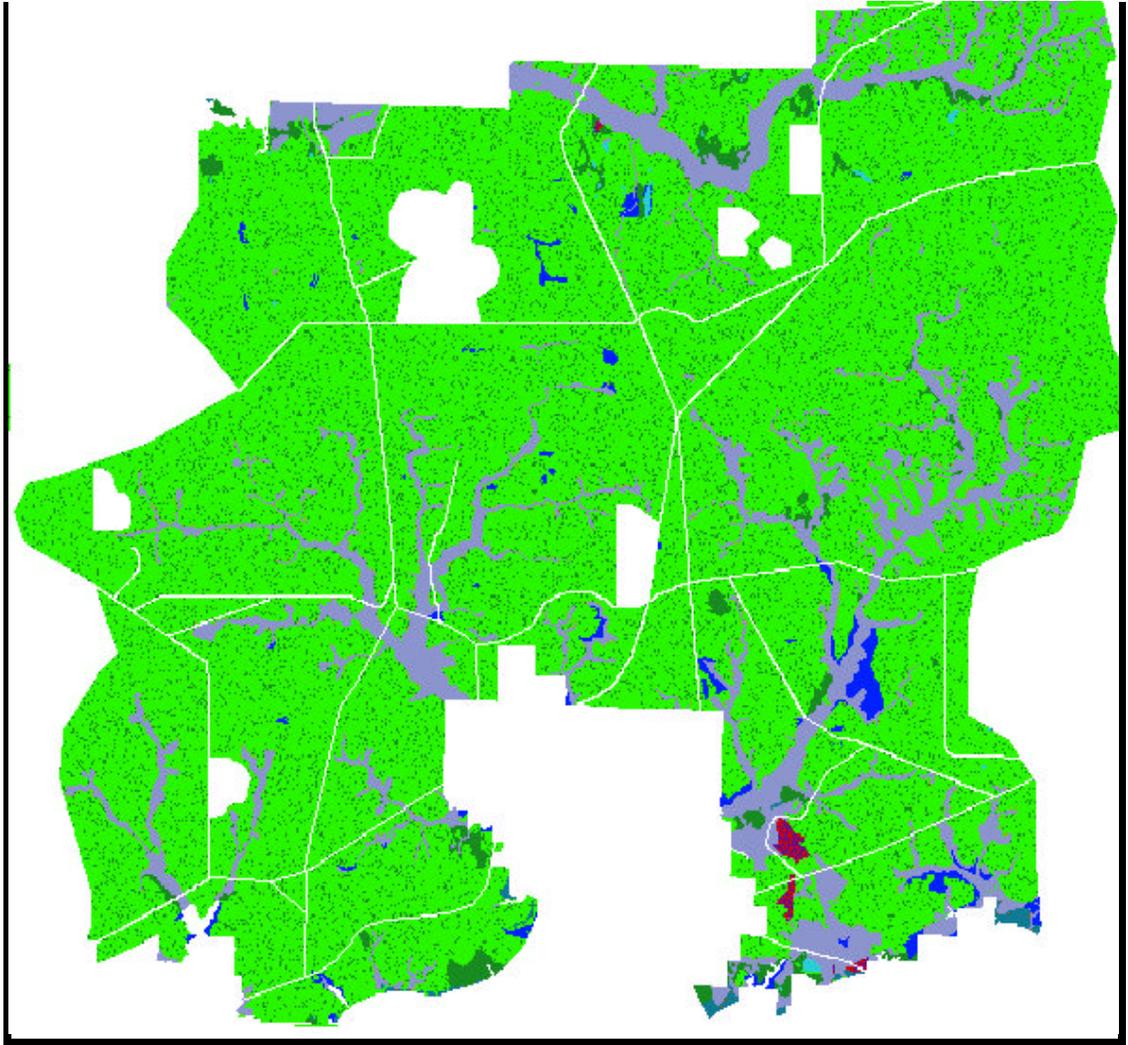


Figure 4-22. The vegetation predicted by the Eglin model following 100 years of fire suppression on the hypothesized historical Eglin landscape, after that landscape has been fragmented by roads, and structures. This movie displays vegetation change over 100 years at 5 year intervals. After 50 years of fire suppression the map roughly corresponds to the present state of Eglin Air Force Base.

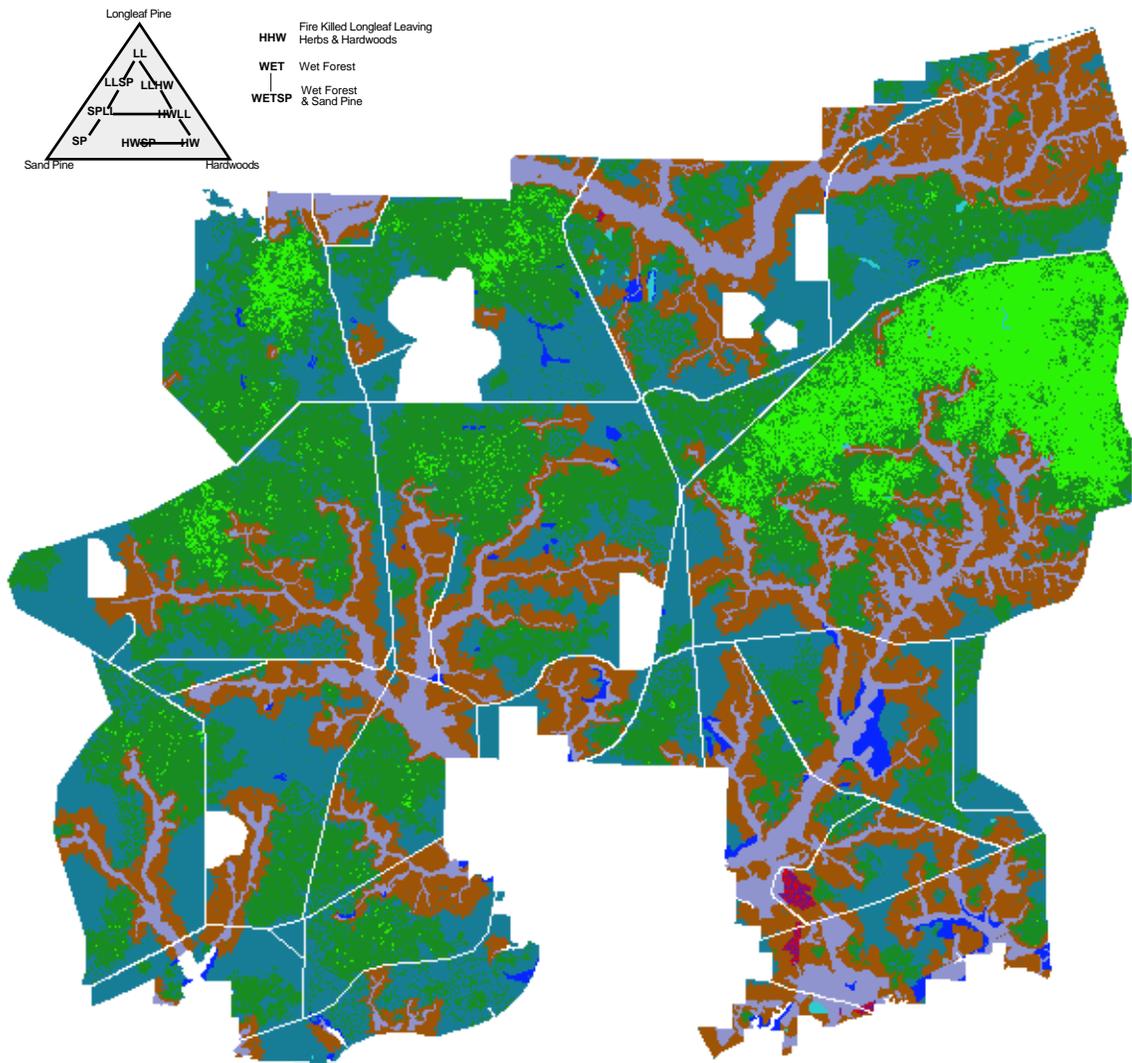


Figure 4-23. The vegetation predicted by the Eglin model following 50 years of fire suppression on the hypothesized historical Eglin landscape, after that landscape has been fragmented by roads, and structures (the white areas). The map roughly corresponds to the present state of Eglin Air Force Base, and was used as a benchmark for restoration strategies.

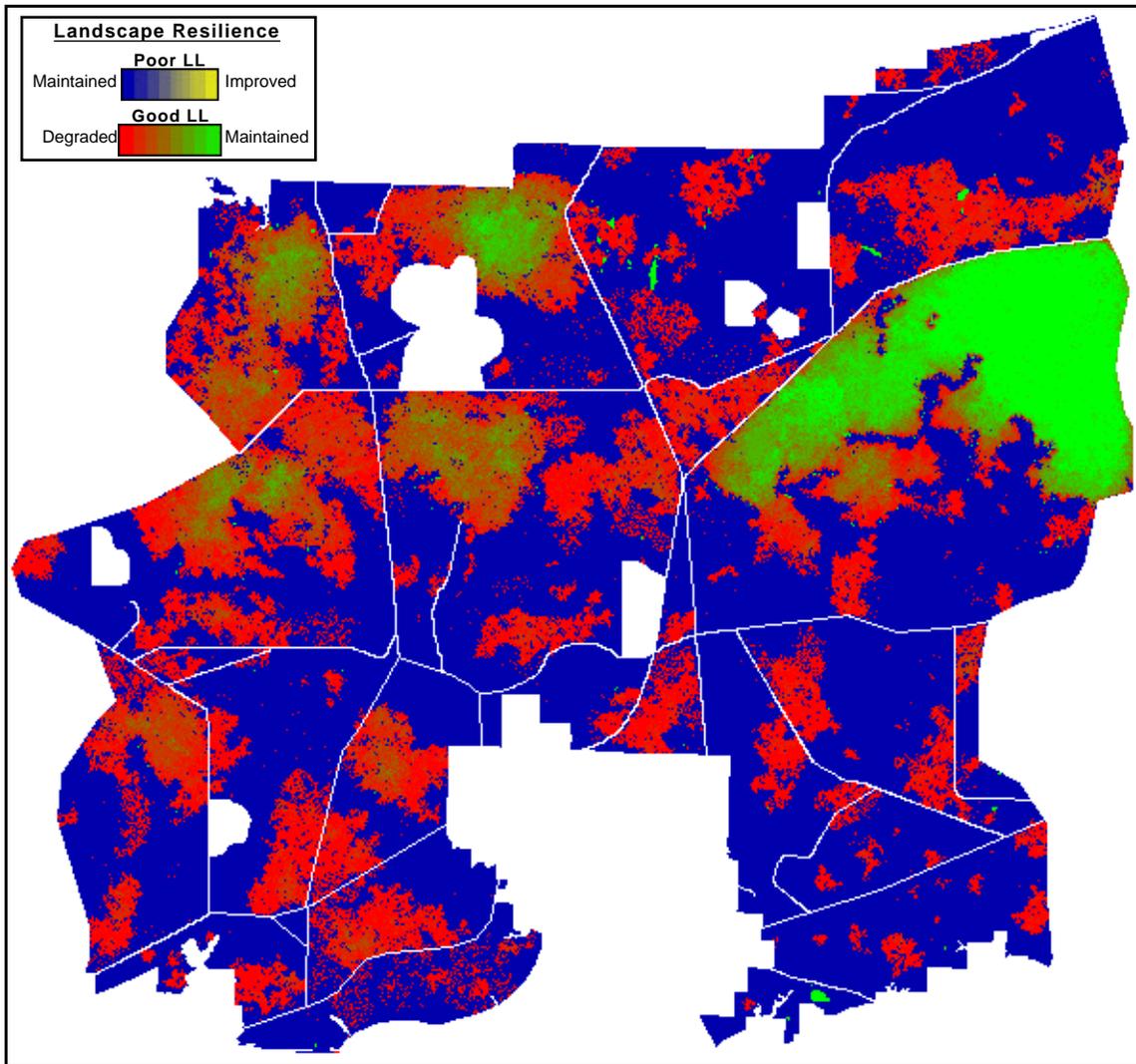


Figure 4-24. Map of spatial resilience of the 'current' landscape under suppressed wildfire. This map shows that the landscape will experience large changes within the next fifty years, if only suppressed wildfire was to occur.

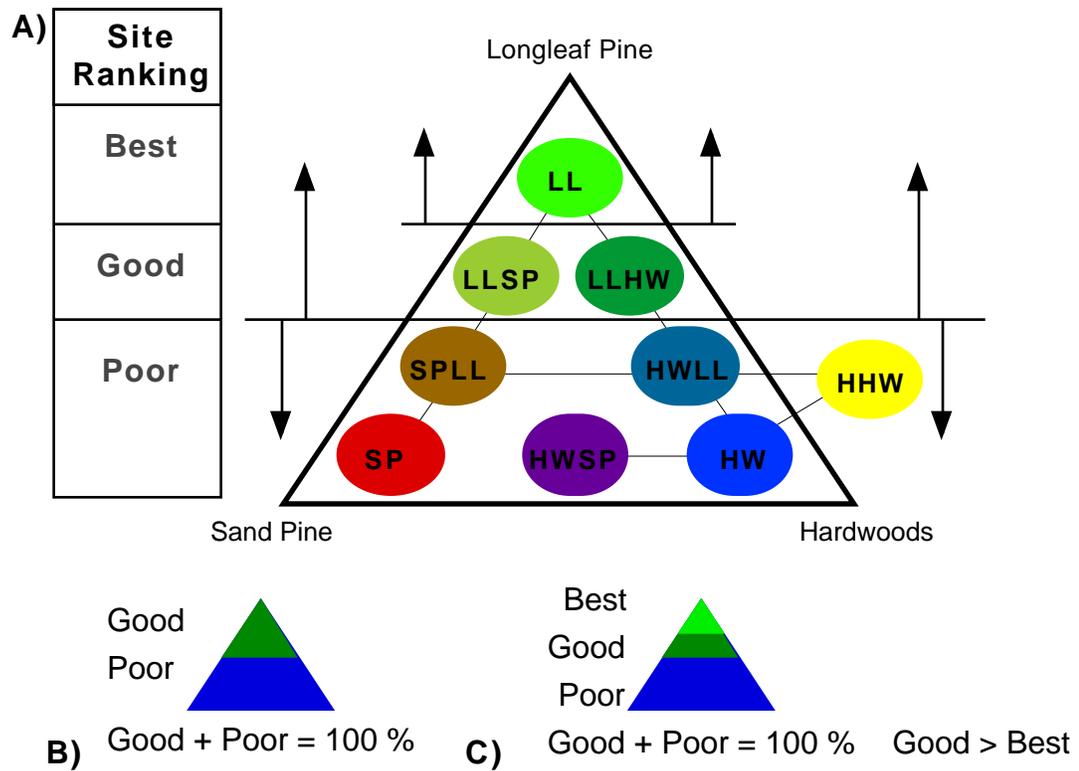


Figure 4-25. A) To compare the relative success of alternative land management strategies, vegetation types were divided into two mutually exclusive classes, 'good' and 'poor', based upon the proportion of longleaf pine in each vegetation type. B) All the sites in which longleaf pine is a dominant component (LL, LLHW, and LLSP) are 'good' sites. All the other sites that could include longleaf are considered 'poor sites' (HWLL, SPLL, HW, HWP, SP and HHW). C) The sub-class of 'good' sites that were longleaf (LL) were classified as the class 'best'. The vegetation types WET and WETSP are excluded from these divisions as they do not contain and cannot change to contain longleaf pine.

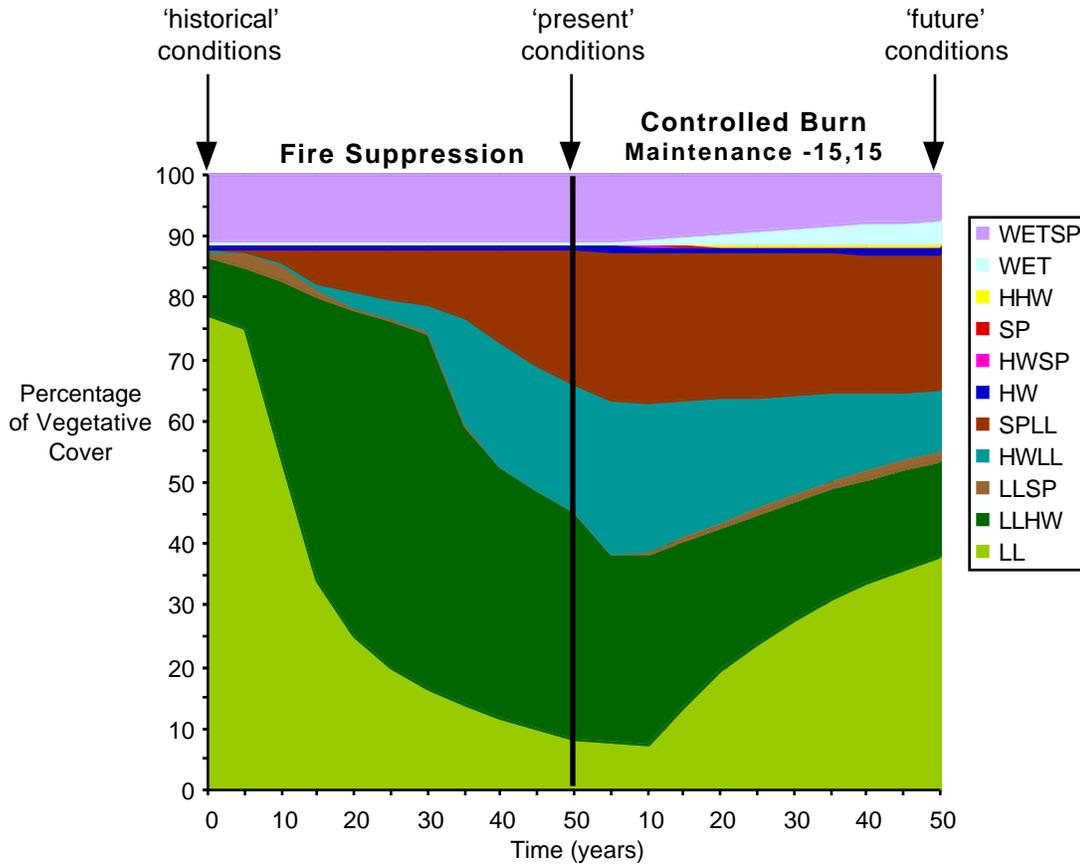


Figure 4-26. Changes in area covered by different vegetation types during a simulation run of the Eglin Landscape Model. For the first fifty years of the model fire is suppressed. At fifty years the management strategy changes and prescribed burns following the 'maintenance' strategy are applied for the following fifty years. Note how prescribed burns successful convert hardwood invaded sites to longleaf, but sand pine continues to invade longleaf sites.

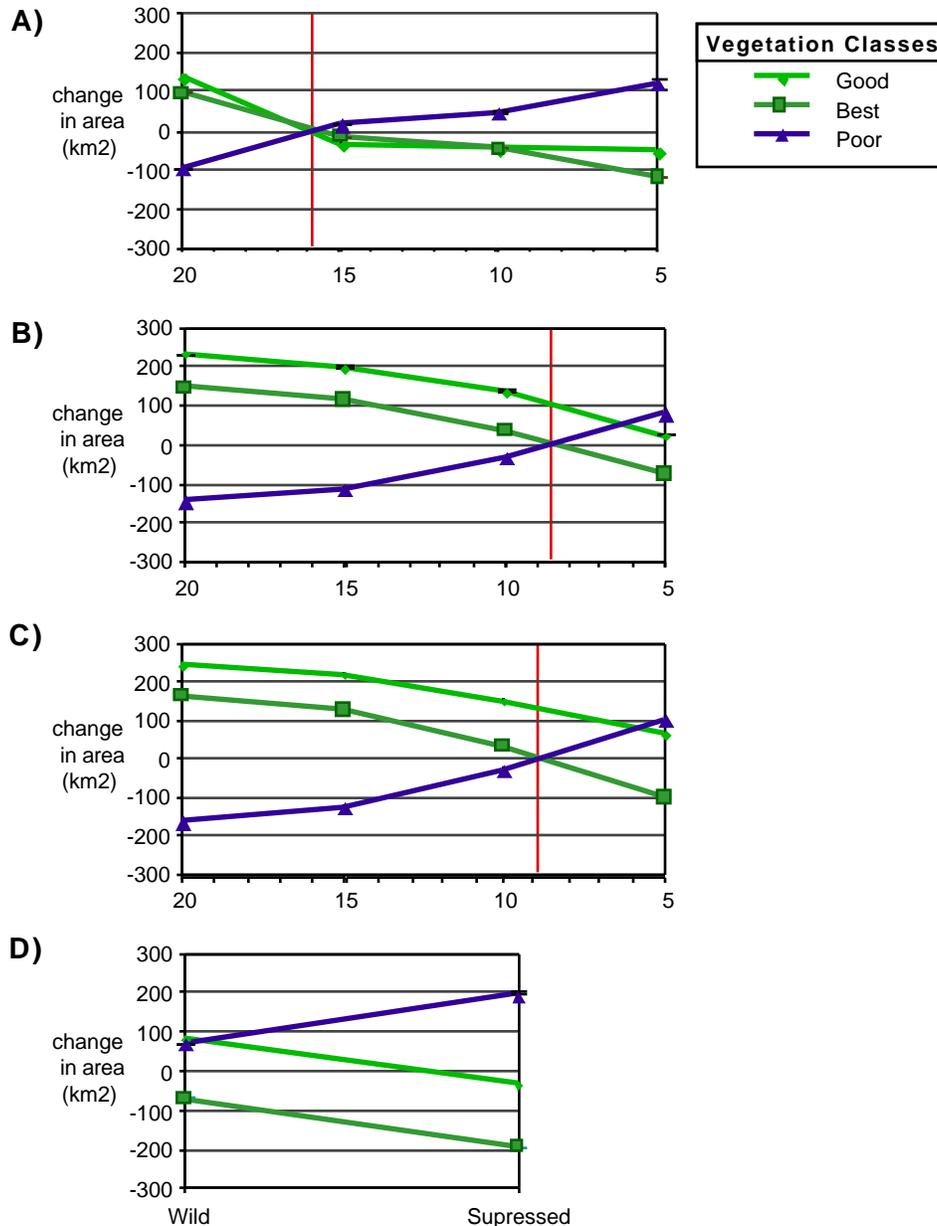


Figure 4-27. Changes in proportion of landscape covered by different vegetation classes in response to varying intensities of the management strategies: ‘conversion’, ‘maintenance’, ‘rotation,’ and ‘fire’. In the prescribed burn cases intensity varies with the number of prescribed burns a year. The range is from 20 small and 20 large burns a year, to 5 large and 5 small burns a year. In the wildfire case it intensity varies the number of initiations between the wildfire case, and fire suppression in which the number of fires started is reduced by a factor of five. A) ‘Rotation’ management strategy. B) ‘Conversion’ management strategy. C) ‘Maintenance’ management strategy. D) ‘Wildfire’ management strategy. Each model scenario was run ten times. The results shown are the average values. The standard errors area displayed, but difficult see because they are small. They are all less than 0.5% of each mean value. The vertical red lines indicate the minimum number of prescribed burns necessary to maintain the existing area of ‘good’ longleaf pine vegetation for each management approach. Neither of the ‘wildfire’ management strategies succeeded in maintaining the initial area of ‘good’ vegetation.

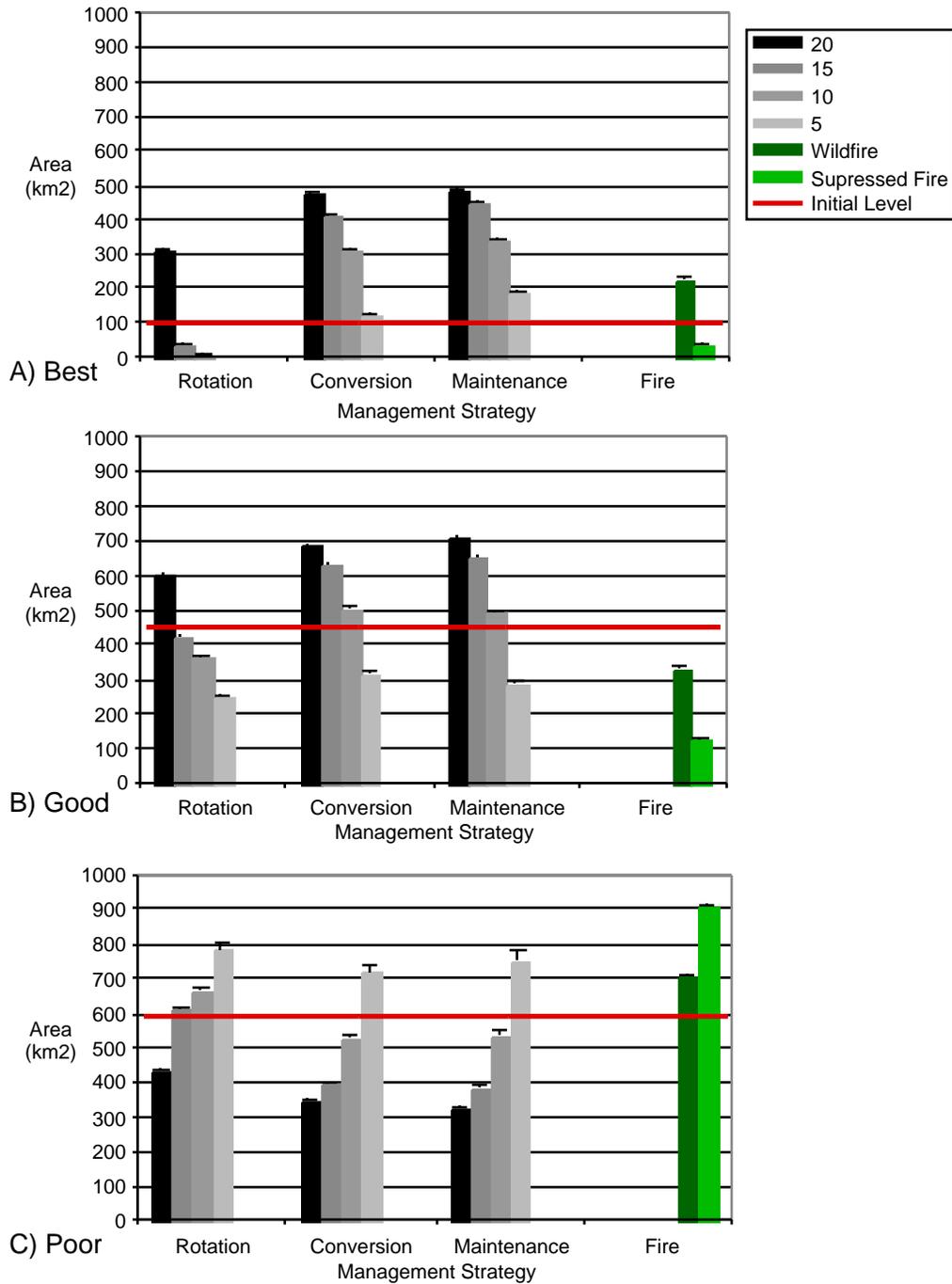


Figure 4-28. Response of landscape classes to management strategies. A) Change in 'Best' sites. B) Change in 'Good' sites. C) Change in 'Poor' sites. The goal of management is to increase the amount of good and best sites, while decreasing the area occupied by poor vegetation. Each model scenario was run ten times, the result shown are the average values. The standard errors is displayed.

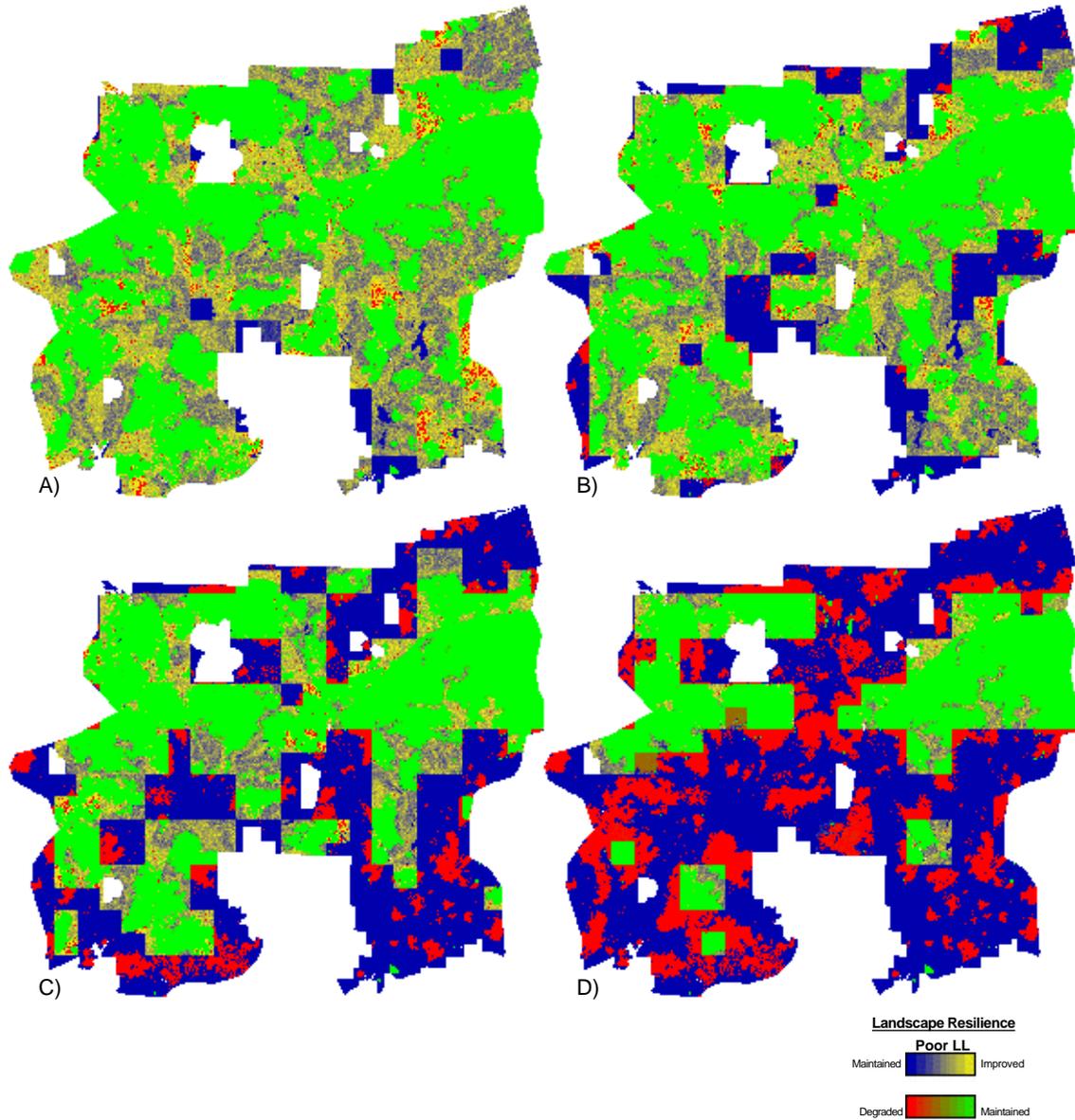


Figure 4-29. Resilience landscapes produced by fifty years of a ‘maintenance’ strategy. For A) 20 large and 20 small burns/year; B) 15 large and 15 small burns/year; C) 10 large and 10 small burns per year; and D) 5 large and 5 small burns/year.

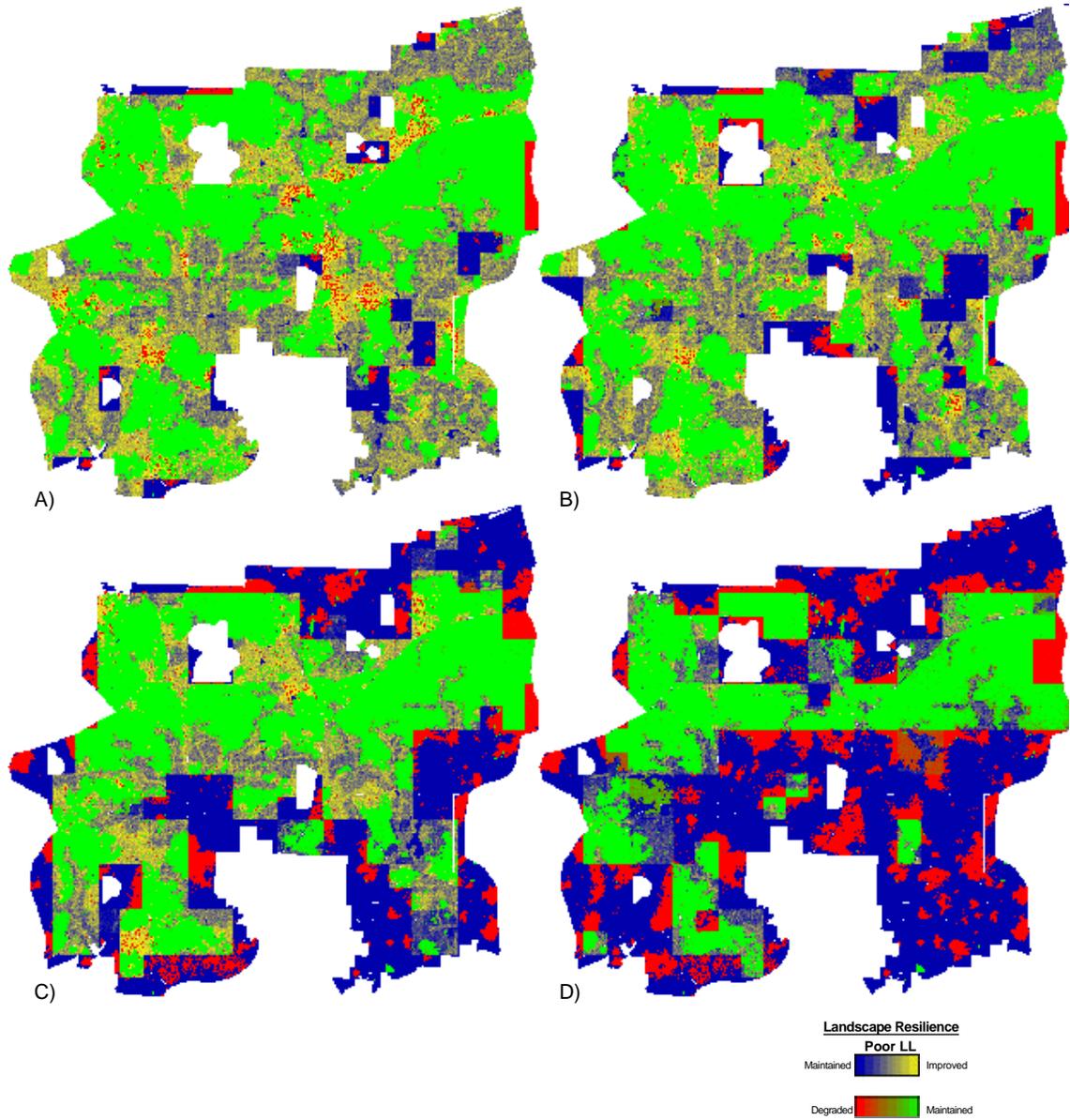


Figure 4-30. Resilience landscapes produced by fifty years of a ‘conversion’ strategy. For A) 20 large and 20 small burns/year; B) 15 large and 15 small burns/year; C) 10 large and 10 small burns per year; and D) 5 large and 5 small burns/year.

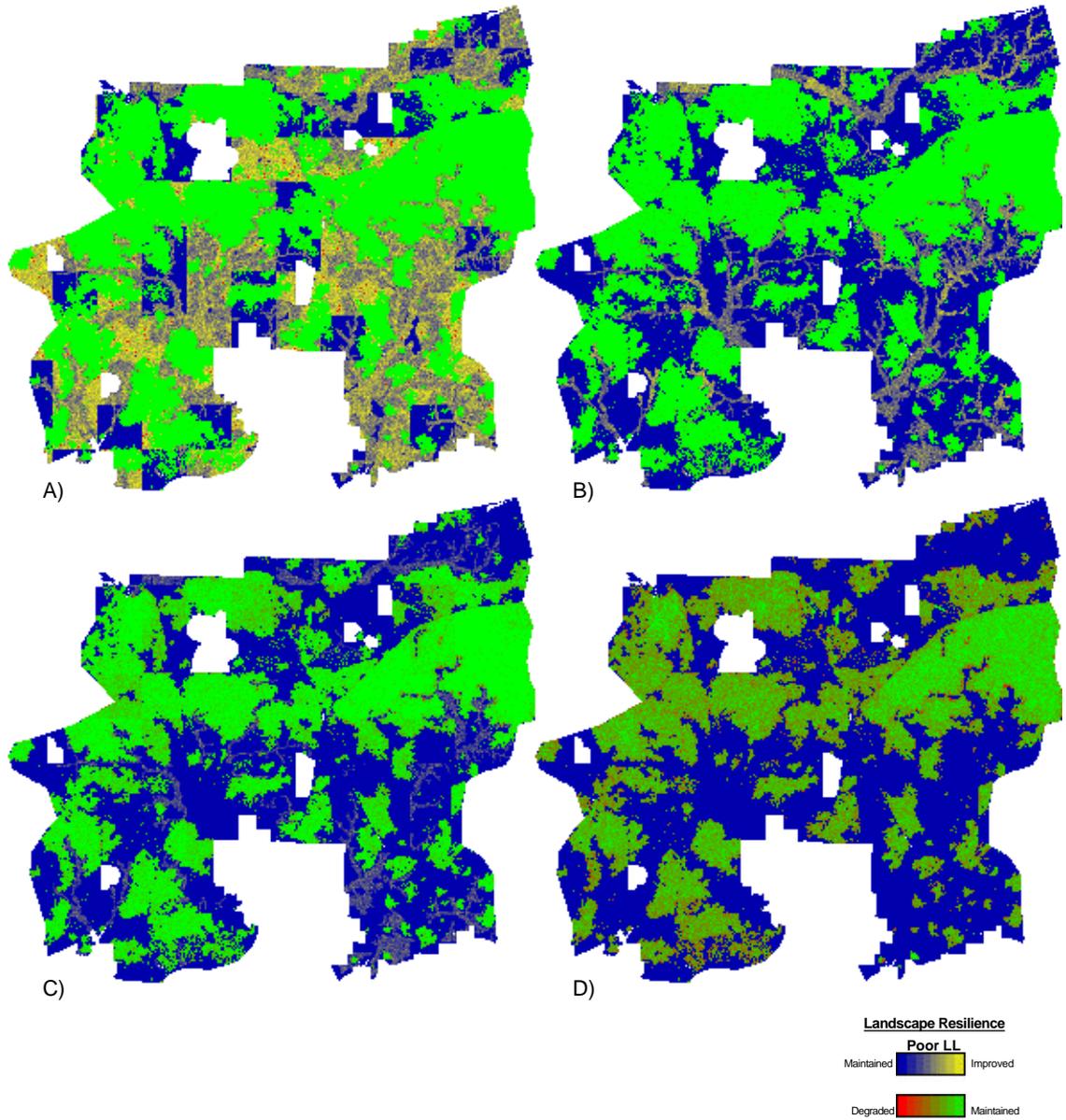


Figure 4-31. Resilience landscapes produced by fifty years of a 'rotation strategy. For A) 20 large and 20 small burns/year; B) 15 large and 15 small burns/year; C) 10 large and 10 small burns per year; and D) 5 large and 5 small burns/year.

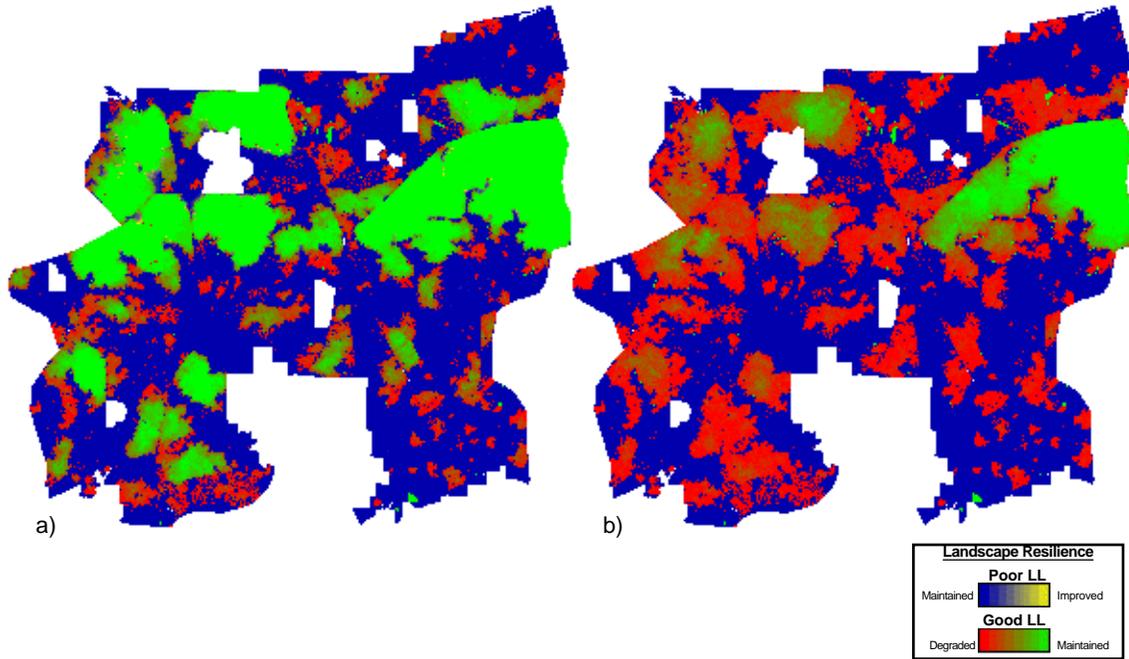


Figure 4-32. Resilience landscapes produced by fifty years of 'fire' strategy. For a) wildfire; and b) suppressed wildfire. Fires are initiated at 1/5 of the wildfire rate.

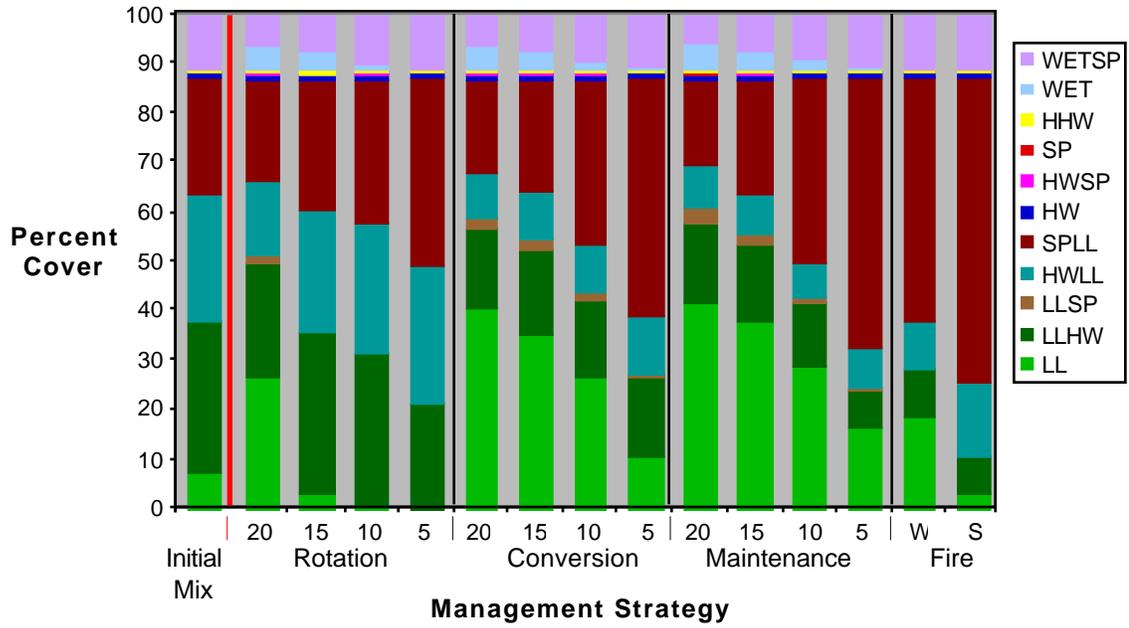


Figure 4-33. Response of vegetation types to different management strategies, after fifty years. Each model scenario was run ten times, the results shown are the average values.

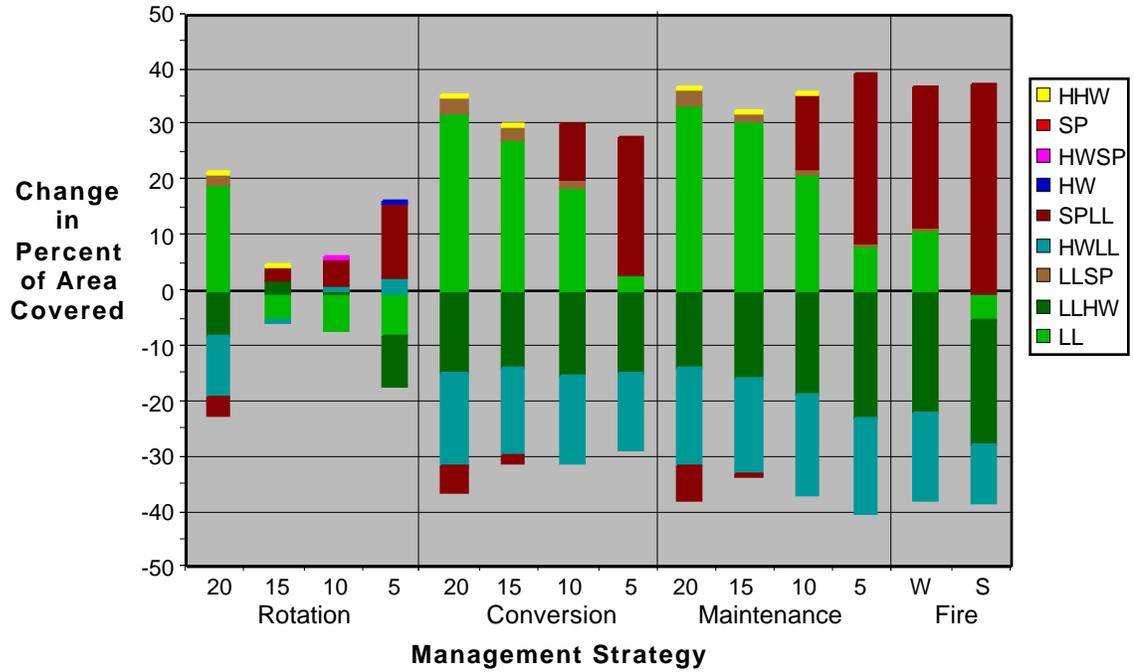


Figure 4-34. Change of sandhill vegetation types from 'present' conditions in response to fifty years of different management strategies, after fifty years. Each model scenario was run ten times; the results shown are the average values. Standard error values are not shown but are less than 1% for all vegetation classes.

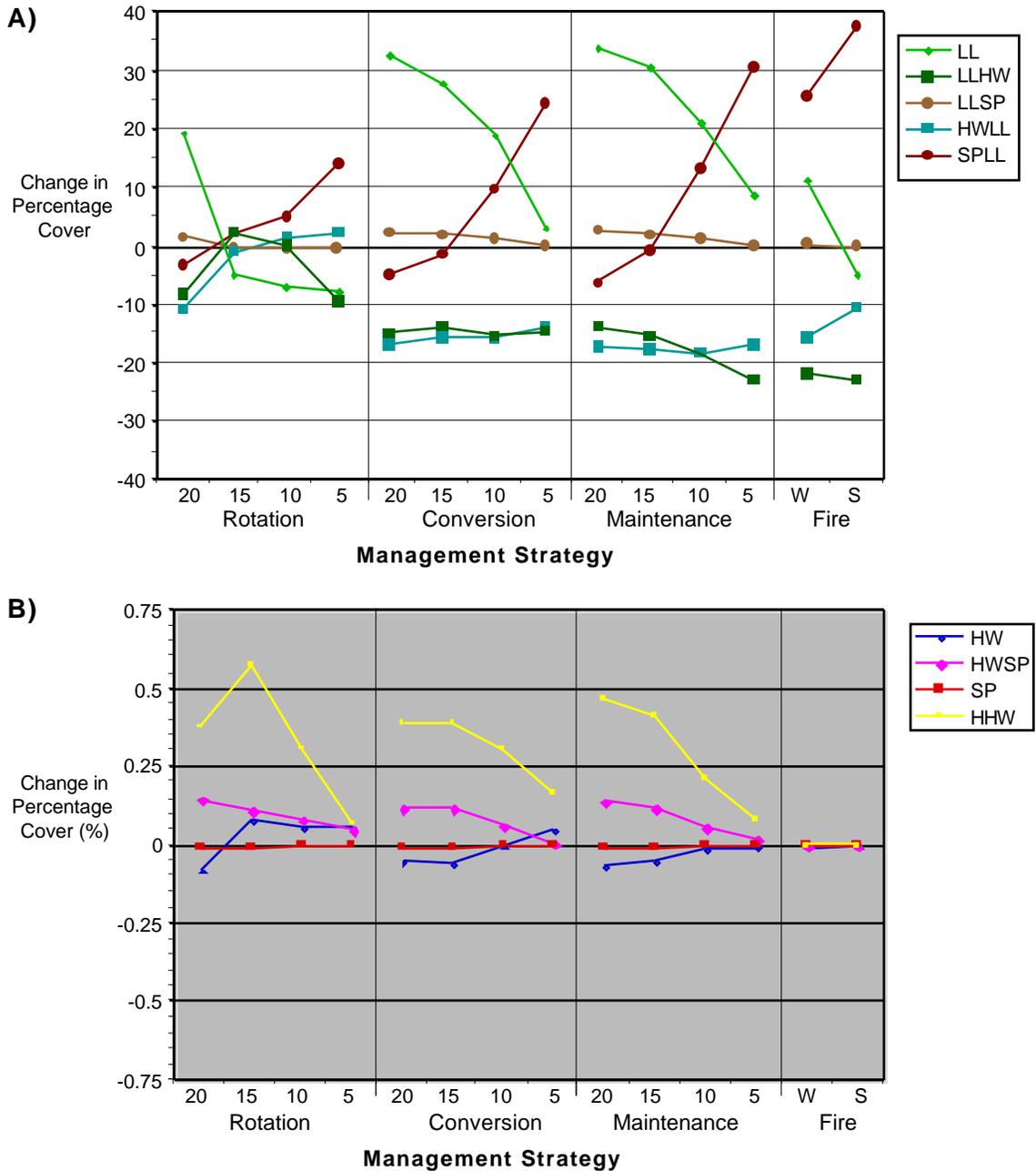


Figure 4-35. Change of sandhill vegetation types from ‘present’ conditions in response to fifty years of different management strategies, after fifty years. Inflection points in trend of vegetation growth or shrinkage are shown by crossing zero axis. Each model scenario was run ten times; the result shown are the average values. Standard error values are not shown but are less than 1% for all vegetation classes. A) Changes in common vegetation classes: LL, LLHW, LLSP, HWLL, and SPL. B) Changes in uncommon vegetation classes: HW, HWSP, SP, and HHW. Note that changes in dominant vegetation are almost two orders of magnitude larger than changes in uncommon vegetation.

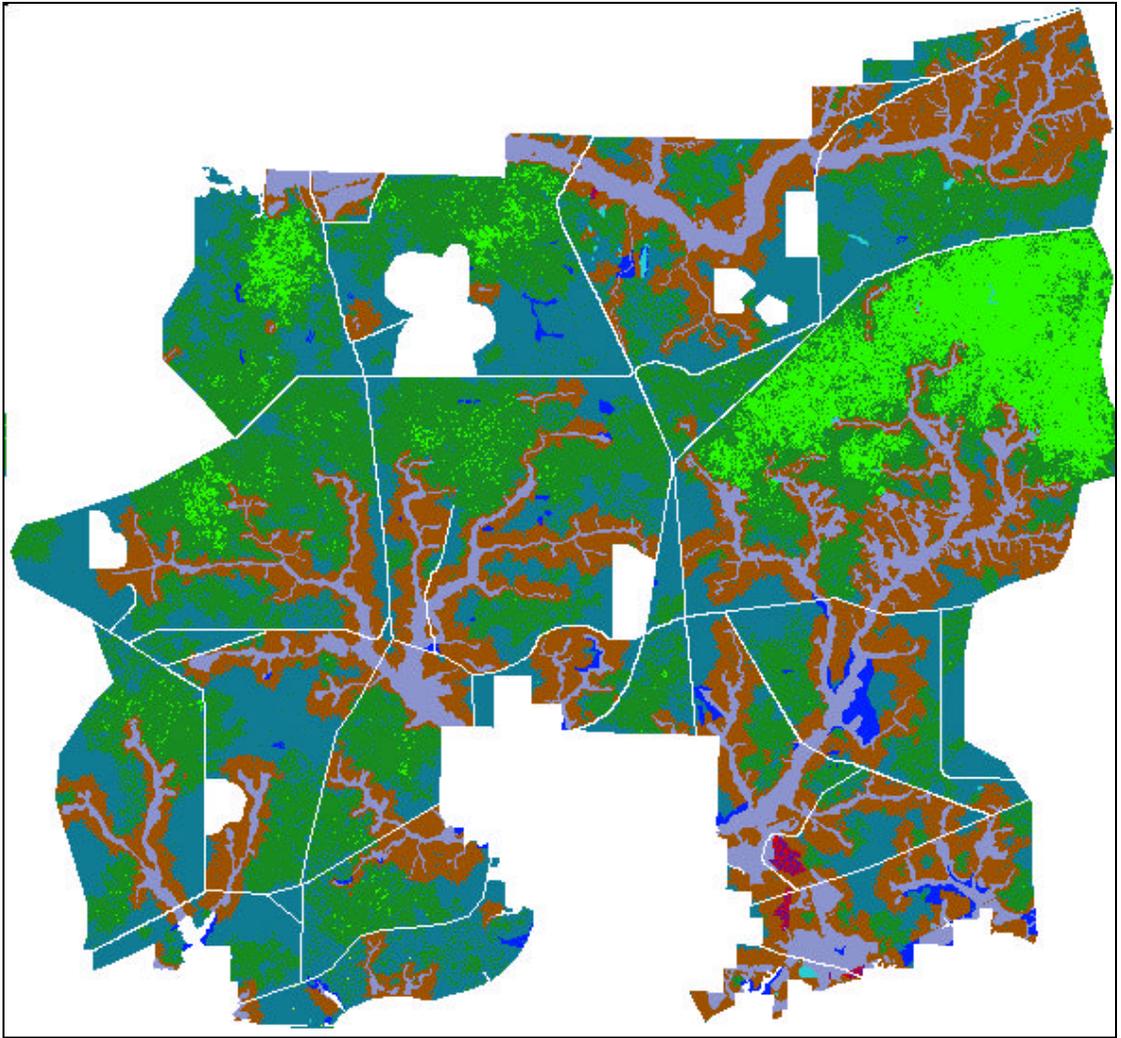


Figure 4-36. Vegetation change from the 'current' landscape under 100 years of the 'maintenance' strategy using 10 large and 10 small fires per year. Vegetation change is shown every two years.

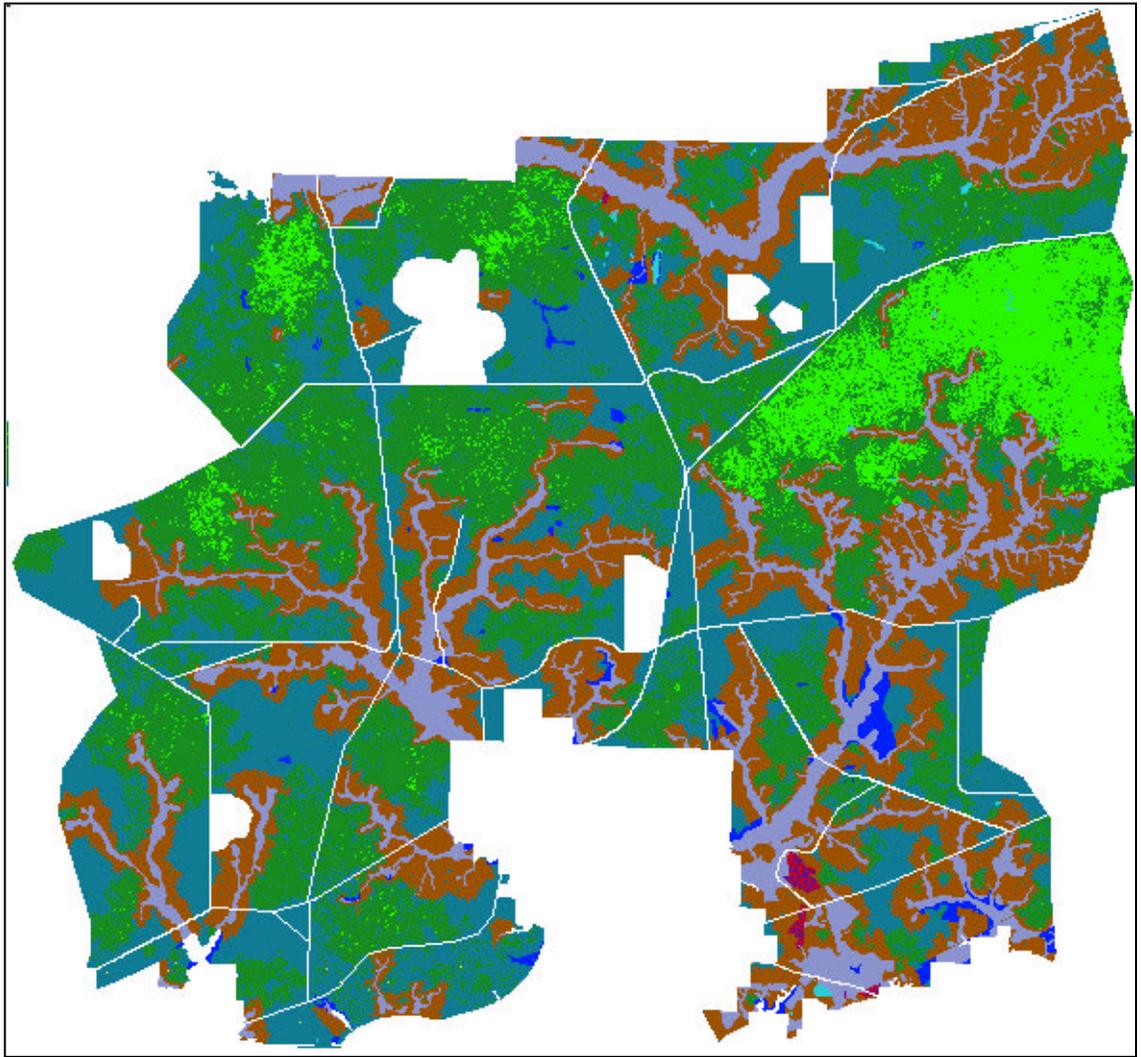


Figure 4-37. An animation of vegetation change of the 'current' landscape under 100 years of the 'rotation' strategy using 10 large and 10 small fires per year. Vegetation change is shown every two years.

FIRE IN BOREAL FOREST: EMERGENT LANDSCAPE DYNAMICS

Introduction

Research on ecological dynamics has often focused upon processes at either a local or global scale. As an example, forest gap models represent interplant dynamics at spatial scales up to tens of meters (Botkin 1993, Shugart and Prentice 1992), and Global Circulation Models (GCMs) represent atmospheric dynamics at spatial scales down to several hundred kilometers (Intergovernmental Panel on Climate Change 1995). However, modeling exists of the meso-scale processes, such as fire, that structure landscapes between these extremes. These meso-scale processes, such as fire, disease and insect outbreaks, mediate between large scale climatic processes and fine scale vegetation processes, which makes understanding them a key component of global change research. This paper examines these linkages by exploring how fire interacts with climate and forest structure in the boreal forest.

Ecological change simultaneously occurs over many scales, from the extremely local, up to the global. Productive research is necessarily constrained to specific scale ranges, but understanding ecological change requires an understanding of the changing nature of ecological processes across scales. In the boreal forest, the dominant structuring processes change with the scale of reference. At the scale of a tree, competitive interactions over tens of meters between trees determine ecological structure, while at a larger scale interactions between fuel accumulation, topography, and climate allow fire to emerge as a dominant structuring process. At still larger scales regional climatic, geomorphological processes, and species migration rates determine forest structure. The emergence of new

structuring processes at larger scales means that it is inappropriate to consider larger scales simply as aggregations of a large number of small-scale entities. Just as it is inappropriate to consider a tree as a collection of branches, it is inappropriate to consider a forest as a collection of trees and gaps. Just as roots and a trunk link branches, fire links separate patches.

Previous attempts to link local to global dynamics often fall into two categories. The first approach aggregates fine scale gap dynamics to represent behavior at larger scales (Shugart and Prentice 1992). However, this approach ignores the contagious meso-scale disturbance processes that are responsible for generating and maintaining patterns of distributions of stands in the forest landscape. The second strategy generates and distributes plant assemblages across a landscape based on climatic conditions predicted by GCMs (Haxeltine and Prentice 1996). However this approach also ignores the transient states that connect landscapes across time. Vegetation is distributed as it would be in a stable, rather than in a transient, dynamics climate. These approaches ignore the processes that connect across scales.

Contagious disturbance processes often provide a bridge between local and global scales. Contagious meso-scale disturbances are processes that propagate themselves across a landscape. They are triggered locally, at scales ranging from tens of meters to kilometers, but their contagious nature allows them to influence ecological structures at scales of up to hundreds of kilometers. These processes include abiotic processes such as fires, hurricanes and floods (Friedman et al. 1996, Johnson 1992, Smith et al. 1994); animal processes such as insect outbreaks (Holling 1992b), and the pulsed grazing of mega-herbivores (Owen-Smith 1988); disease (Crosby 1986); and human habitat modification or harvesting activities (Turner et al. 1993).

I have developed a model of boreal forest dynamics that explicitly incorporates one such contagious disturbance processes – forest fires. Fire is a spatial process that connects the dynamics of large-scale landscape features and local vegetative processes. The models

demonstrate that simple fire and forest processes, interacting over space and time, can self-organize to produce persistent spatial patterns in the absence of any external imposed heterogeneity. This result complements the conventional explanations of forest heterogeneity that argue forest heterogeneity is defined by external topographic and climatic processes.

This paper begins by outlining the nature of fire in the boreal forest. The theoretical background of this work is then discussed before moving on to a description of the fire-forest models. The architecture of a set of models is presented along with a description of their behavior relative to empirically derived data. The paper then discusses the possible ways the fire-forest models suggest climate change could effect the boreal forest. The paper concludes with some remarks on climate change and the boreal forest, and approaches to modeling such change.

Fire in the Boreal Forest

Fire is one of the dominant meso-scale processes controlling the formation and maintenance of forest communities in the North American boreal forest (Heinselman 1981, Johnson 1992, Payette 1992). Therefore to understand how the boreal forest could respond to climate change requires an understanding of how fire could respond to climate change.

Compared to forests, fire is a transient feature of the boreal landscape, but fire produces long-lasting effects. At the local scale fire is a homogenizing force in the boreal forest. Fire burns large areas of forest which regenerate as even-aged stands. At a regional scale, however, fire introduces heterogeneity, because different fires fragment a landscape into many different patches. The pattern of fire induced stand regeneration influences the spread of future fires, because at a specific site the amount of fuel available for a fire and the susceptibility to fire varies with the age of the stand. The spread of fire across the

landscape is also influenced by the interactions of vegetative forest processes with climate and topography.

Topography and Dominant Tree Species

There is a complex set of relationships between fire, tree species, and topography. Poorly drained areas are less susceptible to fire than well drained areas for several related reasons. Poorly drained sites are often wetter than well drained sites, and wetter sites burn less readily than dry sites. In the boreal forest, Jack pine (*Pinus banksiana*) dominates well-drained upland sites while black spruce (*Picea mariana*) is the most common tree in poorly drained areas. Moderately drained areas are composed of mixed stands of both species (Ecoregions Working Group 1989). Intense crown fires remove much of the organic soil layer in upland areas leading them to develop droughty mineral soils (Heinselman 1981). Lowland areas develop wet organic soils (Woo et al. 1977). These soil changes which encourage and discourage the spread of fire in these two different areas, are the result of a complex interaction between trees species, climate, topography and fire.

Climate

Climatic conditions play a major role in fire spread. Fire frequency is associated both with particular yearly climate events which produce conditions which both dry fuel and ignite fires (Bessie and Johnson 1995, Johnson 1992), and with long-term variations in average temperature and precipitation (Swetnam 1993).

In very dry periods, the normally wetter areas become dry reducing the difference between well drained and poorly drained regions, thus allowing larger fires to occur than is possible under average climatic conditions. Similarly, during very wet periods both well and poorly drained areas are unlikely to burn. Consequently the topography and species composition of a site have the greatest influence on fire spread in years of intermediate wetness/dryness, but have a reduced impact during climatically extreme years.

Fire in the Forest of Southeastern Manitoba

This research centers on a sub-region of the boreal forest located in South Eastern Manitoba. This area was chosen for two reasons: the region's high frequency of fires has produced a good historical example of fire-forest interaction that allowed Marples (1998) to develop a detailed and accurate set of fire history maps from the Hecla and Carroll Lake regions of southeastern Manitoba (Figure 5-2).

The study region is dominated by jack pine (approx. 73% of area) with the remaining area covered by black spruce (17%), aspen (7%), and tamarack (2%) (Marples 1998). Topography and soils create a dry to wet gradient. Droughty, upland soils are dominated by jack pine while wetter conditions produce black spruce, tamarack, and bog/fen complexes (Woo et al. 1977). A limited amount of succession occurs where aspen is replaced by more shade tolerant coniferous species (Pastor and Mladenoff 1992). However, fire rather than old age, or insect outbreaks, kills most trees. The region has a fire cycle of approximately 72 years (Marples 1998), which is relatively short for the boreal forest (Johnson 1992).

Severe frequent fires are the dominant processes determining the landscape structure of the southeastern Manitoban boreal forest. Topography, vegetation and climate interact with fire to determine the frequency and spatial configuration of fires. The severity and frequency of fires reduce the importance of other structuring processes in the Manitoban boreal forest, rendering it an ideal locale to explore fire-forest interaction.

Approach

Understanding the interaction between the structure of a forest landscape and forest fire requires the study of large areas for long periods of time. It is necessary to study an area which is large enough to contain several large fires over a period long enough that the majority of the points within the area have been burnt several times. For the boreal forest such requirements result in a study area which covers hundreds of square kilometers and an

observation period of several centuries. Clearly a typical ecological approach involving local observation and experimental manipulation is not feasible, at least during the course of dissertation research. Alternate historical and synthetic approaches to this problem are required.

Examination of the ecological history of several sites using paleoecological methods is one possibility. Such methods allow the reconstruction of periods of fire outbreak, and the species composition of a forest. However long term landscape reconstructions generated from pollen records or carbon deposits have a coarse spatial resolution. This resolution is adequate for the study of regional ecological history, but it is too coarse for the study of the interactions between fire and vegetation pattern (Clark 1990, Delcourt and Delcourt 1991).

An alternative is to develop and test simulation models of fire-forest interactions. This approach allows the examination of large spatial areas, over long periods of time at a high spatial and temporal resolution. This approach is the one I used.

Modeling Approach

It is unproductive to even presume that simulation models can describe the actual forest, for they only include what a modeler places within them, and a real forest will always include more than can be fit inside a computer. Therefore, a more productive approach is to select parsimonious descriptions of forest processes and structures for representation in a model world. By making these descriptions of forest dynamics explicit and animating them, their limitations can be revealed in useful ways, and connections previously hidden can be revealed. Such a process uses model worlds not as simple predictive tools, but as means of testing suppositions (Walters 1986).

The usefulness of simulations is that they allow ideas and suppositions to be expressed rigorously and explicitly, while also allowing them to be tested in ways that are not feasible to actually do in the forest. For example, large areas of forest can be arbitrarily burned for several consecutive years. The flexible nature of reality in model worlds allows

new alternate hypotheses of system functioning to be constructed and tested, often in ways that would be unlikely to occur in a real forest. Model worlds also provide an investigator with a forum for developing and invalidating experiments that can then be applied to empirical forest data.

The boreal forest region of both Europe and North America has been studied well enough to produce extensive sets of time series data, and well tested simulation models. These models provide an excellent base for the development and evaluation of new modeling methodology and analytical techniques (Shugart and Prentice 1992).

Model Organization

A family of three meso-scale landscape simulation models were constructed to examine these spatial-temporal relationships between fire and forest structure. These models, the Null, Interaction, and Fuel models, incorporate a range of ecological processes and structures. The behavior of each of these models was compared against both, other models and empirical data from southeastern Manitoba.

The models range from the simple to the relatively complex. All are spatially explicit models that represent fire as a contagious process occurring over a forest. The simplest is the 'Null' model in which fire burns patches of the forest, but forest pattern does not influence fire spread. The Null model is indeed a null model because it functions as if fire operated independently of a forest's stand structure, fuel type, and fuel volume. In all three other models fire spread is influenced by forest pattern. The 'Interaction' model adds the influence of the forest upon the pattern of fire spread. The 'Fuel' model more finely represents the interactions between forest and fire. The 'Tree Species' model provides further detail to the Fuel model by representing a forest as a mix of black spruce and jack pine tree species rather than as a generalized tree type. The complex models contain more finely represented forest structure and processes than the simpler models, but all the models are organized around the same basic design.

The development of such an integrated set of models rather than a single model allows the appropriate mode of investigation to emerge from the set, rather than being constrained investigation to an initial monolithic model design. The use of a set of models also allows model behavior to be compared across models as well as against empirical data.

Fire & Forest Models

The model represents a region of forest as a rectangular matrix. Each element in the matrix, termed a site, represents an area of forest approximately 150 meters on edge, which is equivalent to an area of 2.25 hectares.

Each site is described by the age of the forest at that site. Site age is considered to be analogous to the physical state of the site. Every simulated year the site ages. The modeled forest region experiences a fixed number of fires initiations/unit area at random locations every year. A fire may spread from a site to adjacent sites. The probability of fire spreading to an unburned site from a burning site is a function of the age of the unburned site. A fire will continue to spread until it fails to spread to any unburned cells. The entire process of fire initiation and spread occurs within a simulated year (Figure 5-3).

No external disturbance enters the area from beyond the model's edges, and fire cannot spread beyond the edges of the simulated forest area. These constraints produce an edge effect, which results in the cells near the edges of the simulated area burning less frequently than the cells near the center of the matrix. The extent of the area experiencing edge effects depends upon the relative size of the simulated fires compared to the total extent of the simulated area. The extent of the landscape in the model is arbitrary, but we examined landscapes composed of 256 by 256 and 512 by 512 sites, approximately 38 km and 77 km on edge respectively, which typically exhibited minimal edge effects over the range of conditions modeled.

The two main features that control the dynamics of the model are the probability of fire spread as a function of tree age (Figure 5-4), and the rate of fire initiations/unit

area/year. In the boreal forest, climate and topographic variation influence the probability of fire spread across time and space, respectively. However to clarify the investigation of fire-forest interactions, in the basic versions of these models climate and topography are assumed to be constant. The initial stand structure creates some transient effects and the extent of the simulated forest creates some edge effect, but appropriate experimental design can minimize these effects (**Peterson** 1994).

Null Model

The Null model is a simplification of the Interaction model, which has been described above. The only difference between the two models is the function that describes the probability of fire spread as a function of site age. Rather than varying as a function of site age, in the Null model the probability of fire spread remains constant (Figure 5-4). Thus, the Null model embodies the null hypothesis that states that fires are not influenced by site age properties.

Interaction Model

The Interaction model represents the probability of fire spread as a function of site age. Different versions of the Interaction model vary the form of this function, but any version of the Interaction model implicitly assumes that forest structure influences the spread of fire (Figure 5-5).

Fuel Model

In the boreal forest, recently burned sites often burn again the year after a fire due to the presence of dead dry combustible material not consumed in the initial fire together with the presence of combustible grasses and herbs. To better represent this forest property, fuel was separated from site age in the simulation model. The model was then restructured to explicitly model fuel dynamics and to represent fire as a function of fuel volume.

Rather than each site being represented by only a site age, each site is represented by the age of the site and its fuel content. The probability of a fire spreading to the site is

defined to be a function of the amount of fuel in the site and its combustibility rather than a function of age. The increased complexity of the Fuel model results in a situation in which the probability of fire spread is a complex function of site age. Rather than a single function, like the Interaction model, there are a variety of possible functions (Figure 5-6).

Alternative Models

The Interaction model provides a template model from which simplified or more complex ones models can be produced. The Null model provides a simplified representation of boreal forest/fire interactions, while the Fuel model and the Tree Species model are more complex. The architecture of the various models in summarized in Table 5-1.

Table 5-1. Alternate models and the defining differences between models. The models are of increasing complexity with the later models encompassing the functioning of the top models.

<u>Models</u>	<u>Key Processes</u>
Null	fire spreads independently of forest age
Interaction	fire spreads as a function of forest age
Fuel	fire spreads as a function of fuel and site dryness

Model Behavior

The analysis of the behavior of the models (Null, Interaction, and Fuel) revealed a great commonality of behavior and some key differences. The preeminent result is that if past fires can influence future fire spread, the forest-fire system self-organizes into a heterogeneous patchy self-maintaining landscape. Such self-organization does not occur in the Null model, while it does occur in all the other models. Compared to this difference other differences between the models are superficial.

Self-Organization

Fire and forest interactions in the Interaction model, in the absence of any other sources of heterogeneity, influence each other to produce a forest landscape characterized

by semi-persistent, self-maintaining, homogenous patches which are renewed rather than destroyed by fire (Figure 5-7). This self-organization process also occurs in the Fuel model, and the following discussion of self-organization in the Interaction model also applies to it.

The discrete patchy nature of the forest landscape evolves from the repeated interaction of fire and forest dynamics. When a fire burns the landscape it produces a patch which is internally homogenous. Repeated fires produce a heterogeneous landscape of internally homogenous patches. These patches greatly influence where fires burn in the future. The homogeneity of patches produces a high probability that the patch will respond more as a whole than a collection of sites. If a patch is young it is likely that any fire in the patch will only burn a small portion of the patch, and if the patch is older it is likely that any fire which burns a portion of the patch will burn the entire patch. The mosaic of different patches reduces the probability of fires spreading between patches due to the asynchrony in their ages. A burning patch is unlikely to spread into a younger patch, and older patches tend to have already burned; therefore a fire is not only likely to burn an entire patch, it also tends to only burn a patch. It is in this fashion that the patchy nature of the landscape reinforces patch persistence.

The memory of the system is measured by the degree to which spatial structure affects fire spread. Past fire events determine present landscape age-structure. In the Interaction model, this structure influences the spread of fire because probability of burn is a function of age. The form of this function determines the intensity and nature of the fire-forest system's memory. Consequently, system memory increases with the rate at which the probability of fire spread increases with age. Both the abruptness and the magnitude of the increase in the probability of fire spread increase the memory of the forest landscape.

Memory strength manifests itself in the landscape through the degree of patch persistence and cohesion. A system with more memory generates longer lasting and more cohesive patches than a system with little memory. The Null model, with its constant

probability of fire spread regardless of site age, is a system with no memory. A comparison of the landscape patterns produced by these two model types clearly shows the qualitatively different landscape memory produces (Figures 5-8 and 5-9).

This landscape property can be readily observed in animations of the model output showing landscape changes through time. Fire generated patches tend to regrow in a coordinated fashion and then repeatedly burn as cohesive units. This patch persistence is a tendency, rather than a certainty. Patches do not persist perfectly. A fire will usually burn only a portion of a patch, along with portions of surrounding patch. However, on the whole, patches persist despite the addition or loss of individual sites (Figure 5-10).

The difference between persistent patches and non-persistent patches is demonstrated in the evolution over time of one-dimensional transects across space (Figures 5-8 and 5-9). Fire patches produced in the Null model do not persist, producing the jagged structure of the space-time transect in Figure 5-8. In the Interaction model patches are more contiguous and persist as wholes, producing a rectangular structure across the space-time transect in Figure 5-9.

The self-organizational behavior of the Interaction model is qualitatively robust across a wide variety of functional forms of the relationships between time since fire and the probability of fire spread probability. Self-organization occurs with when fire spread probability increases as a linear function of time since fire, as well as various non-linear functions such as logistic or step functions. This suggests that system memory, once established, will lead to landscape self-organization unless the landscape's memory is removed by a continual source of structure-destroying randomness (e.g. a highly variable climate).

Fire Patterns

Fire spreads differently in a self-organized landscape, than in a memoryless landscape. Fire patterns produced in the Interaction model tend to be more compact, and less articulated than fires in the Null model (Figure 5-11). This tendency is caused by the

fact that fires in the Interaction model are more likely to burn an entire patch than parts of several patches. Consequently areas in the center of a patch are more likely to burn than are articulated patch edges, because fire is more successful spreading along a front than through a bottleneck. This difference in fire spread between articulated edges and the patch centers, results in fires that tend to burn most of a patch. Parts of the patch that do not burn tend to be on articulated fringes of a patch, and conversely, additional sites that are incorporated to the new patch when the original patch burns tend to have been surrounded by the original patch. These two tendencies towards the shedding of dangling edges and the envelopment of intruding edges serve to produce fires which are more contiguous and less articulated than fires under similar conditions in the Null model (Figure 5-11).

Summary of Model Behavior

Comparing model behavior reveals the robustness of the landscape self-organization that follows from the spatial-temporal influence of fire and forest processes upon one another. Despite many changes in system parameterization and processes self-organization persists. This suggests that the applicability of these results to an actual ecosystem depends upon whether the probability of fire spread is altered by the time since fire to a significant degree relative to the 'forgetting' caused by climate and topography.

The models discussed in this paper exist along a spectrum ranging from relatively simple to fairly complex. With these increases in detail came greatly increased problems of model parameterization and analysis, and, after a point, little benefit in terms of producing different output patterns. The more complex models produced more realistic behavior, but they also failed to produce any major novel behaviors. The key behaviors of each of the model types are described in Table F-2.

Table F-2. Key behaviors of each of the four model types.

<u>Model</u>	<u>Key Behaviors</u>
Null	produces randomly distributed overlapping fires
Interaction	landscape self-organizes into persistent patches
Fuel	landscape self-organizes into persistent patches and fires can burn same area in consecutive years

Empirical Comparison

Methods

I compared the spatial pattern produced by Null and Interaction models to the actual landscape pattern produced by fire in the boreal forest. I computed a burn count map, which calculates the frequency for fire at each point on the landscape. Manitoban data from the Hecla and Carroll Lake regions exists from 1929 to 1989. Fires during this period burned an area equivalent to 90% of the total area studied, or 90% of a fire cycle. To appropriately compare the Null and Interaction models, I ran these models until they burned 90% of a fire cycle, and the data produced by these models was spatial and in aggregate compared against the empirical data.

Results

The burn frequency map for the Null model shows a highly fragmented and variable pattern. The Null model initiates fires at random locations, and these fires spread across the landscape in highly articulated, fractal-like patterns, with larger fires being exponentially rarer than small fires. This produces a pattern of overlapping burned areas of varying size and jagged form intermixed with a large convoluted areas which have not been burned (Figure 5-12).

The burn frequency map for the Interaction model shows a very homogenous pattern of areas burnt only once, with medium sized fragments of unburned and twice burnt areas (Figure 5-13). This pattern is produced because the fire-shaped forest structure constrains the spread of fire in the Interaction model. This 'memory' of past fires means

that a recently burnt area is unlikely to catch fire again, and that an area that has not burned for a long time is likely to burn again. Because of this property, fires tend not to spread into previously burnt areas, but rather confine themselves to areas that have not burnt recently. This produces a burn map of both large and small unburned areas, the larger areas being patches of forest which have been recently burned and small remnant patches of older trees which escaped being burnt by fires which burnt their neighbors. These old 'remnant' patches are protected from fire by existing as isolated patches of susceptible forest within areas that are not susceptible to fire. Therefore, compared to other areas of forest, connected to burnable forest areas, these patches are unlikely to be burnt.

The burn frequency maps of the adjacent Hecla and Carol Lake regions of southeastern Manitoba were combined into one map (Figure 5-14). The area shown in this map is approximately equivalent to the area of the Null and Interaction simulation maps.

In the burn frequency maps, like the site age maps, the precise location of areas with different burn frequencies is not important. The significant features are the spatial pattern of the different burn frequencies, and the relative proportion of different frequencies of burns. Also, as with the Manitoba landscape maps the data collection process has resulted in a decrease in the presence of remnant patches within larger patches and smoothed the articulated patch edges. The burn frequency map of south eastern Manitoba differs from the Interaction model map, but it is much more similar to the Interaction model map than it is to the Null model's map. The Manitoban data shows an area that is composed of large unburned and once burnt regions. Included within these regions are sizable areas that have burned twice, and some that have burned more than twice. Both the Manitoba landscape and the Interaction model have large homogenous once burnt regions, and smaller homogenous twice burnt areas unlike the Null model. However, unlike the Interaction model the Manitoba landscape also has large relatively homogenous unburned areas.

Despite various similarities between relative burn frequencies of model and empirical data, the principle result of comparison between the Null and Interaction models and the empirical Manitoban data is that neither the Interaction model nor the Null model fits the Manitoban data well (Figure 5-15). Without invoking external variation, the Interaction model does fit the data marginally better, because by varying the functional form of the interaction between age and site combustibility the shape of the Interaction curve can be altered, while the Null model's curve cannot. However, neither model fits the data well. This suggests that another process, probably topographic or climate variability is an important driver of fire pattern. Exploring these more complicated models is an opportunity for future work.

Summary of Comparison between Models and Manitoban Data

In conclusion, the Interaction model produces landscape features and fire property similar to those actually found in the boreal forest and it also shows that the fire/forest system can produce a discontinuous patchy structure which persists and maintains itself in the absence of any external heterogeneity. The increasingly realistic models produce more precise models of the forest/fire interactions, but at the cost of increased complexity.

The examination of the role of climate change and topography show that there are links across scales between different temporal and spatial processes in the Manitoban boreal forest. Further simulation and empirical tests of these ideas need to be made to clarify the precise nature of these linkages. However, the comparisons made in this section between the fire models and the Manitoban fire data also illustrate that the interaction of fire and forest processes also produce somewhat realistic stand structure, even in the absence of topographic and climatic factors (Peterson 1994).

The ability of the forest landscapes to self-organize suggests that fire and forests can respond in a punctuated style to other sources of variation, such as climate change, topography, or anthropogenic landscape modification. Subsequently, changes in forest structure, fire regimes, and boundaries may occur suddenly. This clearly has important

consequences for both the management of forest resources and the prediction of the effects of global climate change.

Climate Change and The Self-Organizing Forest

The best climate models consistently project a 1 to 4.5°C increase in global, mean, surface-air temperature with a doubling of atmospheric CO₂ (Intergovernmental Panel on Climate Change 1995, Walker and Steffen 1997). Air temperature at low latitudes is projected to experience little change, but at high latitudes air temperatures could change substantially. Temperature increases of up to 10°C accompanied by a halving in soil moisture levels have been predicted (Manabe and Wetherald 1986). The boundaries of ecological biomes are expected to shift as a consequence of global warming (Haxeltine and Prentice 1996, Zoltai 1988), but the speed and magnitude of these shifts are highly uncertain. Because high latitudes will experience the greatest degree of climatic changes, the boreal forest may experience dramatic changes.

Climate change will influence forests directly by altering conditions for vegetative growth. Increased levels of CO₂ are expected to facilitate plant growth, but moisture stress may limit biomass accumulation. However hotter and, in particular, drier conditions would also increase the ability of fire to spread throughout the forest. The time since the last fire has a large influence upon the species composition of a site, and consequently a change in fire frequency can be expected to change the vegetative nature of a region. These indirect effects of climate change may play a more important role in determining the future configuration of the forest than more direct physiological effects.

I use the set of fire models to explore how forests could respond to a variety of climatic changes that increase the propagation ability of fire. The purpose of these experiments was not to predict how the boreal forest would respond to specific changes in climate, but to outline some of the ways the boreal forest could change.

The behavior of the fire-forest system was studied under both different stable climatic regimes, and a variety of changing climatic regimes. Operating the model under different stable climatic regimes provides an idea of how climate, forest pattern and fire interact. It also provides a basis against which models that include changing climatic regimes can be compared. Models incorporating changing climatic regimes allow the dynamic and transient effects of climate change to be examined. These effects are very important for climate rarely remains stable, and consequently it is unlikely that any system of fire, forest, and climate is in a stable balance (Davis 1986).

Constant Climate Simulations

Simulations of fire-forest interaction under constant climates reveal several important effects that a drier, warmer climate has on forest and fire patterns. Under warmer, drier, fire promoting climates, areas burned by individual fires are larger, and more cohesive (their edges are less articulated, and they contain fewer unburned fragments). The frequency with which a given site is burned increases and thus decreases the average age of the forest (Figure 5-16). These changes could be important modifiers to forest processes not included in the forest models. Seed dispersal, growth rates, and body morphology vary among species suggesting that climatic changes will likely impact different tree species differently. This could shift the competitive balance between tree species and altering the species composition of the forest.

Climate Change Experiments

The steady-state approach to change discussed above ignores the important transient and non-equilibrium effects of climate change. To better examine the dynamics of climate change I modified the Interaction model to incorporate changing climatic regimes.

Climate Model

Climate was modeled as having an inhibitory or excitatory effect upon the spread of fire. A wet cool year would lower the probability of fire spreading, even in sites containing

large amounts of fuel. A dry hot year would raise the likelihood of any site burning, including those that would not burn in a normal year. Climate was assumed to have the same type of excitatory or inhibitory effect over the entire region. Climate represented by a 'climate' variable which every year modifies the likelihood of fire spreading into a site by a given percentage. For example, in a dry hot year all sites may be 30% more susceptible to fire than in a typical year.

Experiments

To map out the various ways in which the forest could respond to climate change simple experiments were conducted during which the forest models experience several types of climatic variation. Climate was varied cyclically, randomly, at different rates, and around a shifting average. These experiments revealed that the self-organized forest landscape has an adaptive capability to respond to change while maintaining its basic structure, and that this adaptive capability has limits.

Results

The adaptive capability or 'resilience' of the forest landscape breaks down when faced with 'rapid' climate change or with extreme climate change. When climate change occurs 'gradually' the patchy nature of the forest landscape acts as a conservative force. Patches limit the spread of any particular fire, constraining its impact upon the landscape. This limited change allows the forest landscape to gradually adapt to climate changes by small punctuated leaps, while avoiding radical change. In a situation of gradual climate change fires burn larger areas, patches become larger, and the forest becomes younger, but these landscape changes occur gradually over time.

When climate change occurs 'rapidly' the resilience of a landscape is overcome and the forest landscape is abruptly transformed by rapid, discontinuous change as large fires burn the forest. Large fires occur when climate change enables fire to easily spread across multiple patches. These fires obliterate the landscape's existing pattern and the memories

of past fires that this pattern contains (Figure 5-17). The landscape memory that maintains a persistent patch structure can be overwhelmed by externally imposed variability.

Under any stable climate, a relatively constant proportion of the landscape is susceptible to fire due to its age. If the climate were to become rapidly drier the susceptibility of forest to fire is increased and previously less susceptible forest becomes susceptible to fire. Fires that were previously constrained to a single patch, since the patch was surrounded by non-susceptible patches, can now spread across multiple patches. If climate change stops and the climate stabilizes a new relatively stable landscape organization will emerge, and again a higher relatively constant percentage will be susceptible to fire as discussed above. Stated theoretically, rapid climate change makes the existing spatial-temporal forest structure unstable. These instabilities allow a catastrophic reorganization of the forest to occur. Following these catastrophic fires, a new forest structure will gradually emerge (Figure 5-18).

In real forests, a simple reemergence of forest structure may not occur. Processes not included in the simulation model such as inter-tree competition and seed dispersal would likely be effected by changes in the scale and frequency of fire. The destruction of existing forest structure by massive fires releases ecological actors from their existing roles, allowing new ecological communities to assemble. Therefore it is possible, even probable that, large fires increase the likelihood that the boreal forest system could abruptly shift from its current state to another alternate organizational state.

Changes in forest community structure seem to have followed massive fires in the past. It is possible that by synchronizing the age structure of large areas of forest, new forest disturbance processes could emerge (Clark 1990). There is evidence that this has happened with spruce budworm outbreaks in the eastern boreal forest of North America (Blais 1983).

The initiation of a spruce budworm outbreak, requires high population levels spread over an area larger than a critical threshold. High population levels require old forest, and

unless old forest exists over a large area an outbreak cannot propagate itself across the forest landscape. Therefore, large fires provide the initiating conditions for spruce budworm outbreaks. Once initiated, budworm outbreaks kill large areas of forest, which regenerate as large areas of even aged stands. These stands establish the necessary conditions for future budworm outbreaks. If such a pattern of budworm forest disturbance was established, budworm could replace fire as the major-self-organizing meso-scale forest process.

Fire's destruction of ecological structure brings opportunity along with destruction. Fire clears the way for ecological communities better suited to new climatic conditions, but it also removes resources and capabilities that may not be easily replaced. The reorganization that follows large fires allows opportunities for new species to invade a region and new processes to arise, but it also locally extinguishes existing species and processes.

It is also important to mention the effects of extreme climate change. Extreme climate change increases the frequency of fire to such an extent that the forest ceases to exist because trees do not live long enough to grow beyond saplings. In such a situation, forested areas would become a completely different type of ecosystem, such as savanna or grassland.

Summary of Climate Change Modeling Experiments

The self-organization forest landscape that emerges from the interaction of forest processes and fire provides the forest landscape with an ability to adapt to change while maintaining its organization. The landscape heterogeneity tends to constrain fire to patches, provides the opportunity of changes to occur in local asynchronous lurches of landscape 'renewal'. However, if the limits of this landscape 'resilience' are exceeded the self-organized pattern of the landscape is broken down by many large fires. The breakdown of 'resilience' occurs abruptly and regionally. Large fires disrupt existing forest processes,

such as seed dispersal and inter-species relationships, while also providing opportunities for the emergence of new forest structuring processes, such as insect outbreaks.

These results have several implications for a world facing the potential of climate change. First, the speed of climate change is important in determining how the forest will respond. If climate changes are gradual, small punctuated change will occur through spatially distributed fires, however if 'rapidly' large fires will provide abrupt discontinuous change across large regions of forest. What constitutes rapid or gradual climate change in the boreal forest is unclear, but future work will attempt to better relate these concepts to empirical data. Secondly, if large fires do occur one should be prepared for new ecological communities to emerge from their ashes, and these new communities may very well be structured by an unexpected set of ecological processes.

My analysis demonstrates the importance of meso-scale disturbance processes in determining the response of ecosystems to climate change. It also illustrates the importance of considering the dynamics of change, rather than steady-state conditions. Models that ignore the effects of temporal and spatial heterogeneity will be fundamentally incomplete.

Conclusions

Severe frequent fires are the dominant processes determining the landscape structure the boreal forest. Topography, vegetation and climate interact with fire to determine the frequency and spatial configuration of fires. However, when the fire-forest system possesses 'memory' it is possible for fire and forest interactions to produce a forest landscape characterized by semi-persistent, self-maintaining, homogenous patches that are renewed rather than destroyed by fire, in the absence of any external heterogeneity.

Memory is a measure of the relative influence of vegetative pattern on fire spread. The greater the influence the stronger the system's memory. A memory of a fire event is stored with the spatial structure of the forest. This memory is transmitted across time by forest growth, until the memory influences the spread of another fire and a modified

version of the old memory is again stored within the forest. Vegetative, or anthropogenic, processes that alter forest pattern, or climatic and topographic variation can degrade the landscape's memory of past fires.

When a forest landscape possesses memory it will self-organize. Despite many changes in system parameterization and model structure, self-organization persists in a robust fashion. The only prerequisite is that the probability of fire spread generally increases with stand age. This suggests that the applicability of these results to an actual ecosystem rests upon whether the time since the last fire effects the probability of fire spread to a significant degree relative the effects of climate and topography.

The self-organizing forest landscape that emerges from the interaction of forest processes and fire provides the forest landscape with an ability to adapt to change while maintaining its organization. The landscape heterogeneity tends to constrain fire to patches, provides the opportunity of changes to occur in local asynchronous lurches of landscape 'renewal'. However, if the limits of this landscape 'resilience' are exceeded the self-organized pattern of the landscape is broken down by many large fires. The breakdown of 'resilience' occurs abruptly and regionally. Large fires disrupt existing forest processes, such as seed dispersal and inter-species relationships, while also providing opportunities for the emergence of new forest structuring processes, such as insect outbreaks.

The results of this research have several implications for a world facing potential climate change. Firstly, it is important to understand the relationship between the speed of climate change and forest processes. Gradual climate change will produce gradual forest change through small spatially distributed fires. However if climate changes rapidly, large fires could produce abrupt change across broad regions of the boreal forest. Secondly, if large fires do occur it is possible that new ecological communities will emerge from their ashes. These new communities may be structured by unexpected sets of ecological processes.

My research demonstrates the importance of fire, and meso-scale disturbance in general, in determining the ecosystem structure and therefore the response of ecosystems to climate change. It also illustrates necessity of examining the dynamics of climate change rather than steady-state conditions. Models that ignore spatial and temporal heterogeneity will be fundamentally incomplete.

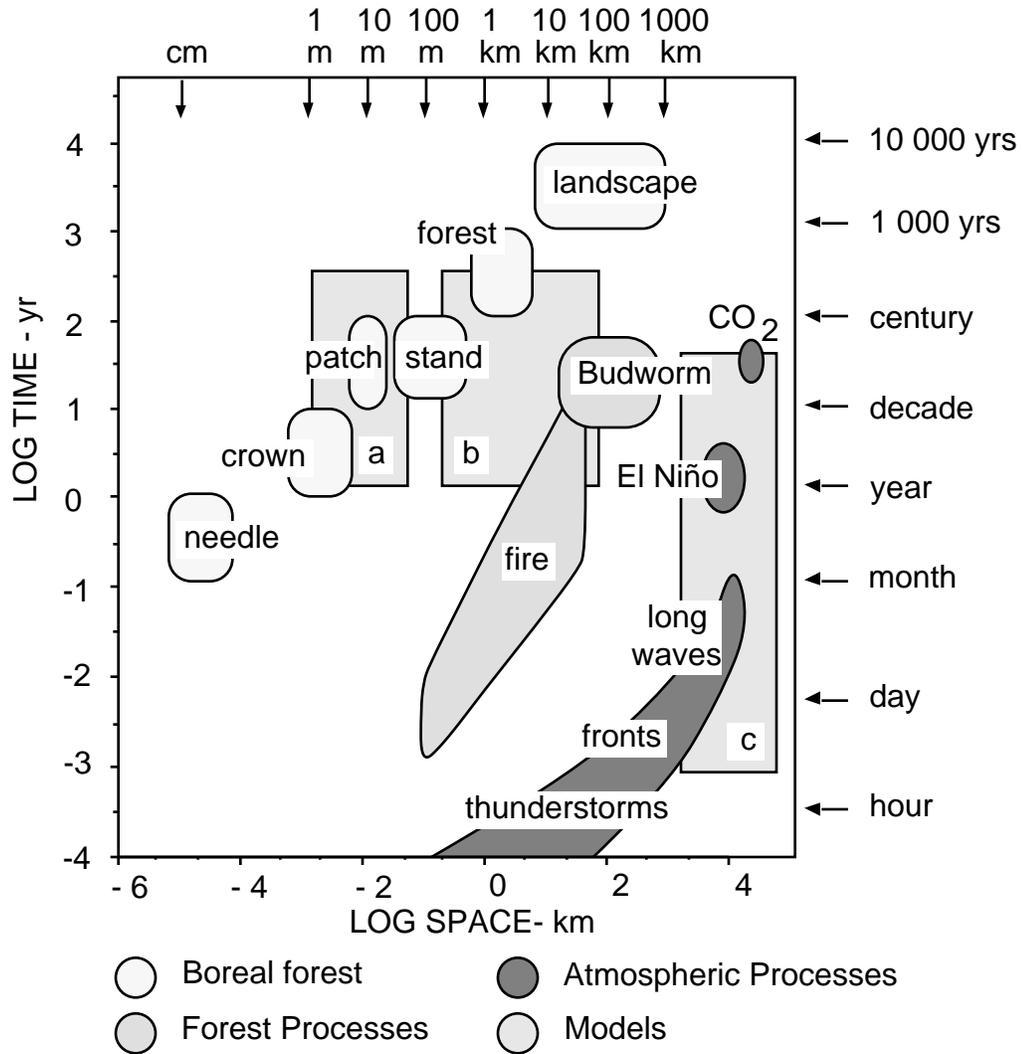


Figure 5-1. Time and space scales of the boreal forest and their relationship to some of the processes that structure the forest. Contagious meso-scale disturbance processes provide a linkage between macro-scale atmospheric processes and micro-scale landscape processes. The scale domains of various simulation models are also shown. The models are: a) Forest gap models (Botkin 1993), (b) Fire models (Peterson 1994), and (c) Global climate models [Intergovernmental Panel on Climate Change, 1995 #354].

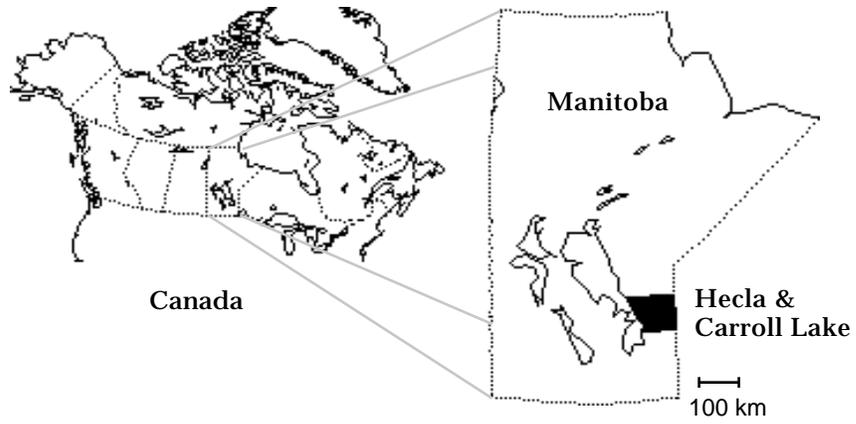


Figure 5-2. Map showing the Hecla and Carroll Lake regions of southeastern Manitoba, Canada. This area was the basis for my modeling work on fire-forest dynamics.

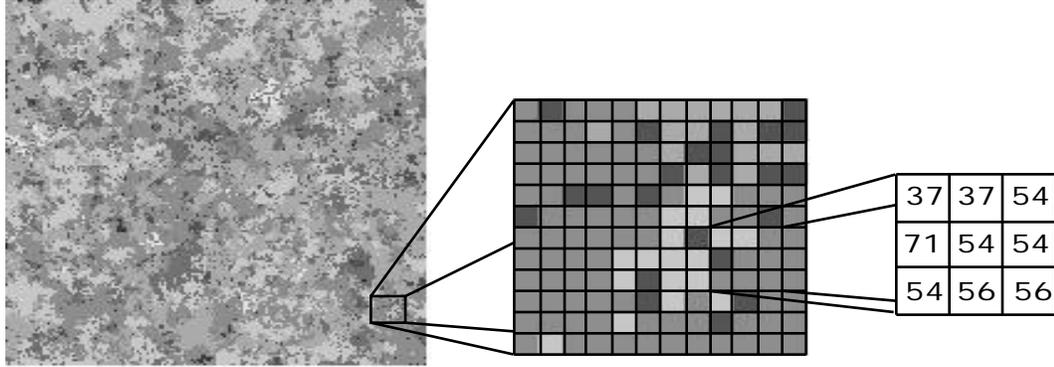


Figure 5-3. A sample model forest landscape composed of a matrix of sites. Fire organizes and maintains the landscape as a mosaic of patches composed of even-aged sites. The sites making up the landscape are each shaded by age. Young sites are lightly shaded while old sites are black. At the right of the figure the ages, in years, of a set of sites are shown.



Figure 5-4. The probability of fire spread is a constant, independent of age in the Null fire model.

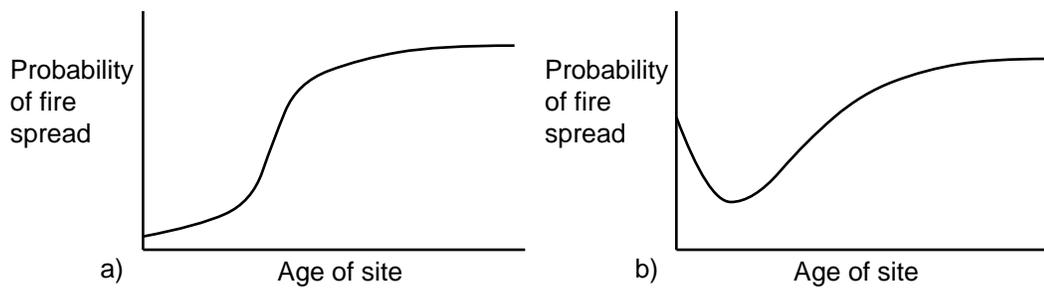


Figure 5-5. Probability of fire spread as a function of age. a) Probability of spread increases logistically in the interaction model. b) Probability of fire spread is the sum of a negative exponential decay function and a logistic growth function.

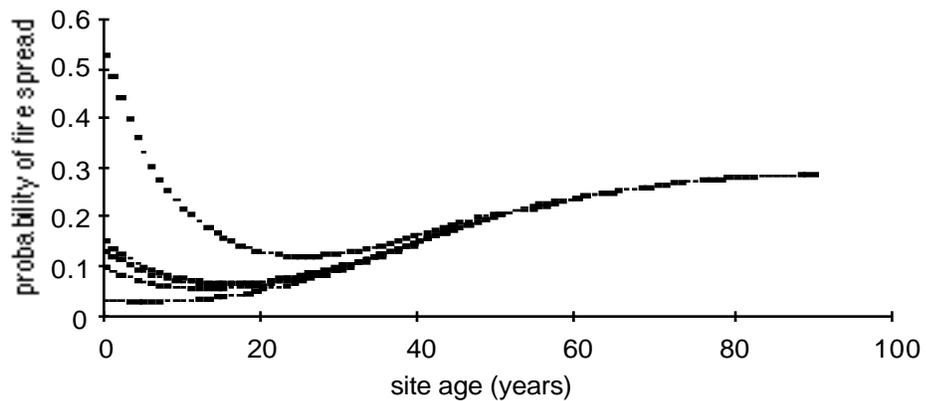


Figure 5-6. Observed relationships between site age and fire spread probability in a Fuel model.

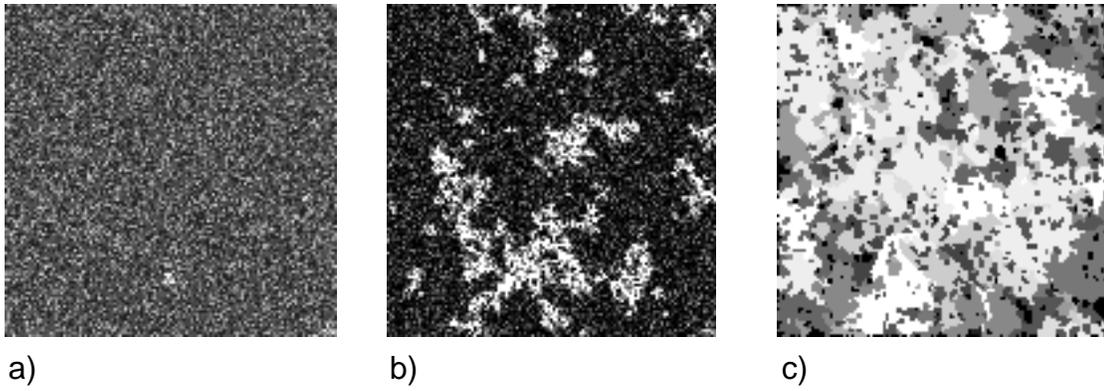


Figure 5-7. A forest landscape of patches emerges from a randomly structured landscape composed of many small differently aged patches. a) Forest at 1 year. b) Forest at 10 years. c) Forest after 52 years.

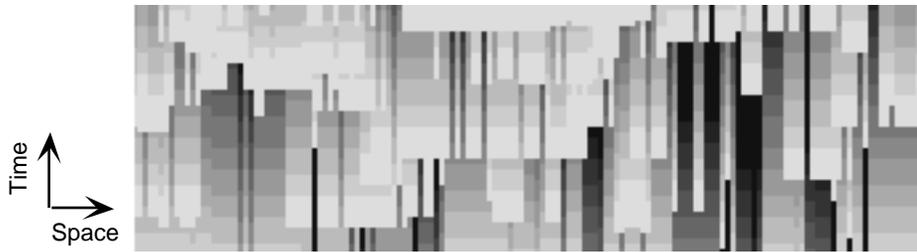


Figure 5-8. Space-time transect of a Null model. Fires burn over many different patches, overlapping with one another. Young sites are lightly shaded, while older sites are darker. Vertical discontinuities indicate fires, while horizontal discontinuities indicate stand boundaries.

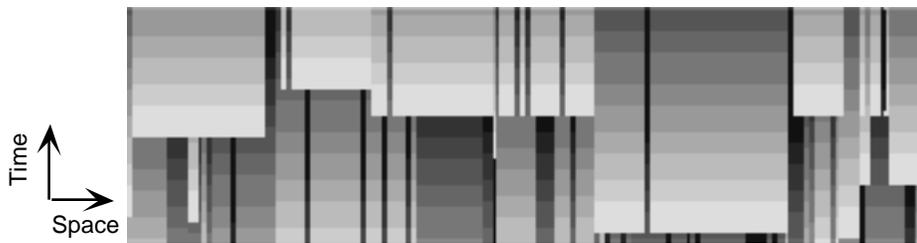


Figure 5-9. Space-time transect of an Interaction model. Burns are more likely to burn an entire patch. The transect exhibits much more order than the Null model.

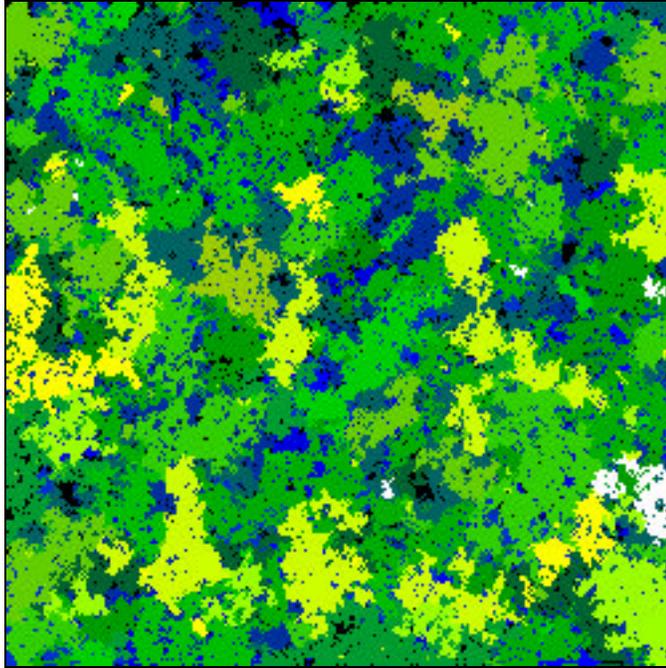
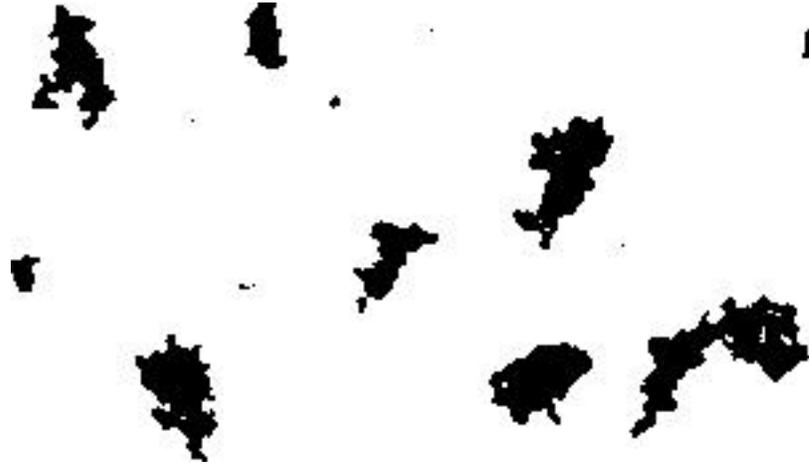


Figure 5-10. A forest landscape of patches maintains its emerges and maintains its structure. This figure is an animation that shows burning patches as white. A site's time since burn is indicated by its color. Site time since fire increases from yellow, through green to blue. Fire maintains the structure of the landscape, and the structure of the landscape maintains the fire regime.



A) Null Model



B) Interaction Model

Figure 5-11. Representative fires from the Null and Interaction models. a) The Null model in which fires burn independently of landscape properties produces fires which are more articulated than the Interaction model. b) The Interaction model produces fires whose pattern is influenced by past burns, and consequently produces more cohesive fires.

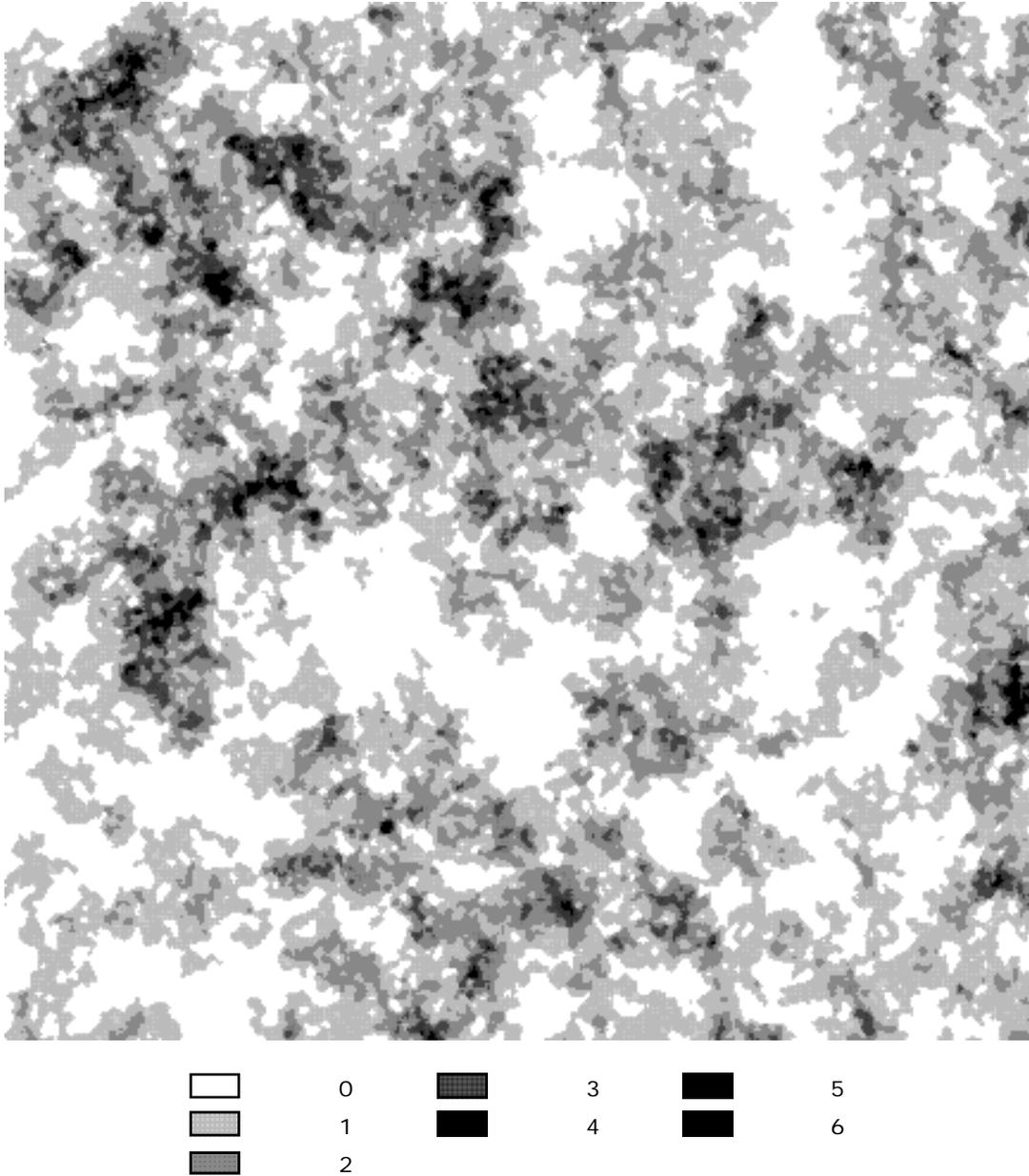


Figure 5-12. The burn count within a simulated region using the Null model over 90% of a fire cycle. The shading of the map corresponds to the frequency of burn.

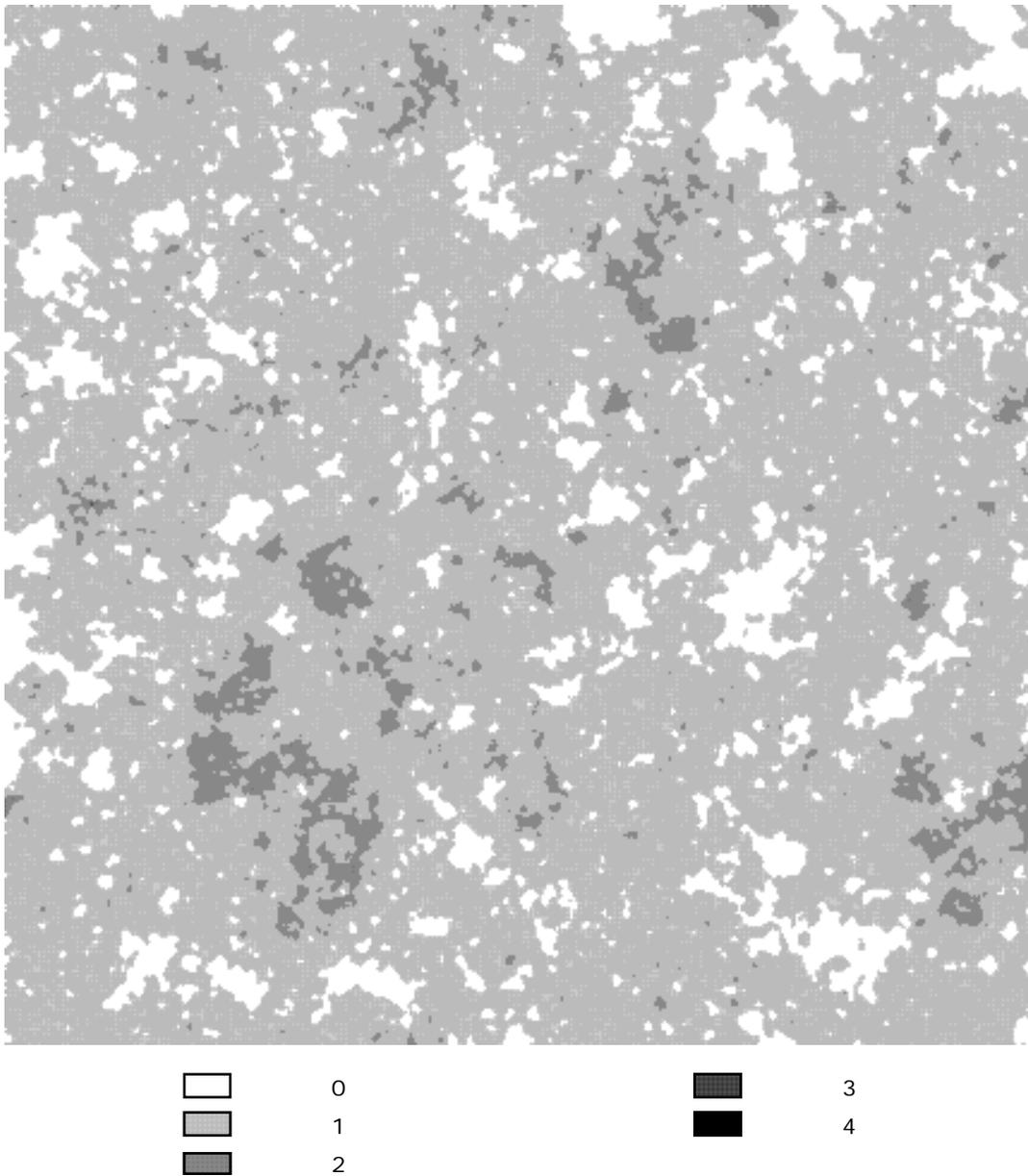


Figure 5-13. The burn count within a simulated region using the Interaction model over 90% of a fire cycle. The darker colors indicate regions burned more frequently than the lighter regions.

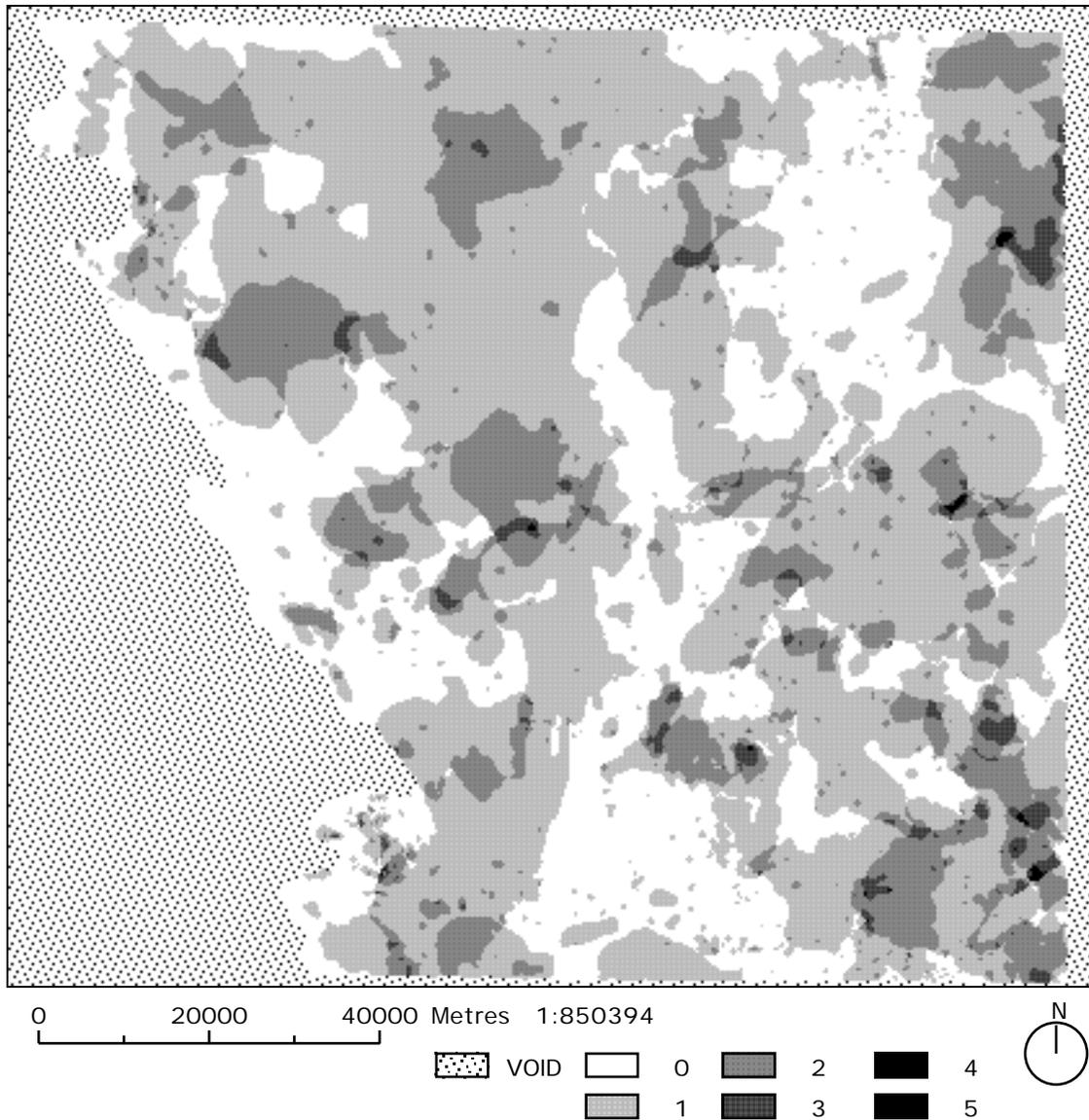


Figure 5-14. The burn count within the Hecla and Carroll Lake regions of southeastern Manitoba (1929-1989). The darker colors indicate regions burned more frequently than the lighter regions. Data is from Marples (1998).

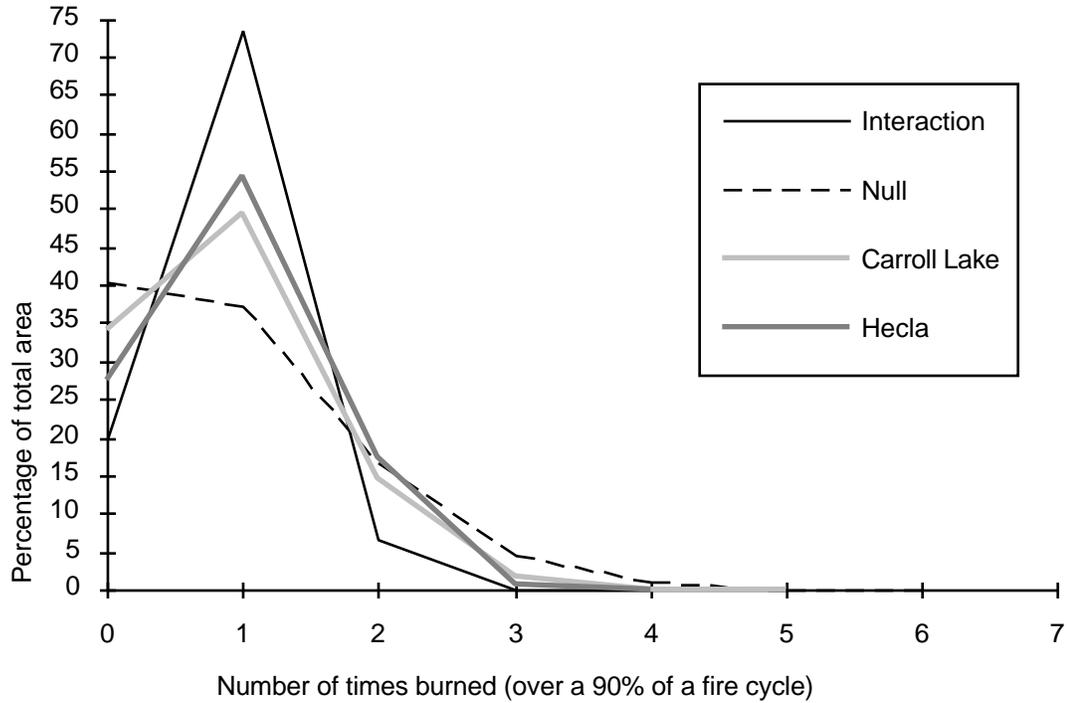


Figure 5-15. The proportion of sites experiencing different burn frequencies within the Hecla and Carroll Lake regions of southeastern Manitoba (1929-1989), and the Null and Prototype fire simulation models. These models have not been configured to mimic the Manitoba region, but what is important is the form of the graphs: the peak of the Manitoba and Prototype model contrasts with the declining curve of the Null model.

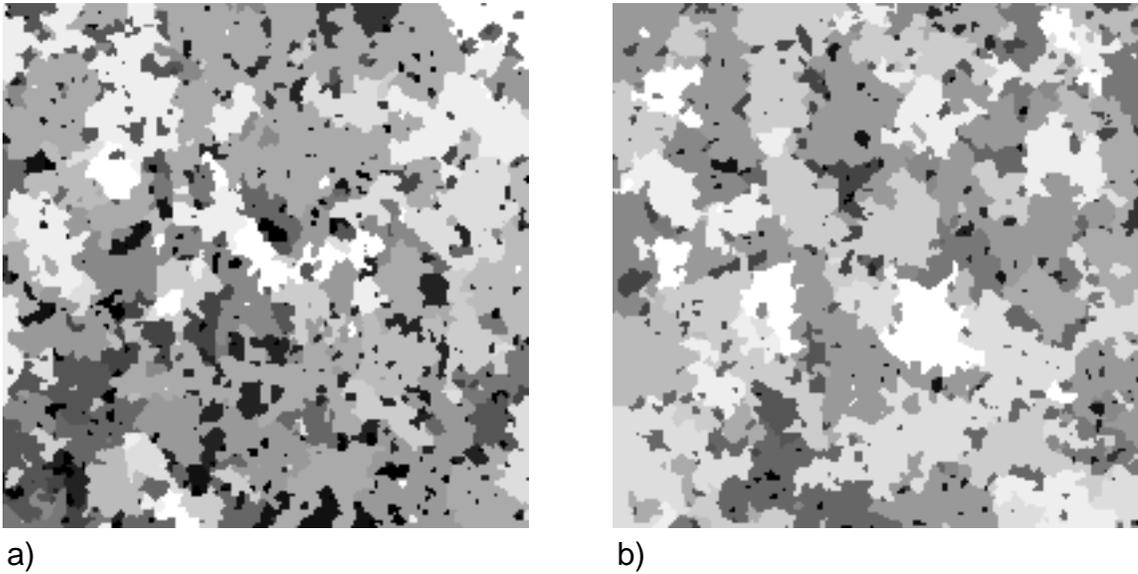


Figure 5-16. Landscape behavior under two different stable climatic regimes. a) A forest landscape under base climatic conditions. b) A landscape under a drier warmer climate. The climate enhances the spread of fire 37.5% compared to base conditions. Under these conditions at a steady state the average age of the forest is 82% of the base conditions, and the average fire size is 15% larger.

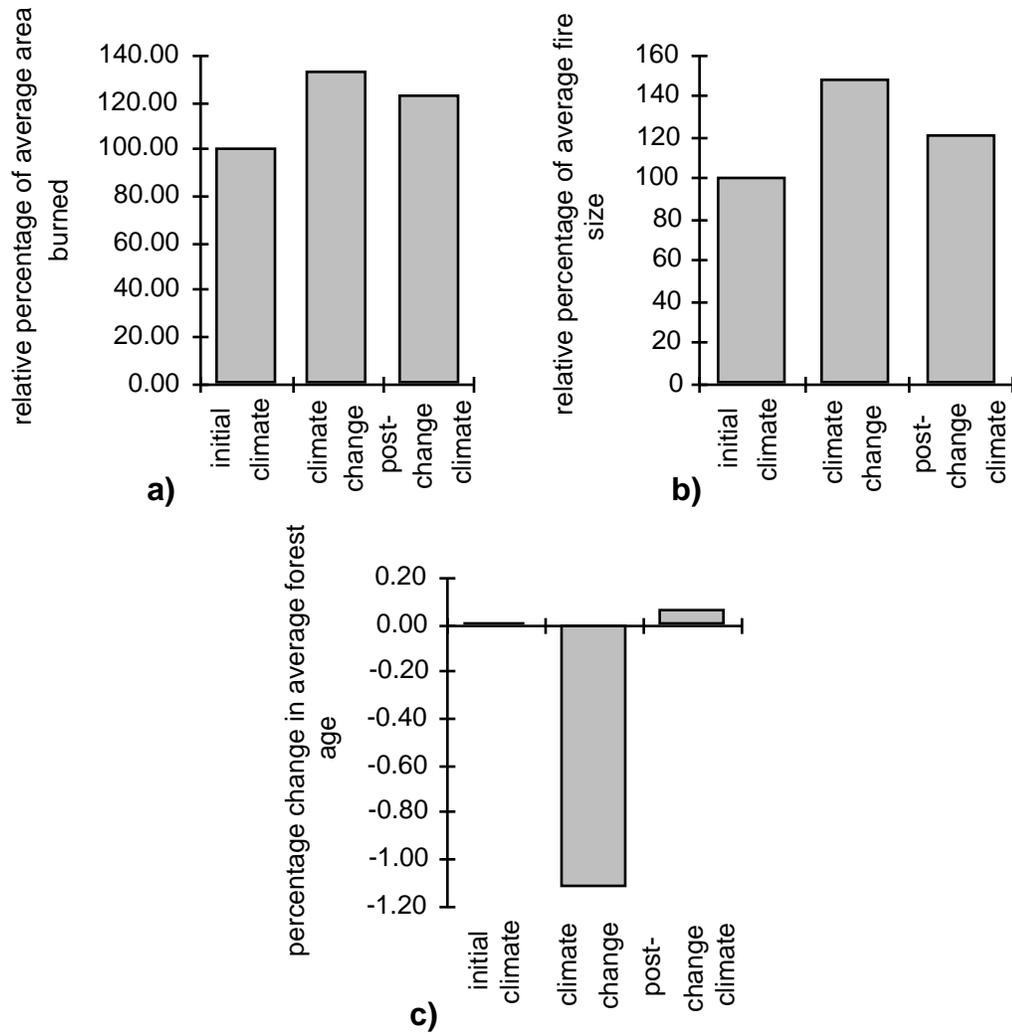


Figure 5-17. Comparisons of effects of climate change in a representative model run. a) Comparison of average total area burned before, during and after a change a climate induced increase in fire susceptibility. b) Comparison of average fire size. c) Comparison of change in average age of the simulated forest (roughly equivalent to biomass).

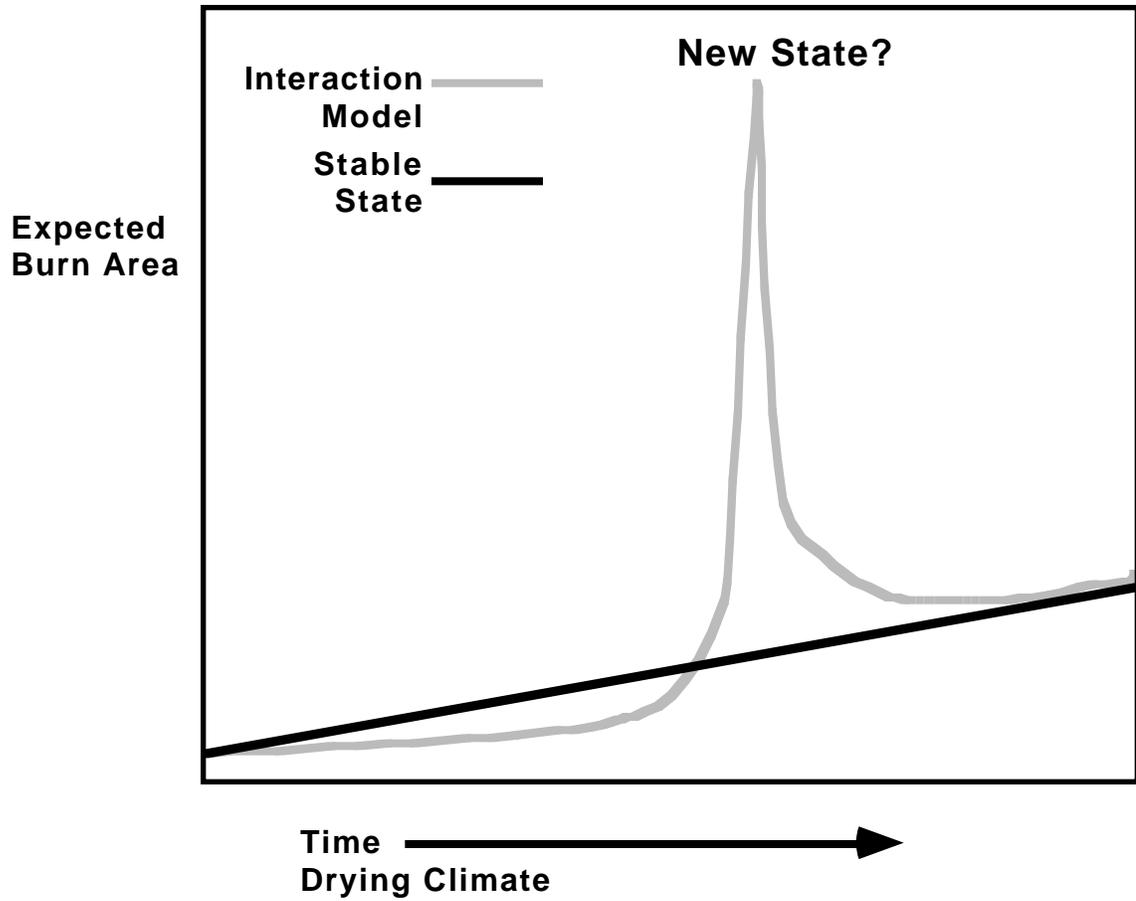


Figure 5-18. Forest structure can adapt to gradual climate change. Rapid, or abrupt, climate change can overwhelm the existing landscape pattern causing much larger fires than at equilibrium. The ability of the Interaction model to resist change, makes it vulnerable to collapse when exposed to large change.

A GENERAL MODEL OF CONTAGIOUS DISTURBANCE

The spatial and temporal analysis of contagious disturbance in chapters 5 and 6 revealed the importance of cross-scale interactions in shaping ecological dynamics. These interactions are inadequately described by existing theories of disturbance, which vaguely describe ecological disturbance as a relatively discrete event in time that disrupts ecological organization (Turner and Dale 1991). Existing theories of disturbance tend to either focus on temporal dynamics at the expense of spatial interactions (Pickett et al. 1989, Bond and van Wilgen 1996), or focus on spatial interactions at the expense of temporal interactions (Andrews 1986, Turner et al. 1993). Some work, specifically in the field of landscape ecology, has focussed on the connections between spatial and temporal ecological dynamics (Gardner et al. 1996), however this work has focussed upon specific questions without developing a theoretical framework to investigate disturbance processes in general.

In this chapter, I present a general model of contagious disturbance. I identify the key features of contagious disturbance, the variables that define those features, and outline how different relationships among these variables produce different disturbance dynamics. I use these attributes to define four sub-models of my general model. These models are not intended to be realistic models of any particular ecosystem, though they may well be. They are intended to represent a variety of abstract types of contagious disturbance. Specific instances of these abstract types can be found in most ecosystems. In this chapter I focus on abstract types rather than specific examples, such those examined in Chapters 5 & 6. These abstract models provide a general framework for thinking about contagious disturbance. These models provide general insights into the consequences of specific ecological organizations, allowing meaningful prediction of disturbance behavior to be

made on limited information, as well as providing a basis for the development of more realistic models of specific ecosystems.

Contagious Disturbance

Contagious disturbances are disturbances that propagate themselves across a landscape. They are triggered locally, at scales ranging from tens of meters to kilometers, but their contagious nature allows them to influence ecological structures at scales of up to hundreds of kilometers. These processes include abiotic processes such as fires and floods (Friedman et al. 1996, Johnson 1992); animal processes such as insect outbreaks (Holling 1992b), and the pulsed grazing of mega-herbivores (Owen-Smith 1988); disease (McNeill 1976); and human habitat modification or harvesting activities (Turner et al. 1993).

The propagation of contagious disturbance depends upon its ability spread into sites that are susceptible to disturbance and disturbed them. Consequently, the extent, form and duration of a contagious disturbance are determined by the spatial distribution of disturbed and undisturbed sites across a landscape. Because disturbance is shaped by the emergent dynamics of the interaction of small-scale processes to produce large-scale pattern, contagious disturbance processes often link ecological pattern and process across a range of scales.

Non-contagious disturbances behave differently. Processes exogenous to the system being disturbed determine the duration and extent of non-contagious disturbances. This difference in driving forces means that contagious and non-contagious disturbance respond differently to change. Changes in landscape pattern alter the nature of a contagious disturbance regime, but will not alter a non-contagious disturbance regime. For example, if lightning sets a tree on fire, that burning tree will only cause a forest fire if there are trees to which it can spread. Consequently, a disturbance initiating processes, such as lightning strikes, may remain constant, but the disturbance regime experienced by a site in a landscape can radically change due to changes in that landscape's spatial connectivity.

Most ecological theory has considered disturbances to be non-contagious. The primary theory of ecological disturbance is patch dynamics that arose from the study of driftwood smashing against rocks in the inter-tidal zone (Levin and Paine 1974). A large amount of work has been done studying contagious disturbances, such as fire and insect outbreaks, but almost none of this work has recognized the important distinction between non-contagious and contagious dynamics. Indeed much of this work has treated contagious disturbances as if they were non-contagious (Green 1989). This work has tended to focus upon the effect of disturbance on an ecosystem rather than the interaction of disturbance and ecosystem dynamics. Disturbances have been treated as if they were events whose frequency and size are determined by external constraint (Johnson 1992), rather than through interaction with ecological dynamics.

Despite the theoretical neglect of contagious disturbance, contagious disturbance processes are ubiquitous in ecology. Contagious disturbance processes, such as grazing animals, tree-falls, floods, landslides, fire, insect outbreaks, and disease epidemics, can have a strong effect on ecological dynamics. In the following sections I present a theoretical model of contagious disturbance.

A General Model of Contagious Disturbance

Based upon the detailed analysis of fire in Florida and Manitoba (Chapters 4 and 5), I have developed a general model of contagious disturbance, that I use to delineate four qualitatively different varieties of contagious disturbances. From the specific details of these models, I have abstracted a general model that has the minimal level of complexity to produce a rich range of contagious disturbance processes. By varying the parameters in this model I can produce different types of contagious disturbance.

Model States

My simple model embodies vegetation processes, disturbance processes and the interactions of vegetation and disturbance. I represent a landscape as a rectangular grid of

sites. Each of these sites can exist in one of three conditions: infected, susceptible, or resistant. A disturbance agent is present in the infected sites. Disturbance can spread from infected to susceptible sites, but disturbance also destroys the infected sites rendering them resistant to disturbance. Resistant sites recover from the disturbance to become susceptible (Figure 6-1).

This model uses the states defined in the classic Kermack-McKendrick models of diseases, also known as SIR models (Kermack and McKendrick 1927). This class of models divides disease hosts into the three states: susceptible, infected and resistant. I generalize these states as the smallest number of states to represent a disturbance prone system. Susceptible sites are sites that can be disturbed. Infected sites are those sites that are being disturbed, while resistant sites are those that cannot be disturbed. While I use the states defined in the SIR models, it is important to note that I do not use the same set of state transition processes. I consider a broader set of processes.

Model Processes

A disturbance regime defines patterns in space and time that govern the transitions among the susceptible, infected and resistant sites. I propose that a contagious disturbance regime is defined by the relationship among contagion, virulence, recovery, reproduction, and initiation rates (Figure 6-2). Contagion is the rate at which the disturbance can spread. Virulence is the speed with which an infected site is destroyed and becomes resistant. Recovery is the speed at which a resistant site once again becomes susceptible to disturbance. The initiation rate, is the number of new disturbances that begin at a site per area per year. Reproduction is the rate at which a disturbance reproduces. It defines the number of neighboring sites that a disturbance can infect. The ratios among these various rates and the rate at which the system recovers from disturbance determine the nature of the interaction between disturbance and system being disturbed.

A disturbance regime is defined by the relationships among initiation, reproduction, contagion, virulence and recovery. However, not all relationships define valid disturbance

regimes. For a process to be a disturbance it must occur at a frequency that is slower than the frequency of the system that it disturbs. If a disturbance's rate of spread or rate of initiation is not quite different from the rate of the recovery then there is no 'disturbance', only an interaction among two processes. The importance of disturbance scaling is illustrated by the difference between fire in the boreal forest and in longleaf pine forest. A site in the boreal forest is typically burned about once a century, while a site in a longleaf pine savanna is burned every few years. For a tree that can live more than century fire is a disturbance in boreal forest, but not in longleaf pine savanna. However, in longleaf pine savanna grasses grow at a rate that corresponds to fire frequency. Fire is a disturbance for trees in the boreal forest, but a disturbance process for grasses and tree saplings in longleaf pine savanna.

Whether a process can be considered to be a disturbance is also a matter of perspective. It disturbance is defined relative to a system that is disturbed. Consequently, when considering the role of a process in nature, whether that process can be considered as a disturbance depends upon the scale at which nature is analyzed. An event that is a disturbance at a small scale may be a normal event at a larger scale. For example, from the perspective of a tree in the boreal forest a fire is a disturbance, because fire is a rare event in its life. However, from the perspective of a forest, fire is a normal process that plays an integral part in maintaining the current organization of the forest (Payette 1992).

The distinction between a disturbance process and a 'normal' process depends upon the analytical boundaries imposed upon a system. In this discussion of contagious disturbance I minimize the dynamics of the system being disturbed only one parameter – the recovery rate. This simplification is appropriate, because the focus of this model is on contagious disturbance. I also impose several constraints on the relationships between the model processes. I define disturbance processes as processes in which contagion occurs faster than recovery, which limits the ability of a disturbance process to destroy the same site more than once during an disturbance event. I also consider recovery to be faster than

initiation, because otherwise the disturbed system has no meaningful internal dynamics. It will be controlled by the external initiation rate. In the next section, I show how different relationships between the processes of reproduction, contagion, virulence, recovery and initiation define four types of disturbance.

Types of Contagious Disturbance

Based upon possible relationships among contagion, recovery and initiation rates I distinguish four types of contagion: disturbance agent, stress accumulation and release, chain reaction, and evolutionary epidemic. Examples of each of these types are, respectively, elephant grazing, landslides, fire, and influenza. These types are not crisply separated from one another. Rather they are points on a continuum. I discuss each of these types in turn, from the simplest to the most complex, and then use the various rates to distinguish them from one another.

Disturbance Agents

The simplest form of contagious disturbance is the disturbance produced by disturbance agents. This type of disturbance is not a truly contagious disturbance, because it does not spread itself across the landscape. It is quasi-contagious, because a disturbance agent moves disturbance across a landscape, rather than disturbance propagating itself.

Disturbance agents move across a landscape, destroying susceptible sites based upon behavioral decisions (Figure 6-3). Examples of disturbance agent type disturbances include grazing ungulates, and loggers. Disturbances produced by disturbance agents are contagious in the sense a disturbance agent moves across a landscape and disturbs that landscape in response to landscape pattern and the disturbance agents internal behavioral rules (Figure 6-4). They are not contagious, because a disturbance agent's behavior determines whether a site is disturbed or not. For example, grazing herbivores may decide to graze in an area, or they may decide to move to another area and graze there. While disturbance agents can produce spatially aggregated disturbances, they also move

disturbance across wide areas. These properties make disturbance agents an intermediate type of disturbance between non-contagious and contagious disturbances.

Initiation rate and regrowth control the pattern of a quasi-contagious disturbance. Virulence and contagion vary with behavior, and there are not any strict trade-offs between them. For example, a grazing ungulate may destroy a site and move on, or it may remain within a site without destroying it. This variation makes it difficult to analyze the dynamics of quasi-contagious disturbance in a general way.

Stress Accumulation and Release

Stress accumulation and release disturbances occur when stress stored at a point is released into neighboring sites. Examples of this type of disturbance are floods, landslides and tree falls. Each of these disturbance processes results from a build up of stress that is then dispersed across a landscape. As I shall explain, if the landscape is already stressed, or the directions in which stress is dissipated are constrained, then disturbance can propagate across a landscape.

Stress accumulation and release is the simplest form of true contagious disturbance. Disturbance events are triggered when stress within a site passes a threshold and the site collapses. When a site collapses its stress is dispersed into neighboring sites (Figure 6-5). This stress is added to these sites. If a site is already in a 'critical' state, which means on the verge of collapse, the addition of further stress will trigger its collapse, dispersing more stress across the landscape. A stress accumulation and release produces disturbance that is similar to the fall of dominoes. The disturbance can only be transmitted through sites that are on the edge of collapse. The stress threshold at which a site collapses determines the amount of stress that is released by a collapse. This conservation of stress on the landscape limits the ability of a stress accumulation disturbance to effect a large area, because any non-critical sites will simply absorb the released stress dampening the spread of disturbance (Figure 6-6).

The reorganization of the landscape following a collapse changes the landscape, producing a fractal pattern that makes it easier for future collapses to spread. This process gradually self-organizes the system to a critical state, at which cascades can occur at any size (Bak and Chen 1992). In a critical state system the distribution of disturbances follows a power law:

$$\text{Frequency}(\text{Area Disturbed}) = \text{Area Disturbed}^{-\alpha}$$

Where alpha is an exponent that specifies the scaling relationship between frequency of a disturbance and its size. What this relationship means is that if a disturbance of size X occurs with a frequency of .01, a disturbance of size 10X will occur with a frequency of $.01 * 10^{-\alpha}$ (Figure 6-7).

A stress accumulation and release disturbance will self-organize a system towards criticality, however the rate at which a system moves towards criticality depends upon the driving rate. The time required to increase the spatial scale over which a power law distribution of disturbance sizes exists also follows a power law (Figure 6-8). This relationship means that it takes exponentially longer for stress accumulation disturbances to organize the landscape in into a spatial pattern that will allow them to propagate across long distances. Consequently, the scale over which a stress accumulation disturbance is able to self-organize depends upon the amount of time that a stress accumulation disturbance can organize a landscape independent of other processes.

The requirement that stress accumulation disturbances propagate only through neighbors that are critical means that these disturbances can only weakly influence distant sites. This suggests that unless stress accumulation disturbances occur in situations isolated from other disturbances, these disturbances will only be able to spread across relative small scales. They will not have sufficient time to self-organize a landscape pattern that has an appropriate pattern of critical sites to allow disturbances to propagate long distances. This is illustrated by tree fall gap dynamics. Tree fall gaps are a type of stress

accumulation disturbance. Because forests are frequently disturbed by larger-scale disturbances, the stress accumulation disturbance model suggests that tree-fall gaps will never be able to organize large patches of connected trees that can tip one another over. This limitation occurs, because the stress accumulation disturbances will not have sufficient time to establish a critically organized spatial pattern at a large enough scale, before other disturbance processes disrupt that pattern. This proposition is meant to illustrate the model's behavior, but it also illustrates how considering contagious disturbance yields that could be tested in real forests that experience different types and frequencies of disturbance.

Chain Reaction

A chain reaction is a disturbance that after it is initiated at a site reproduces itself to infect neighboring susceptible sites. It destroys the sites it infects, which means that its ability to persist depends upon its contagion, the rate at which it can successfully infect new sites, relative to its virulence, the rate at which it converts infected sites to resistant sites (Figure 6-9). Unlike stress accumulation disturbances a chain reaction disturbance can reproduce. An infected chain reaction site is not limited in the number of sites it can infect, consequently it has a increased ability to spread and infect a large number of sites (Figure 6-10). Forest fires and insect outbreaks are examples of chain reactions.

The key relationship controlling dynamics of chain reaction disturbances is the ratio of the initiation rate to the recovery rate. This ratio defines the degree to which the effect of a disturbance, which is a pattern of resistant sites on the landscape, is preserved before a new disturbance occurs. This ratio defines the 'memory' the system possesses. The greater the system's memory the more past disturbances influence the spread of current disturbances. Because resistant sites impede the spread of disturbance this ratio also controls the average size of disturbance. The slower the initiation rate is relative to the recovery rate the larger the average size of the system's disturbances will be (Clar et al. 1996). This ratio also defines the size distribution of disturbance. As the ratio approaches

zero, that is as the initiation rate becomes increasingly slower than the recovery rate, the behavior of the disturbance approaches self-organized criticality (Drossel 1997).

Self-organized criticality means that the system maintains itself near a critical state. A critical state means that disturbance can spread, and if the entire system is in a critical state, it means that disturbance has the potential to spread across the entire system. Near self-organized criticality, the distribution of disturbance sizes fits a power law distribution (Figure 6-11). This pattern can be found in actual forest fire data, both in area burned per year (Figure 6-12), and in the frequency of fire sizes (Malamud et al. 1998).

Under any realistic disturbance regime, self-organized criticality is never actually reached, because the ratio of disturbance initiation and system recovery rates is a finite amount. The ratio of the initiation and recovery rates determines the range of scales over which a disturbance regime follows a power law distribution. A larger ratio will extend expand the scale of the disturbance regime, while a smaller ratio will contract it. An example of this behavior is shown in the output from a fire model (Figure 6-13). If either of these rates changes, so does the scale domain of self-organization. This type of model can therefore be used to predict the consequences of faster vegetation recovery or increased initiation events on the scale of a disturbance regime.

Evolutionary Epidemic

An evolutionary epidemic is an adaptive type of a chain reaction. In a chain reaction the rates of virulence and contagion are fixed. In an evolutionary epidemic virulence and contagion can vary during a disturbance. Functions similarly to a chain reaction. An infected site reproduces disturbance that can infect neighboring susceptible sites.

However, unlike chain reactions reproduction occurs with variation and selection, allowing the virulence and contagion rates of an evolutionary epidemic to vary in response to selection, rather than remained fixed. For example, many disease outbreaks change their attributes during the course of an outbreak. A classic example of is provided by the change in the behavior following the introduction of syphilis to Europe from the New World

(Quetel 1990). Initially syphilis became quite virulent and contagious, spreading rapidly and killing people, but over time its behavior shifted towards a slowly spreading, less virulent chronic disease.

An evolutionary epidemic requires that selection can occur on virulence and contagion. Even if a disturbance agent has the potential to evolve, it will not if the rate of evolution is slower than the rate of spread, which is a combination of contagion and reproduction. Therefore, the greater the ratio of the rate of evolution to the rate of spread, the greater the potential of a disturbance to become adaptive. The importance of evolution occurring at a faster scale than spread is illustrated by influenza. The life cycle of the influenza virus is orders of magnitude faster than the rate at which influenza spreads, and it is a very adaptable evolutionary epidemic (Crosby 1989).

Along with the ability to vary and select disturbance traits, for an evolutionary epidemic to behave differently from a chain reaction, virulence and contagion must not be independent of one another (Ewald 1994). The reason for the necessity of this linkage is that if virulence and contagion do not any trade-off they will each evolve to an optimal level, and the evolutionary epidemic will maintain fixed virulence and contagion rates, which means that it will behave as a chain reaction. If virulence and contagion are independent then their optimal levels are to be non-virulent and highly contagious. All other things being equal, a strain of disturbance that is more contagious than others will reproduce faster than others, its population will grow faster than slower spreading strains, and it will come to the population of disturbance. Similarly, a disturbance that destroys its host rapidly has less opportunity to infect the hosts neighbors, than a strain that has reduced virulence that allows a host to live longer. If there is no tradeoff between virulence and contagion, the virulence and contagion of an evolutionary epidemic will rapidly evolve to a stable state of high contagion and low virulence.

If there is a trade-off between maximizing contagion and minimizing virulence, then evolutionary epidemics can occur. Such trade-offs can be expected, because often a

disturbance must consume a portion of a host site to produce more propagules. Consequently, a disturbance can exhibit many different strategies. A strain can be contagious and virulent by producing many propagules that quickly exhausts and destroying a host. Alternatively, a strain can be non-virulent and non-contagious producing propagules gradually allowing a host to live longer. In such a situation a disturbance process is unable to simultaneously maximize contagion and minimize virulence, and selection moves disturbance properties towards a tradeoff that is optimal for local conditions.

Ewald (1994) has discussed how virulence can evolve based upon the ability of a disturbance to infect new sites. The best trade-off between virulence and contagion will depend upon how many susceptible sites a disturbance agent can potentially infect. If there are very few it makes sense to have low virulence and contagion, in order that disturbance can slowly try and infect those sites, while waiting in the hope that new sites will appear. When there are many potential host sites, selection will favor contagious and virulent disturbances. When there are few available host sites virulence will be selected against (Ewald 1994). As a disturbance spreads across a landscape its virulence and contagion will experience selection, depending upon the availability of susceptible sites in different portions of the landscape. If large contiguous areas of susceptible sites are present virulence can be expected to evolve. If only isolated host sites are present virulence will be decreased.

The ability of a disturbance to adapt itself to the landscape it is in is the central difference between evolutionary epidemic and chain reaction disturbances. If an evolutionary epidemic occurs in a homogenous landscape there is no variation in the selective forces acting upon the epidemic, and its behavior will collapse to that of a chain reaction disturbance. Rhodes and Anderson (1996) recently described epidemics of measles in isolated populations where they were able to document this occurring. In this case, the epidemics behaved like chain reaction disturbances producing power law

relationships between frequency and size of outbreaks, quite unlike measles dynamics in larger populations.

The ability of an evolutionary epidemic to respond to landscape changes has raised the concern that land-use/land-cover changes will produce a 'new' disease. These diseases are not truly new, rather they are behaving in new ways due to alterations in landscape pattern that have selectively encouraged the evolution of different disease behaviors (Schrag and Wiener 1995). Possible candidates for such diseases include Lyme disease and Hantavirus (Daily and Ehrlich 1996). Simple models of evolutionary epidemics can be used to investigate the consequences of landscape change and possible approaches to disturbance control. It may even be possible to apply such models to analyze evolutionary change that occurs during the course of biological invasions.

Comparisons of Contagious Disturbances

The four types of contagious disturbance discussed above have some similarities and differences that can be characterized in terms of the five key contagious processes: initiation, reproduction, contagion, virulence, and recovery. Additionally, variation in these processes defines the behavior of each of the types of disturbance. The type of disturbance being considered determines the nature of influence of the changes in these processes, and consequently how different types of contagious disturbance will respond to changes in their structuring processes.

In this section, I establish connections among the different types of contagious disturbance. The interactions among the key contagious processes can be divided into three main categories: those that effect disturbance spread, those that effect disturbance behavior, and those that alter a disturbance's relationship with the disturbed system. I explore each of these combinations in turn.

Disturbance Spread

The ability of a disturbance to spread is determined by the combination of its reproductive ability and its contagion. Reproductive capacity is lowest among disturbance agents and stress accumulation, as they do not reproduce during the course of a disturbance, and greatest in chain reactions and evolutionary epidemics, which have overproduction of propagules. The spread of disturbance is conservative in disturbance agents and stress accumulation disturbances. Disturbance agents are unable to reproduce during a disturbance event; they only move disturbance from one place to another. Stress accumulation disturbances are also unable to reproduce; it only redistributes stress from one site to another. The spread of disturbance is reproductive in chain reactions and evolutionary epidemics, because both types of disturbance produce disturbance propagules that can infect neighboring sites.

The ability to spread determines what geometric form a disturbance event can take. As ability to spread increases, disturbances can take more space filling shapes, while when ability to spread is limited, disturbance must take more linear forms or be unable to spread. The consequences of shifting patterns of spread for different disturbance types are shown in Figure 6-12. The reproductive and conservative spread disturbances respond differently to constraints imposed upon the manner in which they may spread. If conservative spread disturbances are forced to concentrate, they are able to persist longer and disturb larger areas. However, if they can spread in all directions, their impact is quickly dissipated. The opposite is true for reproductive spread disturbances, if they are channeled into narrow areas they interfere with their own ability to spread. Conversely, their spread is catalyzed by being able to disperse in all directions, because they are exposed to more potential sites to infect.

Disturbance Behavior: Constant vs. Adaptive

Disturbance types can also be classified based upon the flexibility of their behavior, as well as by their ability to spread. In chain reaction and stress accumulation and release

disturbances, contagion and virulence remain constant for a given disturbance. However, both disturbance agent and evolutionary epidemic disturbances can vary their contagion and virulence during a disturbance event (Table 6-1).

Table 6-1. Types of contagious disturbance can be classified based upon the mode of disturbance spread and the adaptive or constant nature of contagion and virulence.

	Conservative Spread	Reproductive Spread
Constant Virulence & Contagion	Stress Accumulation and Release	Chain Reaction
Adaptive Virulence & contagion	Disturbance Agent	Evolutionary Epidemic

This adaptive capacity makes it difficult to analyze the general behavior of disturbance agents and evolutionary epidemics, but it does suggest that the interaction of behavior and landscape properties should be able to produce multiple stable states of disturbance landscape interaction. For example, disturbance agents could potentially choose to either graze in aggregated groups or as dispersed individuals. This behavioral choice would alter the spatial distribution of vegetation across the landscape. Aggregated grazing would produce patchy vegetation, while dispersed grazing would produce a more homogenous landscape. All other things being equal, these behavioral choices would then be self-reinforcing, for patchy vegetation would tend to encourage animals to aggregate in the good patches, while a homogenous landscape would encourage dispersal. Similarly, an evolutionary epidemic could exist in either as a periodic epidemic or as a continuous endemic infection. Both of these states could also become self-reinforcing, as epidemics would select virulent and contagious strains that could rapidly spread through a large population of susceptible, while endemic disease would select strains that can survive long enough to infect a non-resistant host.

Disturbance and Ecological Dynamics

The dynamics of disturbance are also strongly influenced by the behavior of the system that they disturb. Disturbance types can be classified by their interaction with the system being disturbed.

Stress accumulation disturbances are tightly coupled to the system that they disturb. Initiation, reproduction and recovery rates are interdependent upon one another. Stress accumulation is a product of the system's development. The rearrangement of stress across the landscape, drives both recovery and disturbance initiation.

The other types of disturbance are separate from the systems that they disturb. Disturbance processes occur independently of ecosystem recovery from disturbance. All these disturbance types are influenced by the recovery of resistant sites to susceptible status. These effects of regeneration are greater from chain reactions and evolutionary epidemics, for these disturbances require susceptible sites to transmit themselves across a landscape. Disturbance agents can move across resistant sites, to initiate disturbance in distant susceptible sites. While the presence and distribution of susceptible sites influence the disturbance regime produced by disturbance agents, the influence of spatial pattern is greater for chain reaction and evolutionary epidemic disturbances.

Table 6-2. Summary of key attributes of disturbances and their relationship with disturbance type.

Disturbance Type	Disturbance Spread	Disturbance Behavior			Dynamics of System Disturbed
		<i>Virulence and Contagion</i>	<i>Initiation of Disturbance</i>	<i>Disturbance Stopping</i>	
Disturbance Agent	Conservative. Movement of disturbance agent	Adaptive Driven by an agent's behavior	Behavior of disturbance agent	Behavior of disturbance agent	Resistant sites become susceptible
Stress Accumulation and Release	Conservative Stress dissipated into neighbors	Constant	Internal stress passes a threshold	Stress dissipated without starting triggering collapses.	Stress accumulates and is redistributed by disturbance.

Chain Reaction	Reproductive Over production and dispersal	Constant	External initiation	Failure to infect more sites	Resistant sites become susceptible
Evolutionary Epidemic	Reproductive Over production and selection	Adaptive Varies as landscape selects on trades-off between virulence and contagion.	External initiation	Extinction or product of density and virulence drops below a threshold.	Resistant sites become susceptible

Disturbance Patterns

Disturbance types produce distinctive spatial patterns. Variation in these patterns can be explained by the relationships between the contagion processes. I focused my analyses on disturbances that maintain constant values of virulence and contagion. It is difficult to develop general descriptions of disturbances that vary their virulence and contagion, because such analyses requires a consideration of rates of evolution, learning, and other behavioral attributes.

In this section, I analyze the dynamics of stress accumulation and release and chain reaction disturbances. The patterns produced by stress accumulation and release and chain reaction disturbances are quite different, and consequently so are their responses to changes in their driving processes. These dynamics also describe the special case of the adaptive disturbances operating under stable conditions, however the response of these adaptive disturbance processes to environmental change is much more varied than the constant disturbance types.

Stress Accumulation and Release

The spatial patterns produced by stress accumulation and release disturbances exhibit strong scaling patterns that are controlled by a few parameters. As was discussed above, the spatial pattern of these disturbances is fractal (Bak et al. 1988), and the

frequency of disturbances is related by a power law to disturbance size (Figure 6-7). In other words, stress accumulation disturbances produce pattern that is self-similar across a fixed range of scales in space (fractal disturbance pattern) and in time (frequency follows a power law). This connection between spatial and temporal pattern is not surprising when the degree to which landscape pattern and disturbance spread are linked in stress accumulation disturbances.

In the stress accumulation model, the same process drives both ecosystem recovery and disturbance initiation. Stress accumulates, because of system development. This connects the rates of recovery, initiation, and reproduction to one another, so that change in one of these variables also changes the others. Contagion and virulence are also linked to one another, since collapse is what triggers contagion. These linkage means that variables cannot be altered independent of one another, which results in little room for variation in cascade dynamics.

Stress accumulation and release models can be made more complex, and realistic, by adding an exogenous driver of stress, along with the endogenous stress accumulation. For example, to model the effect of storms on tree-fall gap formation, a model would need to include the external stress of wind along with the internal stress of tree size or age. But such complex models are outside the scope of this chapter.

The chief forms of variation in stress accumulation disturbances are constraints of spread imposed by the geometry of the landscape, which have already been discussed (Figure 6-14), and the amount of stress a site can accumulate before collapsing. The amount of stress a site dissipates when it collapses influences the fractal dimension of the disturbances (Bak 1996). The greater the relative of stress dissipated by a site's collapse, the greater the fractal dimension of a disturbance. This connection arises because the larger the amount of stress accumulated within a site, the greater the number of neighboring sites it has the ability to disturb when it collapses.

Chain Reaction

Chain reaction disturbances are more complex than stress accumulation and release disturbances. The independence of the processes determining the dynamics of chain reaction disturbances allows these disturbances to produce a variety of spatial and temporal patterns of disturbance. These patterns are controlled by the three processes that define a chain reaction regime: recovery, contagion, and initiation rates.

The ratio of recovery to contagion determines the memory an ecosystem has of past disturbances, because this ratio determines how long it takes before a past disturbance no longer influences a site, and therefore controls the ability of a disturbance to spread across a landscape. Similarly, the ratio of recovery to initiation determines whether a disturbance can influence its own spread. If the disturbed system recovers at a rate near to that at which disturbance spreads, the same disturbance can disturb the same site more than once. If these rates are decoupled, then a single disturbance event cannot disturb the same site more than once. These two ratios can be used to define a set of disturbance patterns (Figure 6-15).

When the recovery occurs much slower than contagion, recovery must occur between rather than during disturbances. This decoupling between the rates of recovery and contagion causes disturbance to produce patches of disturbance on the landscape. The dynamics of these patches depends upon a system's memory. As system memory increases, the tendency for existing patches to burn as complete units also increases (see Chapter 5).

Memory causes the patches to constrain the spread of disturbance among patches, and enhance the spread of disturbances within patches, producing a self-organized landscape with persistent spatial structure. As memory decreases, when recovery and initiation scales become decoupled, the size of patches increases, until patches impose no constraint or enhancement on disturbance spread. In this case, the system approaches self-

organized criticality, in which the system exhibits disturbances whose frequency is a power law of their size (Drossel 1997).

When recovery is not decoupled from contagion, and recovery occurs at a scale similar to the rate of initiation, the system behaves chaotically. Such a system has transient fine scale spatial pattern, whose scale is dependent of the ratio of initiation to recovery, but this pattern is continually disrupted by new disturbances. This produces chaotic pattern, which appears to be random, but actually has hidden order. This type of system is not really a disturbed system, as the scale similarity between the disturbance processes and the system's recovery mean that by definition, the process being called a disturbance is not a disturbance, and it should be considered as an integral part of the systems dynamics. As this ratio increases, the structure of the landscape increases, until eventually producing waves or if disturbance can spread in two dimensions spiral waves. An example of this type of disturbance is forest wave regeneration on mountains (Iwasa et al. 1991).

Response to Environmental Change

The interaction of vegetative recovery and disturbance initiation self-organizes a landscape pattern. The scale of this self-organization determines the response of a system to a change in external drivers. The degree of memory in the system, that is the ratio of initiation and recovery, determines how a system responds to a given degree of change. Systems with more memory (stronger self-organization) are more resilient to small climatic changes than systems that are constrained chiefly by external drivers. However, if systems are exposed to larger changes in their external drivers the opposite is true.

The ability of a disturbance to spread determines its ability to change the scale over which it operates. Consequently, evolutionary epidemics have a strong ability to span a huge range of scales, while a disturbance producing agent has a limited ability to influence scales other than the scale at which the agent operates. Secondly, the ability of disturbance to adapt means that the same disturbance regime will behave radically differently in different environments. This suggests that when either an exiting disturbance that can

adapt is introduced into a new environment, or an existing environment is radically changed, one can expect not just the pattern but the behavior of the disturbance to change. Finally, the dynamics of the system being disturbed determine the response of the disturbance-producing agent to changes in the arrangement or dynamics of the system. Any rearrangements a system will alter stress accumulation disturbance, while changing rates at which new susceptible sites are available to a disturbance will strongly alter a chain reaction or evolutionary epidemic.

Summary

In this chapter I have presented my version of a general model of contagious disturbance and defined disturbance agents, stress accumulation and release, chain reactions and evolutionary epidemics as four key sub-types of contagious disturbance. I have identified initiation, reproduction, contagion, virulence and recovery as the five key properties of a contagious disturbance regime, and shown how changes in the relationship of these variables alters the behavior of contagious disturbances. These models provide general insights into the consequences of specific ecological organizations, allowing qualitative predictions to be made about the behavior of a poorly understood disturbance process by fitting it into the classification of rates and their relationship. These models can provide Null models for the investigation of contagious disturbances in specific ecosystems. In addition these models provide a framework for constructing more realistic alternative models of specific disturbance processes.

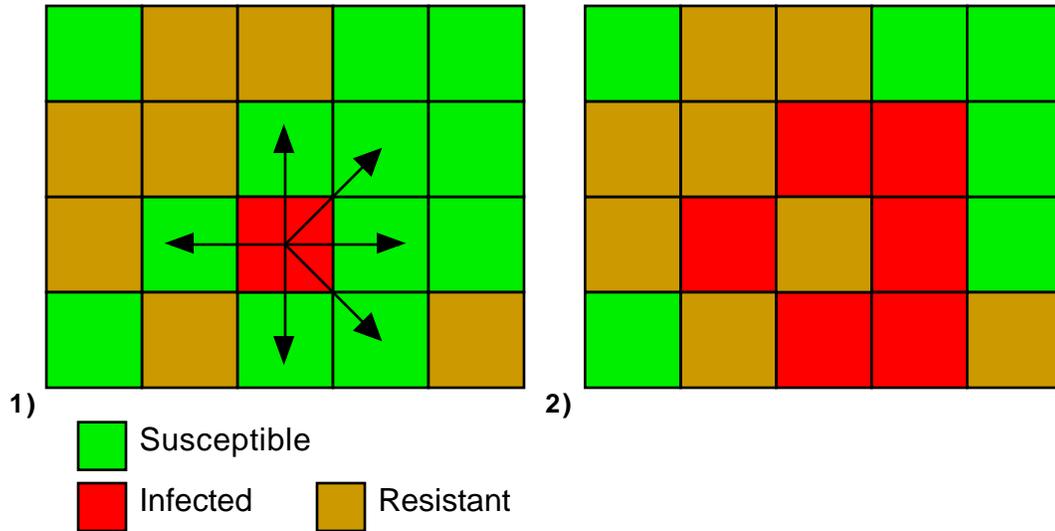


Figure 6-1. A general model of contagious disturbance. A landscape is represented by a matrix of sites. There are three classes of sites relative to the disturbance. Sites that are susceptible to the disturbance, those that are infected with the disturbance, and those that are resistant to the disturbance. 1) A disturbance initiated at a site can spread to its susceptible neighbors. 2) The disturbance has spread from its initial site. The initial site is destroyed and now resistant to disturbance, the newly infected sites can infect their susceptible neighbors. A disturbance spreads until it fails to infect new sites, and destroys its sites.

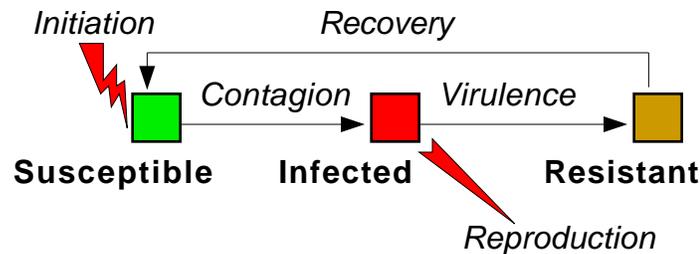


Figure 6-2. The dynamics of a disturbance are defined by the transitions among states and the initiations and reproduction of disturbance. Initiation infects sites, contagion spreads infection, and reproduction replicates infection. Virulence defines the rate at which infection destroys a site, and recovery the rate at which a site recovers from infection.

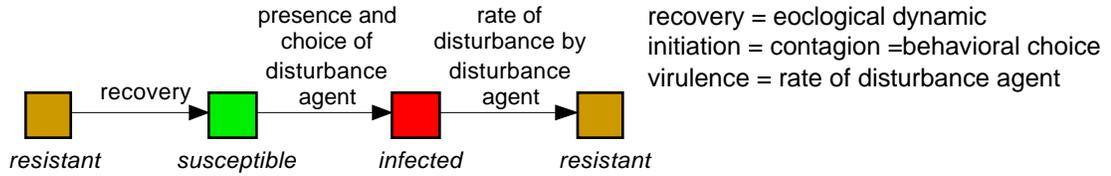


Figure 6-3. Disturbance agent dynamics. The disturbed system recovers following its own dynamics. Contagion and initiation are almost identical, both being based upon the disturbance agents behavior. Virulence is also a property of the disturbance agent, which also may follow behavioral rules.

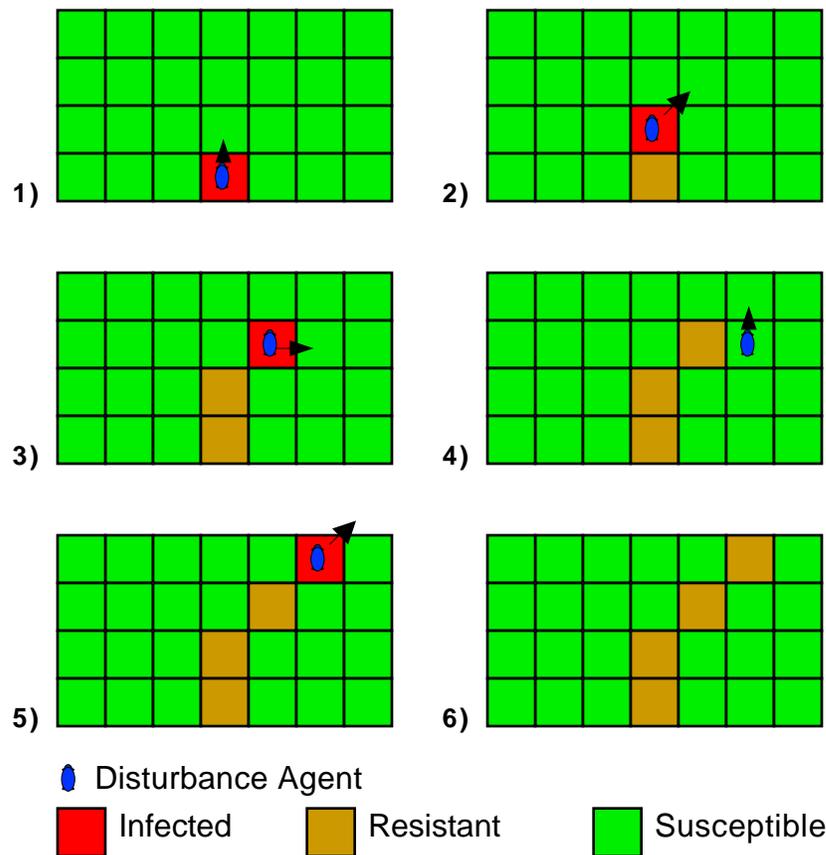


Figure 6-4. A disturbance agent moving disturbance across a landscape. A disturbance producing agent moves across the landscape, from site to site, based upon internal decision rules. It may destroy susceptible sites. In 4) the disturbance agent does not destroy the site, but moves over it. A disturbance event continues until the disturbance agent stops disturbing a site again. A disturbance begins when a disturbance agent decides to begin disturbing a site again.

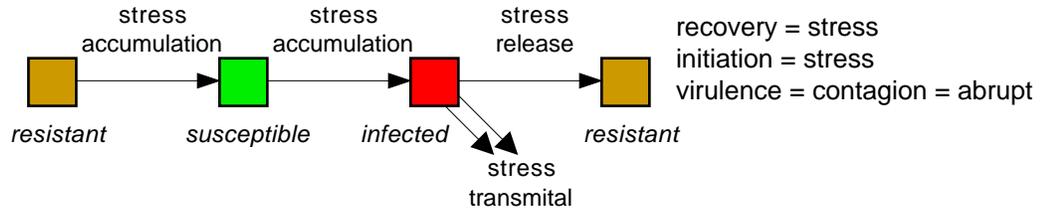


Figure 6-5. Stress accumulation and release dynamics. Stress is conserved among the site types, and stress accumulation defines the rates of recovery and initiation. There are two stress accumulation rates the exogenous driving rate and the internal abrupt transmission of stress from an infected site to other sites.

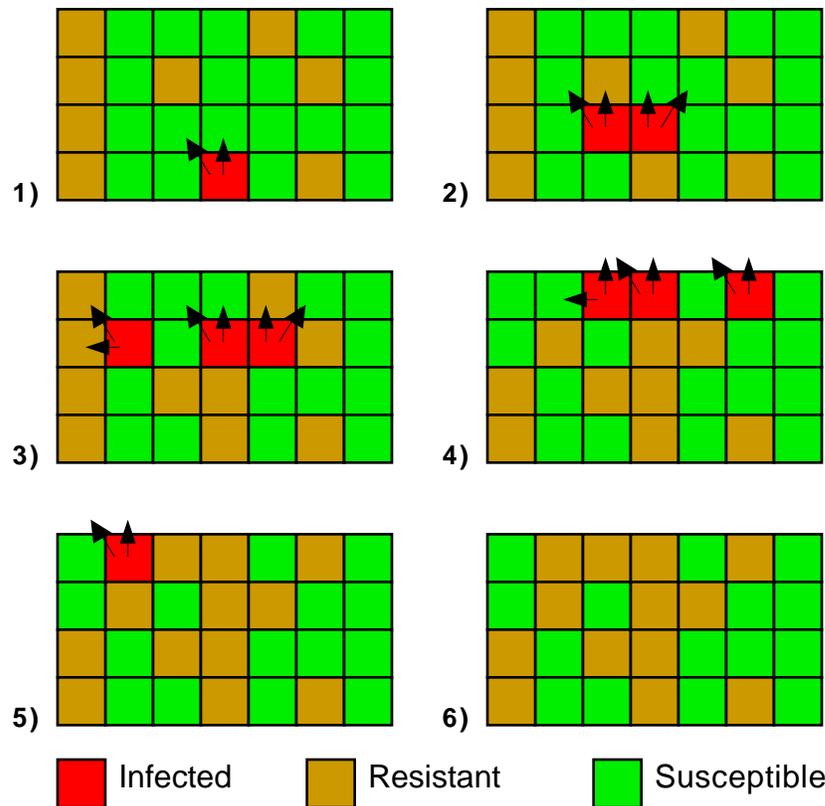


Figure 6-6. A stress accumulation and release disturbance spreads across the landscape. 1) A stressed site collapses distributing its accumulated stress into two neighboring sites. 2) These sites also collapse, spreading stress. 3) Stress causes one site to recovery and three others to collapse. 4) Three resistant sites recovery, while three susceptible sites collapse. 5) One site collapses, while the other stress is distributed off the landscape. 6) A reorganized landscape.

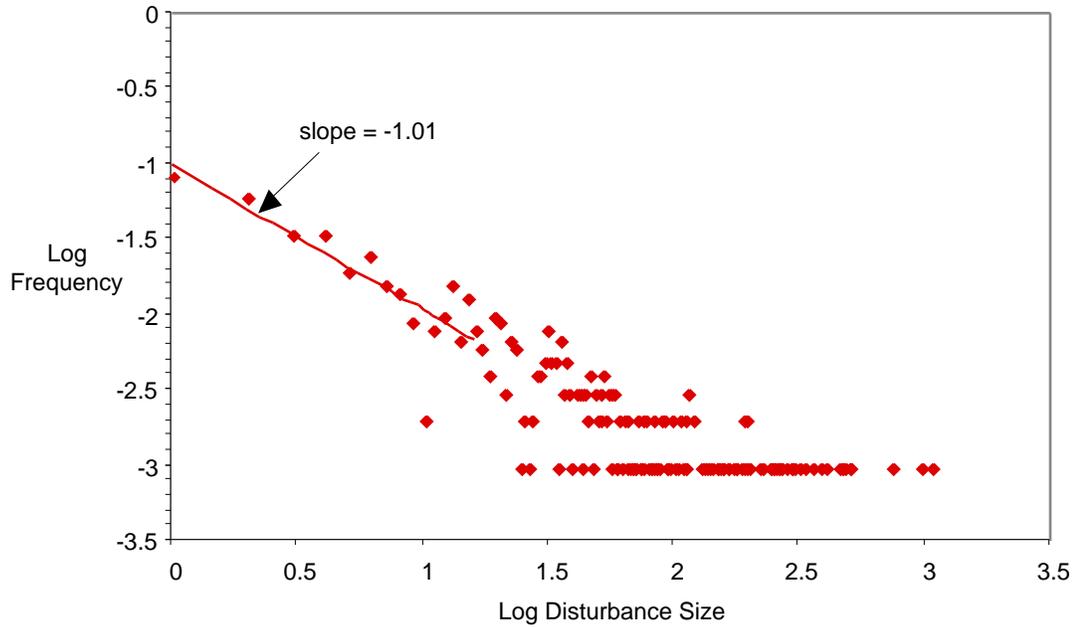


Figure 6-7. The distribution of disturbance sizes between 9000 and 10000 time units, follows a power law, $\text{Frequency} = \text{Area}^{-1.01}$ ($R^2=.68$, $N=16$). Over this smaller spatial scale range, where this scaling rule applies, the scaling exponent of 1.01 indicates that approximately equal areas are disturbed by disturbances of every size. Larger disturbances do not follow the scaling law, because there has not been sufficient time for self-organization to extend over larger spatial scales.

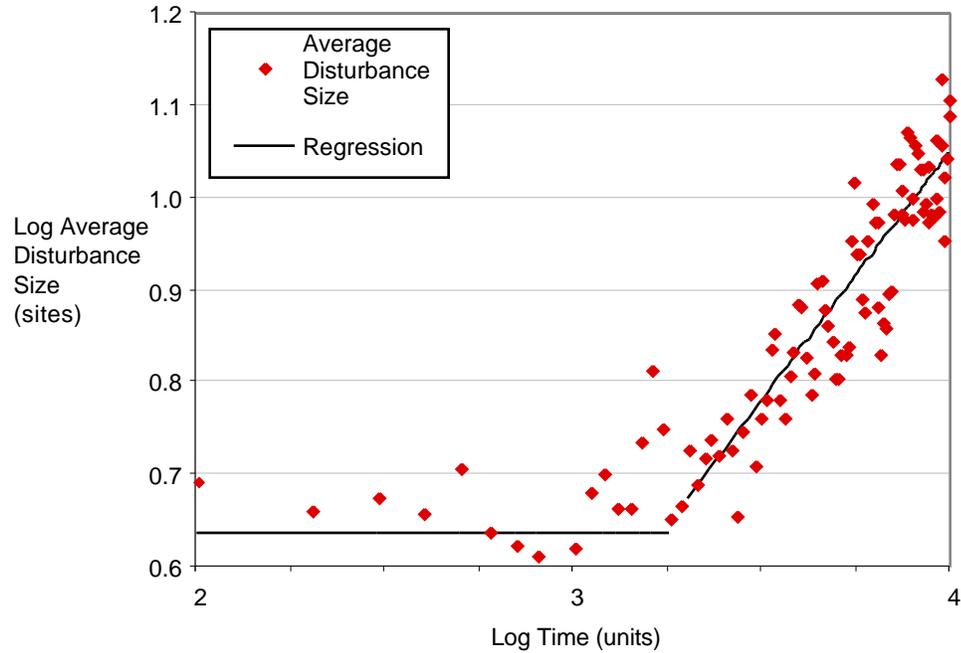


Figure 6-8. The distribution of average disturbance sizes from five simulation runs over 10000 time units using a bin size of 200 units. After 2000 units, the landscape becomes self-organized at small scales. From then on the scale of self-organization expands. This is shown by the increasing power law scaling of the average size of disturbance against time. This relationship is $\text{Average Size} = \text{Time}^{0.53}$ ($R^2 = .91$, $n = 80$).

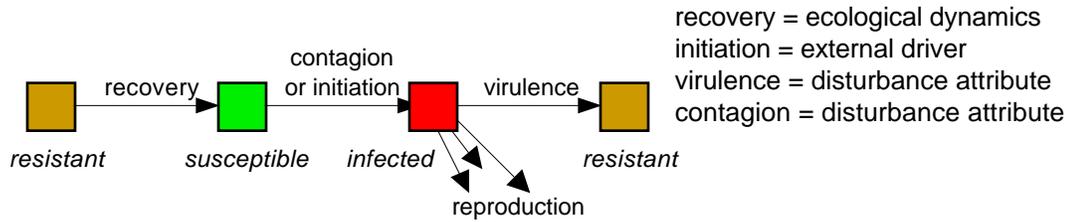


Figure 6-9. Chain reaction disturbance dynamics. The disturbed system recovers following its own dynamics. Contagion and virulence are independent constant properties of a specific chain reaction. The initiation rate is an external driver.

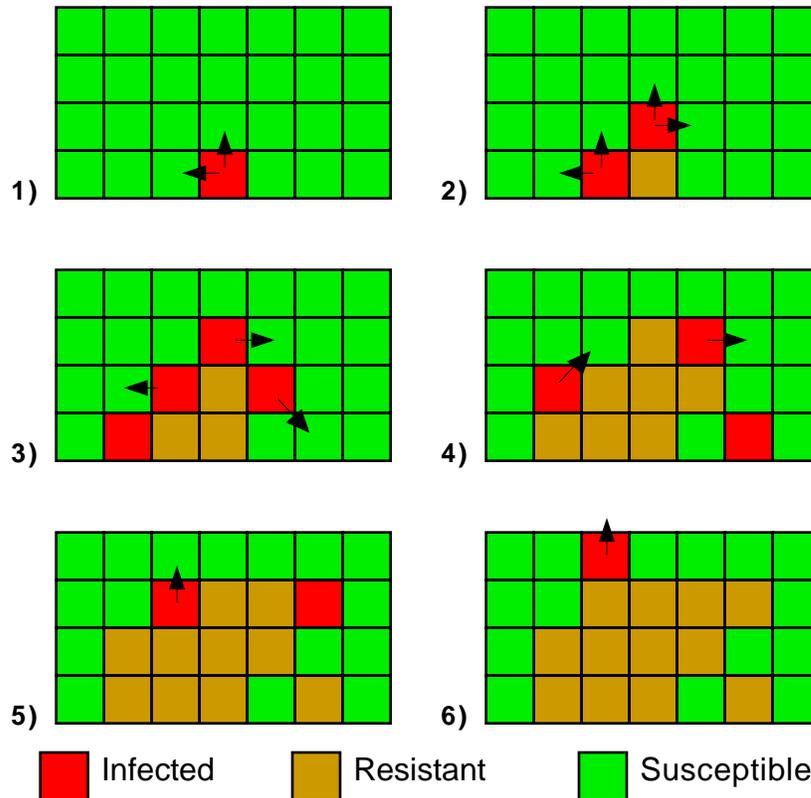


Figure 6-10. The spread of a sample chain reaction disturbance. Disturbance infects susceptible sites as a function of its contagion. Infected sites become resistant as a function of the disturbance's virulence. The disturbance persists until the last infected fails to infect any other sites, and the disturbance is extinguished. In this example, disturbance moves off the landscape is 6).

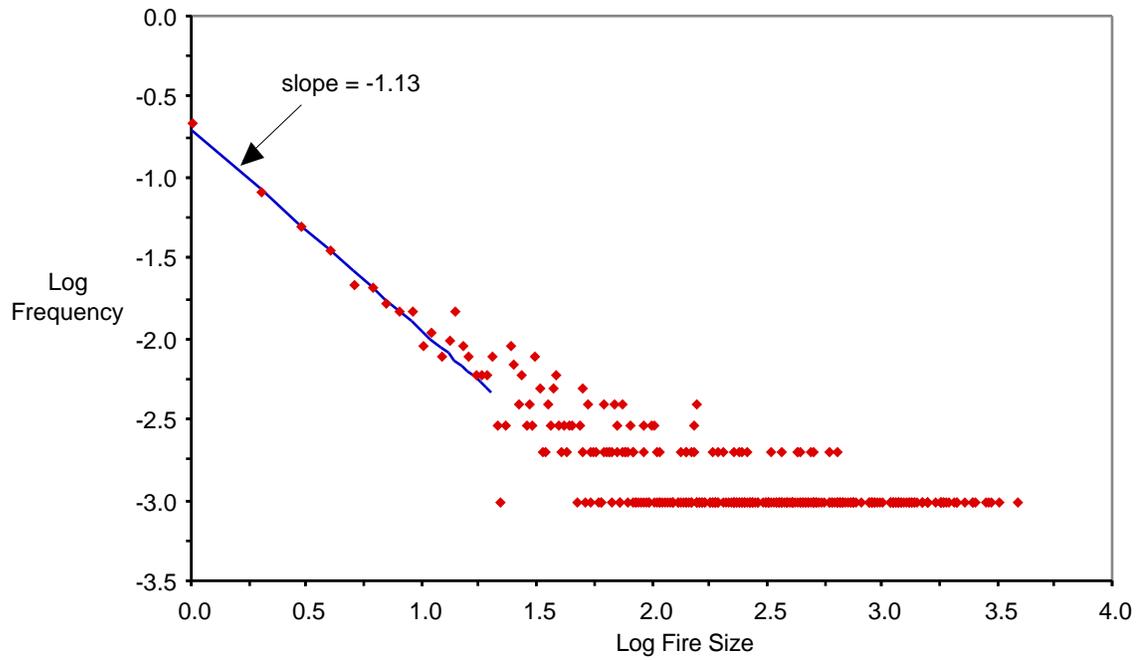


Figure 6-11. The distribution of disturbance in a chain reaction fire model follows a power law - Frequency \sim Area^{-1.13} ($R^2 = 0.83$, $N=32$). This scaling relationship applies at small scales, but cannot be applied over the entire range of fire sizes. The model is an interaction model from Chapter 5.

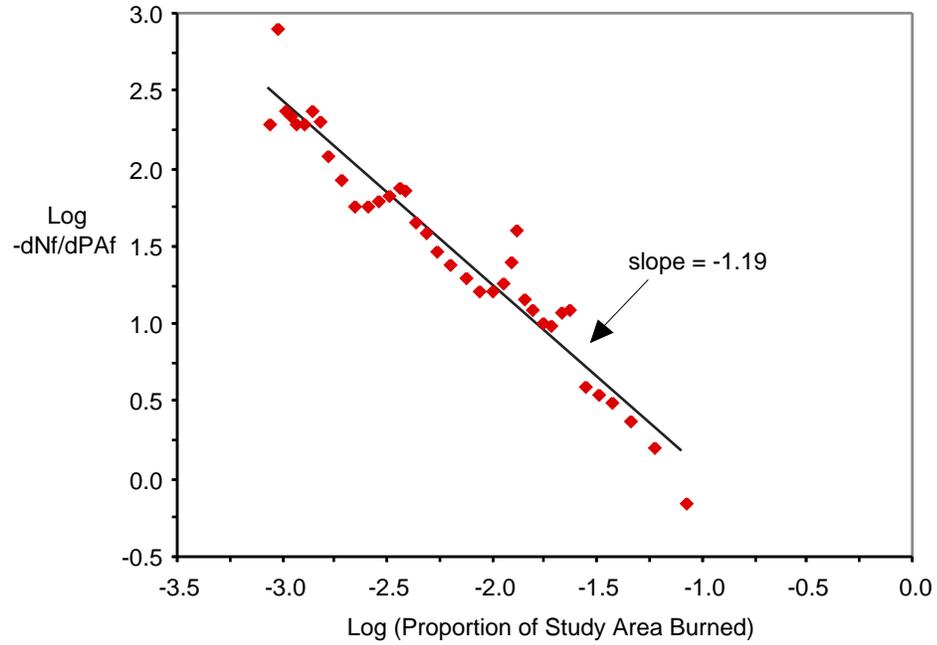


Figure 6-12. The distribution of annual area burned in SE Manitoba follows a power law. Frequency of Area Burned \sim Area Burned^{1.19} ($R^2 = 0.932$, $N = 37$). Data from Marples (1998).

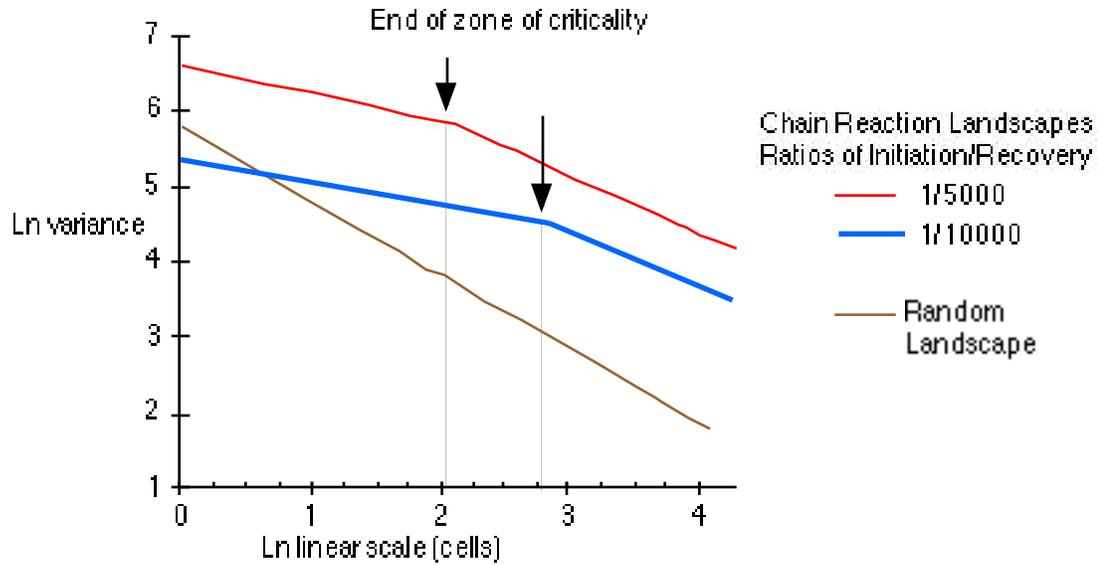


Figure 6-13. The scales of pattern in two chain reaction landscapes and a random landscape shown by changes in variance with window size of analysis. Variance follows a power law over small scales, and then follows the power law corresponding to a random distribution. A random landscape follows a power law with a slope of one, which corresponds to equal variation at all scales. The location of the boundary between the patchy and the random power law scale is defined by the ratio of initiation rate and recovery rate. The greater the scale separation between these two rates the larger the self-organized scale range. These data were generated from landscapes produced by an interaction model, which is described in Chapter 5, run at different disturbance initiation rates.

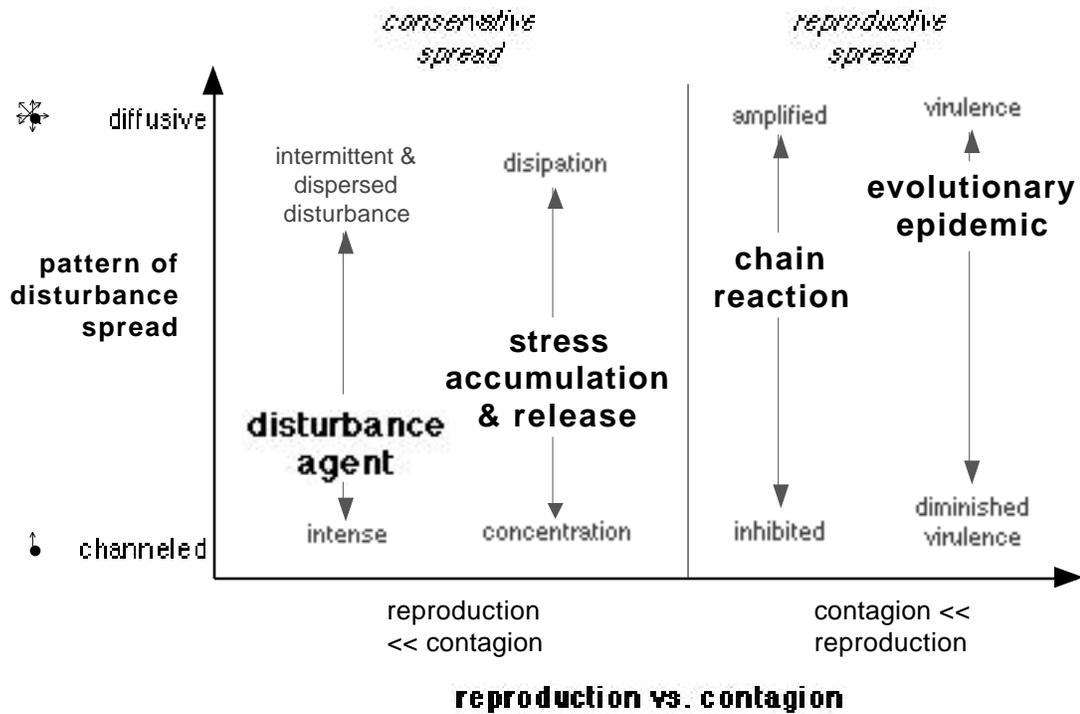


Figure 6-14. A comparison of the reproductive potential of different types of disturbance and the degree to which they can spread across the landscape. Quasi-contagious disturbances do not reproduce, cascade disturbances move, chain reactions can reproduce, and evolutionary epidemics can reproduce rapidly. The greater the reproductive potential the easier it is to influence larger scales.

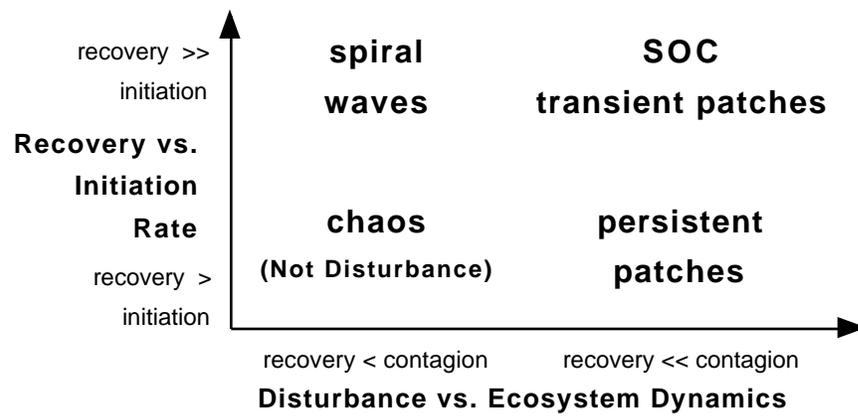


Figure 6-15. Patterns of self-organization produced by different ratios of disturbance recovery to initiation, and recovery to contagion. This comparison assumes that virulence is fixed, and is at about the same scale as contagion. By definition a disturbance process should occur at a scale distinct from a system's 'normal' ecological dynamics.

ECOLOGICAL RESILIENCE, BIODIVERSITY AND SCALE

Introduction

One of the central questions in ecology is how biological diversity relates to ecological function. This question has become increasingly relevant as anthropogenic transformation of the earth has intensified. The distribution and abundance of species have been radically transformed as massive land-use changes have eliminated endemic species (Turner et al. 1993), and the expansion of global transportation networks has spread other species (McNeely et al. 1995). This biotic reorganization is co-occurring with a variety of other global changes, including climate change, alteration of nutrient cycles, and chemical contamination of the biosphere. Maintaining the ecological services that support humanity, and other life, during this extensive and rapid ecological reorganization requires understanding how ecological interactions among species produce resilient ecosystems.

Species perform diverse ecological functions. A species may regulate biogeochemical cycles (Vitousek 1990, Zimov et al. 1995), alter disturbance regimes (D'Antonio and Vitousek 1992, Dublin et al. 1990), or modify the physical environment (Jones et al. 1994, Naiman et al. 1994). Other species regulate ecological processes indirectly, through trophic interactions such as predation or parasitism (Kitchell and Carpenter 1993). The variety of ecological functions that a species can perform is limited, and consequently ecologists frequently have proposed that an increase in species richness also increases functional diversity, producing an increase in ecological stability (Tilman 1996).

The idea that species richness produces ecological stability was originally proposed by Darwin (1859), reiterated by MacArthur (1955), and modeled by May (1973). Recently, Tilman and colleagues (Tilman 1996, Tilman et al. 1996) experimentally demonstrated that in small systems, over ecologically brief periods, increased species richness increases the efficiency and stability of some ecosystem functions, but decreases population stability. Despite the demonstrated link between species richness and ecological stability over small scales, the nature of this connection remains uncertain.

Models of Ecological Organization

Many competing models attempt to describe how an increase in species richness increases stability. Following previous authors, I divide these models into four classes: 'species richness-diversity' (MacArthur 1955), 'idiosyncratic' (Lawton 1994), 'rivet' (Ehrlich and Ehrlich 1981), and 'drivers & passengers' (Walker 1992, Walker 1995). They all explicitly or implicitly assume that a species has ecological function, and that the function of a species can be represented as occupying an area of multi-dimensional ecological function space (Grinnell 1917, Hutchinson 1957, Sugihara 1980). For illustrative purposes, I compress multi-dimensional functional space into one dimension in which breadth represents the variety of a species' ecological function (Clark 1954). For example, a species such as a beaver, that strongly influences tree populations, hydrology, and nutrient cycles has a broad function, while a fig wasp that pollinates a single species of fig would have a narrow function. I represent the intensity of a species' ecological function by height. For example, a 'keystone species' (Paine 1969, Power et al. 1996) has a stronger influence than a 'passenger' species (Walker 1992).

The following section emphasizes the differences between these models before discussing their similarities. I then extend these models of diversity and ecological function by incorporating the concepts of scale and resilience.

Species-Diversity

Darwin (1859) proposed that an area is more ecologically stable if it is occupied by a large number of species than if it is occupied by a small number. This idea was formalized by MacArthur (1955), who proposed that the addition of species to an ecosystem increases the number of ecological functions present, and that this increase stabilizes an ecosystem (Figure 7-1).

While many experimental studies have demonstrated that increasing the number of species increases the stability of ecosystem function (Ewel and Bigelow 1996, Frost et al. 1995, Holling et al. 1995, Naeem et al. 1994, Schindler 1990, Tilman 1996), apparently no investigations of the relationship between species richness and stability have indicated that additional species continue to increase stability at a constant rate, indicating that the species-diversity model is excessively simplistic. Consequently, in this paper I examine models that propose more complex relationships between species richness and ecological stability.

Idiosyncratic

A competing model of the relationship between species and ecological function proposes that strong ecological interactions among species result in an ecosystem that is extremely variable, and contingent on the particular nature of inter-specific interactions (Lawton 1994). This model proposes that the degree of stability in a community depends idiosyncratically upon which species are present (Figure 7-2). For example, fire ants have had large impacts on ecosystems of the southeastern United States (Porter and Savignano 1990), but have a much different role in the Pantanal of Brazil and Paraguay (Orr et al. 1995). Such situations suggest that ecosystem function is contingent on the ecological history of a region and the evolutionary history of interacting species. However, ecosystems are not only products of historical contingency, ecosystem ecology has demonstrated that many ecosystems are similarly organized.

Many ecosystem studies have revealed that despite dissimilar species compositions, ecosystems can have striking ecological similarities. For example, lake studies have demonstrated that similar ecological function can be maintained over a wide mix of species and population densities (Frost et al. 1995, Schindler 1990). Mediterranean climate ecosystems provide a good example of functional convergence. The world's five Mediterranean climate regions, despite geographic and evolutionary isolation that has produced radically different floras and faunas, are extremely similar in ecological structure and function (di Castri and Mooney 1973, Kalin Arroyo et al. 1995). This convergence suggests that species are organized into functional groups, and that these groups are determined by regional ecological processes. Both the 'rivet' (Ehrlich and Ehrlich 1981) and 'drivers and passengers' (Walker 1992) models of functional diversity assume that some sort of functional redundancy exists, but they differ in the importance they assign to functional groups.

Rivets

Empirical evidence suggests that the effect of species removal from or addition to an ecosystem varies. Ehrlich & Ehrlich's (1981) rivet hypothesis, which is similar to Frost et al.'s (1995) model of compensating complementarity, likens the ecological function of species to the rivets that attach a wing to a plane. Several rivets can be lost before the wing falls off. This model proposes that the ecological functions of different species overlap, so that even if a species is removed, ecological function may persist due to the compensation of other species with similar functions (Figure 7-3).

In the rivet model, an ecological function will not disappear until all the species performing that function are removed from an ecosystem. Overlap of ecological function allows an ecosystem to persist. Compensation masks ecosystem degradation, because while a degraded system may function similarly to an intact system, the loss of redundancy decreases the system's ability to withstand disturbance or further species removal.

Drivers and passengers

Walker's 'drivers and passengers' hypothesis accepts the notion of species complementarity and extends it by proposing that ecological function resides in 'driver' species, or functional groups of such species (Walker 1992, Walker 1995). It is similar to Holling's (1992) 'extended keystone hypothesis'. Walker defines a driver as a species that has a strong ecological function. Such species significantly structure the ecosystems in which they and passenger species exist. Passenger species are those that have minor ecological impact. Driver species can take many forms. They may be 'ecological engineers' (Jones et al. 1994), such as beavers (Naiman et al. 1994), or gopher tortoises (Diemer 1986), which physically structure their environments. Or drivers may be 'keystone species' (Paine 1969), such as sea otters (Estes and Duggins 1995) or asynchronously fruiting trees (Terborgh 1986), that have strong interactions with other species (Power et al. 1996). Walker (1995) proposes that since most ecological function resides in the strong influence of driver species, it is their presence or absence that determines the stability of an ecosystems ecological function (Figure 7-4).

Model synthesis

While the 'rivet' hypothesis assumes that ecological function is evenly partitioned among species, Walker's model assumes there are large differences between 'drivers' that have strong ecological function and passengers that have weak ecological function (Figure 7-4). Both hypotheses recognize that different types of ecological functionality are required to produce ecological stability, and that as additional species are added to an ecosystem the increasing redundancy of function decreases the rate at which ecological stability increases. The existence of some type of ecological redundancy is supported by experiments conducted in Minnesota grasslands, tropical rainforests, artificial mesocosms, and lakes (Ewel and Bigelow 1996, Naeem et al. 1994, Schindler 1990, Tilman et al. 1996).

Tilman and colleagues, for example, demonstrated that more diverse plots (4 m X 4 m) have greater plant cover and more efficiently utilize nitrogen. They demonstrated that

ecological function was more stable in diverse communities despite, or perhaps because of, large fluctuations in populations of species (Tilman 1996, Tilman et al. 1996). These results echo those of Frank & McNaughton (1991) who demonstrated that more diverse natural grass communities recovered faster than less diverse communities following drought.

In a series of experiments, Ewel and co-workers constructed a set of tropical ecosystems with different levels of species richness and compared their functioning to adjacent rainforest. They demonstrated that relatively few species, if drawn from different functional groups, can duplicate the ecological flows of a diverse rainforest (Ewel et al. 1991). Herbivory per leaf area was lower and less variable in species-rich plots (Brown and Ewel 1987). They also demonstrated that a variety of ecosystem variables, such as soil organic matter, increase rapidly as one adds different functional types to a plot (Ewel and Bigelow 1996), and that simple agro-ecosystems function quite similarly to much more species-rich rainforests, at least in areas of about 1/3 ha (80 m X 40 m) for five years (Ewel et al. 1991).

Naeem and co-workers (1994) assembled replicate artificial ecosystems at a number of levels of species richness. They demonstrated that carbon dioxide consumption, vegetative cover, and productivity increased with species richness. These increases were greater between 9 and 15 species than between 15 and 31 species, providing support for the hypothesis that an increase in species richness increases ecological redundancy. Water and nutrient retention did not vary with species richness.

Frost and co-workers (1995) demonstrated that ecological function is preserved if population declines of zooplankton species are compensated for by population increases in other species with similar ecological functions. Their results suggest that lakes with fewer species in a functional group would exhibit decreased ability to compensate for population declines in other species. Similarly, Schindler (1990) observed that the largest changes in

ecological processes and food web organization occurred when species that were the only remaining member of a functional group were eliminated.

These studies demonstrate that the stability of many, but not all, ecological processes increases with species richness. They also suggest that the ecological stability is generated more by a diversity of functional groups than by species richness. These results suggest a possible synthesis of the various models relating stability to species richness.

The model that best describes an ecosystem appears to depend upon the variety of functional roles that are occupied in that system, and the evenness of the distribution of ecological function among species. An ecosystem consisting of species that each perform different ecological functions will be less redundant than an ecosystem consisting of the same number of species that each perform a wide variety of ecological functions. Similarly, if there is little difference between the ecological impact of different species, there is little point in differentiating 'driver' and 'passenger' species; they can all be considered 'rivets'. I propose that these models of how species richness influences the stability of ecological function can be collapsed into a simple model that can produce specific versions of these models by varying the degree of functional overlap and the degree of variation in ecological function among species (Figure 7-5).

The experimental results discussed above suggest ecosystems possess considerable functional redundancy. Indeed, it is difficult to envision how ecosystems without redundancy could continue to persist in the face of disturbance. I assume that since no species are identical, redundancy does not reside in groups of species, but rather it emerges from the interactions of species. Therefore it is not possible to substitute species for one another, rather there are many possible combinations and organizations of species that can produce similar ecological functions. Redundancy quickly emerged in the experimental ecosystems, but these experiments were all conducted over relatively small areas and short time periods. Ewel and his co-workers conducted the longest and largest experimental manipulations of diversity, but even five years and a 1/3 ha are small in comparison to the

spatial and temporal dynamics of an ecosystem, or even the life-span and home range of a medium sized mammal.

Understanding of stability and ecological function developed at small scales can not be easily extended to larger scales, since the type and effect of ecological structures and processes vary with scale. At different scales, different sets of mutually reinforcing ecological processes leave their imprint on spatial, temporal and morphological patterns. Change may cause an ecosystem, at a particular scale, to suddenly reorganize around a set of alternative mutually reinforcing processes. For example, Hughes (1994) described an epidemic that caused a 99% decline in the population of an algae-eating fish in Jamaican near shore coral community. The loss of these herbivores caused the community to shift from being dominated by corals to being dominated by fleshy macro-algae. Similar reorganizations are demonstrated in paleo-ecological (Carpenter and Leavitt 1991), historical (Prins and Jeud 1993), and long-term ecological research (Hughes 1994).

Resilience

Assessing the stability of ecosystems that can reorganize requires more than a single metric. One common measure, what has been termed engineering resilience (Holling 1996), is the rate at which a system returns to a single steady or cyclic state following a perturbation. Engineering resilience assumes that behavior of a system remains within the stable domain that contains this steady state. When a system can reorganize, that is shift from one stability domain to another, a more relevant measure of ecosystem dynamics is ecological resilience (Holling 1973). Ecological resilience is a measure of the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures. Note that this use of resilience is different from its use by others (e.g. Pimm 1984), who defines resilience as what I term engineering resilience (Holling 1996).

The difference between ecological and engineering resilience can be illustrated by modeling an ecological 'state' as the position of a ball on a landscape. Gravity pulls the ball downwards, and therefore pits in the surface of the landscape are stable states. The deeper a pit the more stable it is, because increasingly strong disturbances are required to move an ecological state away from the bottom of the pit. The steepness of the sides of a stability pit corresponds to the strength of negative feedback processes maintaining an ecosystem near its stable state, and consequently engineering resilience increases with the slope of the sides of a pit (Figure 7-6).

Ecological resilience assumes that an ecosystem can exist in alternative self-organized or 'stable' states. It measures the change required to move the ecosystem from being organized around one set of mutually reinforcing structures and processes to another. Using the landscape metaphor, while engineering resilience is a local measure of slope of the stability landscape, ecological resilience is a measure of regional topography. The ecological resilience of a state corresponds to the width of its stability pit. This corresponds to the degree to which the system would have to be altered before it begins to reorganize around another set of processes (Figure 7-7).

Ecological and engineering resilience capture different system properties. Ecological resilience concentrates on the ability of a set of mutually reinforcing structures and processes to persist. It allows ecologists or managers to focus upon transitions between definable states, defined by sets of organizing processes and structures, and the likelihood of such occurrence. Engineering resilience, on the other hand, concentrates on conditions near a steady-state where transient measurements of rate of return are made following small disturbances. Engineering resilience focuses upon small portions of a system's stability landscape, while ecological resilience focuses upon its contours. Engineering resilience does not help assess either the response of a system to large perturbations, or when gradual changes in a system's stability landscape may cause the

system to move from one stability domain to another. For these reasons I concentrate on ecological resilience.

Multiple Stable States

Ecological resilience assumes that multiple ecological states do exist, however since an influential paper by Connell and Sousa (1983) cast doubt upon the evidence for multiple stable states the concept has not been widely utilized in ecological studies. In recent years, an increasing number of works in a variety of ecosystems have suggested that multiple stable states are a general feature of ecosystems. In all instances, periodic flips from one state to another are mediated by changes in slow variables that suddenly trigger a fast variable response, or escape. The following cases provide examples of alternative stable states.

Meta-population dynamics: A connected set of populations can exist at either a high-density connected state or a low-density fragmented state. In a landscape composed of potential habitats, the population of a particular habitat depends on its neighboring sites. If the population at a site becomes extinct, the probability of recolonization increases with the aggregate size of the surrounding populations. This effect produces a positive feedback between the density of a region's population and the likelihood that this region's population can maintain itself. Consequently, a regional population can rapidly decline if its population begins to fail to recolonize potential sites, because this further reduces the probability of recolonizing sites (Hanski et al. 1995).

Shallow Lakes: In shallow lakes the interactions among turbidity, nutrients loading, vegetation and fish produce two alternative stable states (Scheffer et al. 1993). Lakes can be clear and dominated by aquatic vegetation or turbid and dominated by algae. Plants stabilize provide refugia for phytoplankton consuming fish, and stabilize sediment reducing turbidity, and the re-suspension of nutrients. Turbidity blocks light for plants, and resuspended sediment makes nutrients available to algae. Lakes usually switch between

states due to a combination of changes. For example, a clear lake can become turbid, due to an increase in nutrient loading, a decrease in algae eating fish, an inflow of sediment, or the removal of vegetation. Diverse processes, including fluctuations in water level or an increase in animal foraging that resuspends benthic material, can drive these changes (Scheffer 1998). Similarly, a turbid lake can be transformed into clear lake if the population of bottom foraging fish is reduced or if the population of the predators of algae-eating fish is reduced.

Reefs: Either corals, surface algae or macro-algae can dominate reefs. Changes in nutrient concentrations, the creation of clear surface, and the intensity of fish and sea urchin predation on algae regulates switches between states (Done 1992). Disturbance events, such as storms, can trigger shifts between stable states. Disturbance can alter many ecological processes simultaneously. For example, a storm may destroy existing structure creating new areas for recruitment, introduce pulses of nutrients that may produce eutrophication, and reduce populations of algal predators (Hughes 1994). Fishing and variation in recruitment can strongly influence fish populations, while the interaction of density dependent recruitment and circulation patterns allows sea urchins to exist at self-maintaining high or low density states (McClanahan et al. 1996). These interactions suggest that reefs can exist in three self-maintaining states, coral-fish, turf algae-urchins, and macro-algae (Done 1992).

Sea otters, sea urchins and kelp forests: In the northern pacific, rocky near-shore communities can be either dominated by dense stands of macro-algae or algae eating sea urchins. The presence of these states is controlled by the presence of sea otters that prey upon sea urchins. In the absence of sea otters, urchins predation tends to prevent kelp forests from establishing, while when sea otters are present, their predation on sea urchins, allows key forests to become established (Estes and Duggins 1995).

Fire in North Florida: In North Florida either oaks (*Quercus* spp.) or pines (*Pinus* spp) can dominate sandhill vegetative communities. Fire mediates the competitive

relationships between these two states. Longleaf pine (*Pinus palustris*) is a particularly fire tolerant pine species. Mature longleaf pines shed needles that provide good fuel for ground fires, and young longleaf pines can survive ground fires. Young hardwoods are intolerant of fire, and mature hardwoods shed leaves that suppress the build-up of fuel for ground fires. This lack of fuel tends to suppress fire in hardwood stands, encouraging the growth of more hardwoods, while fuel accumulation in stands of pine tend to encourage fire, suppressing hardwoods and encouraging the growth of pine (Abrahamson and Hartnett 1990, Glitzenstein et al. 1995, Rebertus et al. 1989).

Fire spreads itself from burning sites, into combustible sites. A fire that is surrounded by non-combustible sites will be unable to spread and will extinguish itself. The mutual reinforcement between fire and longleaf pine will only occur if the fires are started frequently and fires are able to spread across a large area. Otherwise, sites will burn infrequently, and fire susceptible vegetation will be replaced by fire suppressing vegetation. The ability of fire to spread, and consequently the rate at which patches of hardwood or pine either grow or shrink, is determined by the distribution of hardwoods and pine across the landscape. The succession of a forest site will be determined by the relative proportion of hardwood and pine in the area surrounding that site.

Elephants, fire and savanna: Dublin et al (1990) propose the elephants and fire interact with competition between grasses and trees to produce two alternative stable states in east African savanna. Fire shifts woodland to grassland. Grassland is maintained by herbivores, particularly elephants preying upon young seedlings. However, this predation is not sufficient to shift woodland to grassland, as it is only effective at low seedling densities. Low herbivore density and infrequent fire allow woodland regeneration to occur (Dobson 1995). For example, when Rinderpest eliminated a large number of grazers, woodlands experienced a pulse of regeneration (Prins and Jeud 1993).

Irreversible State Transitions

Occasionally, due to the loss of an important system component transition between multiple states results in the elimination of a former stable state. The extinction of species that perform a critical ecological function can cause such irreversible transitions.

Pleistocene extinctions have been proposed as examples of such transitions:

Australian Extinctions: Sediment cores from Australia show that about 100,000 years ago pollen from fire tolerant plants and mangroves increased while other species declined. These increases are likely due the increases in burning that are also documented by an increase in charcoal in river sediment cores. Increases in fire frequency would have allowed fire tolerant plants to spread, while at the same time leaving more bare soil to be eroded and deposited as coastal sediment providing increased habitat for mangroves. Similar climatic conditions had existed previously without increases of fire, which suggests that the arrival of humans may have been responsible (Kershaw 1988).

Flannery (1994) proposes that it was over-hunting of Australia's large marsupial herbivores that caused this change, rather than anthropogenic modification of fire regimes. During the time in which humanity is thought to have been in Australia, fifty large and medium sized marsupial herbivores became extinct, along with several large herbivorous birds and turtles. If these herbivores lived similarly to existing large herbivores (Owen-Smith 1989), then their extinction also likely eliminated their maintenance, through grazing, physical disturbance and nutrient cycling, of a variety of vegetative pattern across the landscape. The removal of this small-scale patterning, and a build-up of fuel may have facilitated the occurrence of larger, and more intense fires. Such fire reduces local nutrient cycling, by causing larger scale erosion. Flannery (1994) suggests that this process caused the expansion of heathlands of fire tolerant species at the expense of fire-intolerant vegetation adapted to herbivory. Without large herbivores to prevent and fragment vegetation, an ecosystem of fire and fire dominated plants could expand at the expense of a system of large herbivores and herbivore adapted plants. Flannery argues that hunting,

irreversibly by removing large herbivores and volatilizing accumulated nutrients, switched the system from a more productive state, dependent upon rapid nutrient cycling to a less productive state, with slower nutrient cycling, maintained by fire.

Slow Dynamics

The dynamics of a system with a single stable state may approximate a system with multiple stable states, if perturbation can cause the system to persist in a slowly changing unstable state. While such a system does not have true alternative states, its dynamics and management may be similar. Semi-arid grazing systems provide an example:

Semi-arid savanna grazing: Competition between grasses and woody vegetation is mediated by stocking rates of cattle that graze grass but not woody vegetation. At low cattle densities grass dominates, however as stocking density increases grazing may shift the competitive balance in favor of woody vegetation. If high stocking densities persist, the grass will be unable to persist and the system will be dominated by woody vegetation. This state is relatively self-maintaining, and a reduction of stocking densities does not allow grass to replace woody vegetation. However the woody vegetation dominated state is not stable, because rainfall variation and the death woody allow grasses to invade woody sites.

Woody vegetation dies back very quickly in dry years, but recovers only slowly in wet years. Grass can recover much quicker. Grass biomass can expand up to 10-fold during a season utilizing water not used by the slow growing woody vegetation. Additionally, as woody vegetation gradually dies it creates patches that can be colonized by grasses. Over time, these patches allow fire to invade a woody patch. The grass state of this rangeland is the only stable equilibrium of this system, but when this state is perturbed by over grazing, the system will make a slow transition through a woody dominated period before it returns to a grass dominated state. High stocking levels over a time period of 5-20 years allow woody plants to replace grasses. However, during the following 30 years, the death of woody vegetation allows fire to invade, replacing woody vegetation with grasses.

This type of slowly changing unstable state is not a true alternative stable state, but to a rancher who is making decisions about stocking levels, it may as well be (Ludwig et al. 1997).

These examples suggest that transitions among multiple states characterize many ecosystems. This supports the use of ecological resilience to analyze ecological function, and suggests that one of the important roles of species in ecosystems is managing the maintenance, and reorganization of ecosystems.

Scale

Ecosystems are resilient when ecological interactions reinforce one another, and dampen disruptions. Such situations may arise due to compensation when a species with an ecological function similar to another species increases in abundance as the other declines (Frost et al. 1995), or as one species reduces the impact of a disruption on other species. However, different species operate at different temporal and spatial scales, as is clearly demonstrated by the scaling relationships that relate body size to ecological function (Peters 1983).

I define a scale as a range of spatial and temporal frequencies. This range of frequencies is defined by resolution below which faster and smaller frequencies are noise, and the extent above which slower and larger frequencies are background. Species that operate at the same scale interact strongly with each other, but the organization and context of these interactions are determined by the cross-scale organization of an ecosystem. Consequently, understanding interactions among species requires understanding how species interact within and across scales.

Many disturbance processes provide an ecological connection across scales. Contagious disturbance processes such as fire, disease, and insect outbreaks have the ability to propagate themselves across a landscape, which allows small scale changes to drive larger scale changes. For example, the lightning ignition of a single tree can produce

a fire that spreads across thousands of square kilometers. Such disturbances are not external to ecological organization, but rather form integral parts of ecological organization (Holling 1986). Disturbance dynamics affect and are affected by species and their ecological functions (D'Antonio and Vitousek 1992). Consequently, the processes regulating contagious disturbances are as much determinants of ecological resilience as are more local interactions among species.

Current models of the relationship between species richness and stability implicitly model species and their ecological functions at the same scale, however ecological systems are not scale invariant. A growing body of empirical evidence, theory and models suggests that ecological structure and dynamics are primarily regulated by a small set of plant, animal, and abiotic processes (Carpenter and Leavitt 1991, Holling et al. 1995, Levin 1992). Processes operate at characteristic periodicities and spatial scales (Holling 1992a). Small and fast scales are dominated by biophysical processes that control plant physiology and morphology. At the larger and slower scale of patch dynamics, inter-specific plant competition for nutrients, light, and water influence local species composition and regeneration. At a still larger scale of stands in a forest, meso-scale processes of fire, storm, insect outbreak, and large mammal herbivory determine structure and successional dynamics from tens of meters to kilometers, and from years to decades. At the largest landscape scales, climate, geomorphological, and biogeographical processes alter ecological structure and dynamics across hundreds of kilometers and over millennia (Figure 7-8). These processes produce patterns and are in turn reinforced by those patterns; that is they are self-organized (Nicolis and Prigogine 1977).

Ecological processes produce a scale-specific template of ecological structures that are available to species (Krummel et al. 1987, Morse et al. 1985, O'Neill et al. 1991). Ecological structure and dynamics vary with scale, which means that while different species may occur at the same site, they will experience that site quite differently if they live at different scales. The body mass of an animal strongly influences the scales at which it

perceives and interacts with its environment. For example, a wetland may be inhabited by two different herbivores, a mouse and a moose, but these species perceive and experience the wetland differently. A mouse may spend its entire life within a patch of land smaller than a hectare, while a moose may move among wetlands over more than a thousand hectares (Figure 7-8). This scale separation reduces the strength of interactions between mice and moose relative to interactions among animals that operate at similar scales (Allen and Hoekstra 1992). In the next section, I propose a conceptual model that relates species richness, ecological resilience, and scale.

Species, Scale and Ecological Function

Species can be divided into functional groups based upon their ecological roles (Clark 1954, Körner 1996). Species can also be divided into groups based upon the specific scales that they exploit. Physiological ecology (Peters 1983) has developed allometric rules that relate the average adult body mass of a species to various ecological attributes, such as energy use, movement, home range size, and foraging behavior (Figure 7-8). These scaling relationships suggest that the ecological scales at which species operate often strongly corresponds with average species body mass, making body mass a useful proxy variable for determining the scales of an animal's perception and influence (Holling 1992a). Body mass can be used to divide species into groups based upon the range of scales they exploit, just as ecological function can be used functionally divide species. I propose that the resilience of ecological processes, and therefore of the ecosystems they maintain, depends upon the distribution of functional groups within and across scales.

I hypothesize that if species in a functional group operate at different scales, they provide mutual reinforcement that contributes to the resilience of a function, while at the same time minimizing competition among species within the functional group (Figure 7-9). This cross-scale resilience complements a within-scale resilience produced by overlap of ecological function among species of different functional groups that operate at the same

scales. Competition among members of a multi-taxa functional group may be minimized if group members that use similar resources exploit different ecological scales. Ecological resilience does not derive from redundancy in the traditional engineering sense, rather it derives from overlapping function within scales and reinforcement of function across scales.

I illustrate these two features of resilience by summarizing the effects of two functional groups on ecosystem dynamics and diversity in two different systems. The first summarizes the results of field and modeling investigations of the role of avian predators in the dynamics of spruce/fir forests of eastern North America. The second summarizes field and modeling studies of the role of mammalian seed dispersers in the tropical forests of East Africa.

Avian Predation of Insect Defoliators

The combination of within and cross-scale resilience allows an ecological function such as predation of keystone defoliators to be maintained despite sudden variations in resource availability or environmental conditions. It is well known that if a particular insect becomes more common, species that would not normally exploit it may switch to using it (Murdoch 1969). This occurs as the increasing relative abundance of a resource makes its utilization less costly. I argue that as resources become increasingly aggregated they become available to larger animals that are unable to efficiently exploit dispersed resources. This mechanism introduces strong negative feed-back regulation of resource abundance over a wide range of resource densities.

A well studied example of such a situation is found in the forests of New Brunswick, Canada. There outbreaks of a defoliating insect, spruce budworm (*Choristoneura fumiferana*), periodically kill large areas of mature boreal fir forest. The initiation of these outbreaks is controlled by the interactions between the slowly changing volume of a growing forest susceptible to budworm, the more quickly changing densities

and feeding responses of budworm's avian predators, and rapidly changing weather conditions (Clark and Holling 1979, Morris 1963).

Avian predation on budworm regulates the timing of budworm outbreaks by having its largest influence when budworm densities are low and forests stands are young. At least thirty-one species of birds prey upon budworm (Holling 1988). These bird species can be divided into five distinct body mass classes or body mass lumps, separated by gaps in their body mass distributions (Holling 1992a). The existence of budworm predators in these different body size classes makes the influence of predation robust over a broad range of budworm densities. This robustness emerges not because they exhibit redundant functional forms of predation, but rather because the scales at which predators are effective overlap, spreading their impact over a wide range of densities and spatial aggregations of budworms.

The predatory effectiveness of a bird is largely determined by its body size. The amount of food a bird can consume - its functional response (Holling 1959) - is a function of its body size, and a bird's search rate is greatly influenced by the scale at which it searches. Kinglets (*Regulus* sp.), Chickadees (*Parus* sp.) and Warblers (Emberizidae), small birds with an average body mass of about 10 g, concentrate on recognizing prey at the scale of needles or tufts of needles. Medium-sized birds focus their foraging upon branches, while larger birds such as Evening Grosbeaks (*Coccothraustes vespertinus*, 45 g) react to stand-level concentrations of food such as irruptions of seeds during good mast years or stand-level budworm outbreaks. The movement of birds over a landscape also is scaled to its body size. Larger birds forage over wider areas than smaller birds. Consequently, both the body mass of birds attracted to budworm and the distance from which they are attracted will increase as the size of local aggregations of budworm increase. A diversity of foraging strategies within and across scales thus provides a strong and highly resilient predation on budworm populations (Holling 1988), particularly at low densities of budworm within stands of young (< 30 years old) trees.

Members of functional groups maintain and therefore determine the resilience of ecosystems by spreading their influence over a range of scales. When a functional group consists of species that operate at different scales, that group provides cross-scale functional reinforcement that greatly increases the resilience of its function. This interpretation of the partitioning of ecological function suggests that what is often defined as redundancy, is not. The apparent redundancy of similar function replicated at different scales adds resilience to an ecosystem, because disturbances are limited to specific scales functions that operate at other scales are able to persist. The production of resilience by cross-scale functional diversity can be illustrated in a model of seed dispersal.

Mammalian Seed Dispersal in an African Tropical Forest

In Uganda's Kibale National Park, seed dispersers vary in size from small mice that range over areas of less than a hectare, to chimpanzees that range over tens of square kilometers. In a simple model of seed dispersal, when the area disturbed annually and the total amount of dispersal are held constant, the population growth rate of mammal-dispersed trees is determined by the distance over which its seeds are dispersed and the size of disturbance. A diverse set of dispersers, functioning at different scales, allows the tree population to persist despite disturbance. If, however, large, long-distance seed dispersers are absent the tree population declines, especially when large disturbances occur (Figure 7-10). Mammal-dispersed trees are more aggregated when dispersal is only by small mammals that move the seeds small distances. When disturbance sizes are large, this limited dispersal is unable to maintain populations of mammal dispersed trees (Peterson and Chapman, unpublished data).

Due to cross-scale functional reinforcement, and the non-linear fashion in which ecosystem behavior can suddenly flip from one set of mutually reinforcing structures and processes to another, the gradual loss of species in a functional group may initially have little apparent effect, but their loss would nevertheless reduce ecological resilience. This decrease in resilience would be recognized only at specific spatial and temporal scales, and

even then may be compensated for within or across scales. However, the ecosystem would become increasingly vulnerable to perturbations that previously could have been absorbed without changes in function or structure.

An indirect consequence of species loss is that it limits the potential number of ways a system can reorganize. Especially troubling is the possibility that the loss of large species that generate meso-scale ecological structure, such as moose (Pastor et al. 1993) or elephants (Dublin et al. 1990), may also eliminate forms of ecological organization. This may have occurred during the Pleistocene extinctions of mega-herbivores (Flannery 1994, Owen-Smith 1989, Zimov et al. 1995). These losses appear to be particularly difficult to reverse even with large scale ecological engineering projects (Flannery 1994).

Potential Tests of Cross-scale Resilience

The cross-scale model discussed above incorporates scale and resilience into a model of biodiversity and ecosystem function. The scaling relationships that it proposes can be tested through the analysis of empirical data, simulation, and field experimentation.

The proposition that ecological function is distributed across scales can be tested by analyzing the distribution of ecological function of a ecosystems species, and determining if species belonging to the same guild or functional group are dispersed across scales as the model predicts. The proposition that competition within a scale drives the dispersion of guilds across scales can be tested by determining if species are more evenly morphologically dispersed within a scale than across scales.

The model of cross-scale resilience can be tested by creating simulations that use various assemblages of species, divided by function and scale, to assess the resilience of a system to a fluctuating environment. I advocate two approaches, one focusing on the role of scale in function, and the other focusing on the plausibility of my model of ecological organization. The first approach is the one followed in the model of Kibale Forest described above. An ecological function that is performed by a number of species at

different scales can be modeled, and then this model may be perturbed by disrupting function and species composition to analyze ecological resilience. The idea that ecological resilience derives from cross-scale functional redundancy resulting from strong within-scale interactions can be tested by simulating an evolving community of organisms that compete for a set of resources. Allowing the resource preference and scale of the organisms to evolve allows one to evaluate the hypothesis that competitive interactions could lead to the distribution of similar function across scales and functional diversity within scales.

Finally, field experiments can be designed to test the response of species to resource availability at different scales. The model hypothesizes that limited, non-aggregated resources will be utilized by species that live at small scales (i.e., small birds such as warblers), while if resources are aggregated they will be used by larger species. The model predicts that resource utilization by animals is determined by the density of resources at their foraging scale. Since density is a scale-dependent measure, as resources are increasingly aggregated the model predicts that they will be used by larger animals.

These tests will provide partial, but incomplete evaluation of my model. To more fully test this theory, and better understand ecological resilience in general, requires long-term and extensive experiments that manipulate species composition and ecological structure at different scales.

Conclusions

I argue that ecosystems are usefully considered not as fixed objects in space, but as interacting, self-organized sets of processes and structures that vary across scales. This approach integrates existing models of the relationship between species and ecological function, and extends these models to incorporate scale. Ecological organization at a specific scale is determined by interactions between species and processes operating within that scale. Competitive interactions are strongest among species that have similar functions

and operate at similar scales. These interactions encourage functional diversity within a scale, and the distribution of ecological function across scales, enhancing cross-scale resilience. I suggest that it is possible to identify critical scales of landscape change that may be altered by species extinctions or introductions, or alternatively to identify which species may be affected by changes in landscape structure. Ultimately, I argue that understanding interactions between the scaling of species and scaling of ecological processes should be a central goal of ecology.

This model of cross-scale resilience has several consequences for ecological policy. The history of resource exploitation and development reveals that ecological crisis and surprises often emerge from unexpected cross-scale interactions (Holling 1986, Regier and Baskerville 1986). Management of natural resources often produces high short-term yields and, either purposefully or unintentionally, creates ecosystems that are less variable and diverse over space and time. Management channels ecological productivity into a reduced number of ecological functions and eliminating ecological functions at many scales. This simplification reduces cross-scale resilience, leaving systems increasingly vulnerable to biophysical, economic or social events that otherwise could have been absorbed – disease, weather anomalies, or market fluctuations. In Jamaica, for example, offshore fishing reduced the diversity of herbivorous sea urchins, leading to the replacement of coral reefs by macro-algae (Hughes 1994). Similarly, in New Brunswick, forestry eliminated landscape and age-class diversity leading to a long period of chronic spruce budworm infestation (Regier and Baskerville 1986). In both of these cases, management reduced the resilience of these ecosystems, leaving the existing people and biota vulnerable to abrupt ecological reorganization. To avoid repeating the ecological management disasters of the past, it is necessary that ecologists understand how the scale-dependent organization of ecosystems and functional reinforcement across scales combine to produce ecological resilience.

I propose that ecological resilience is generated by diverse, but overlapping, function within a scale and by apparently redundant species that operate at different scales. The distribution of functional diversity within and across scales allows regeneration and renewal to occur following ecological disruption over a wide range of scales. The consequences of species loss may not be immediately visible, but species loss decreases ecological resilience to disturbance or disruption. It produces ecosystems that are more vulnerable to ecological collapse, and reduces the variety of possible alternative ecological organizations. Ecological resilience must be understood if humanity is to anticipate and cope with the ecological crises and surprises that accelerating global change will bring.

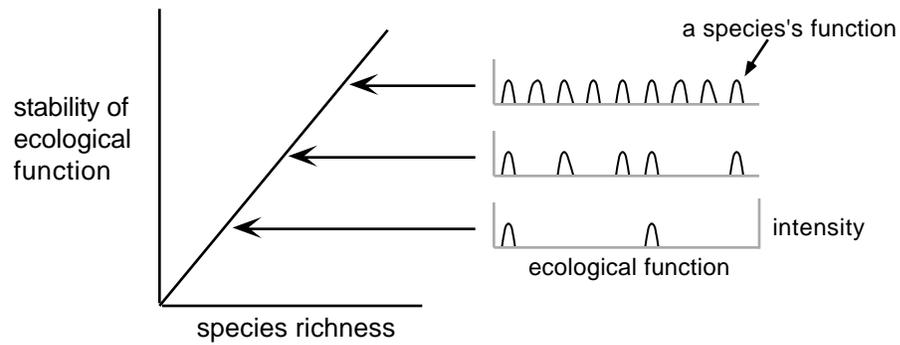


Figure 7-1. A representation of the Darwin/MacArthur model: Increasing species richness increases the stability of ecological function. This model, and the other models I discuss, implicitly represents species ecological function as occupying a portion of a multi-dimensional ecological function space that is analogous to niche space (MacArthur 1955). As species accumulate they fill this space. The width and height dimensions of the inset diagrams represent the breadth and intensity of a species' ecological function. This model assumes that function space is relatively empty and therefore species can be continually added to a community without saturating it. It also assumes that the strength and breadth of ecological functions does not vary among species.

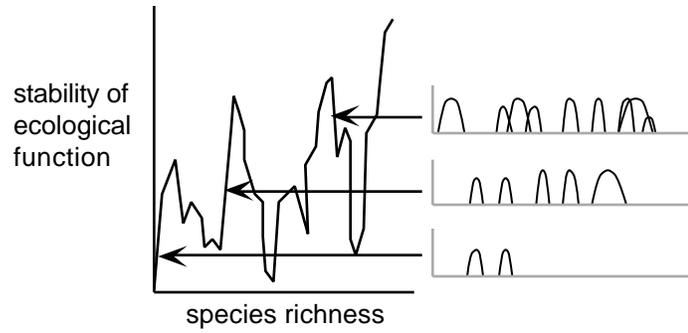


Figure 7-2. A representation of the Idiosyncratic model (Lawton 1994). In this model ecological function varies idiosyncratically as species richness increases. This model argues that the contribution of each species to ecological function is strongly influenced by interactions among species. Therefore, the effects of the introduction or removal of species to an ecosystem can be either insignificant or major, depending upon the nature of the species introduced or removed, and the nature of the species with which it interacts.

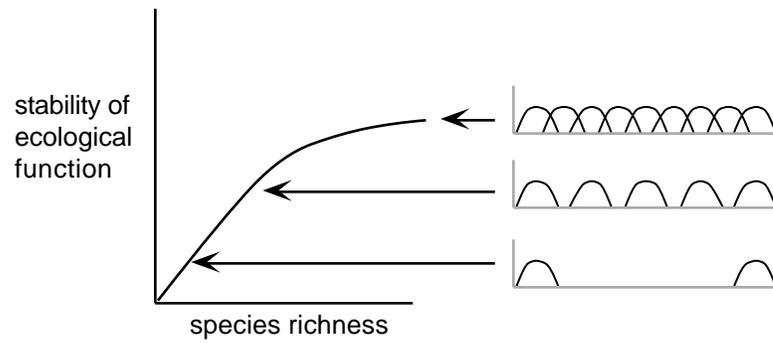


Figure 7-3. The 'rivet' model of ecological function (Ehrlich and Ehrlich 1981), presumes that ecological function space is relatively small. Therefore, as species are added to an ecosystem, their functions begin to overlap or complement one another. This overlap allows ecological function to persist despite the loss of a limited number of species, since species with similar functions can compensate for the elimination or decline of other species. However, the increase of stability gained by adding new species decreases as species richness increases, and functional space becomes increasingly crowded.

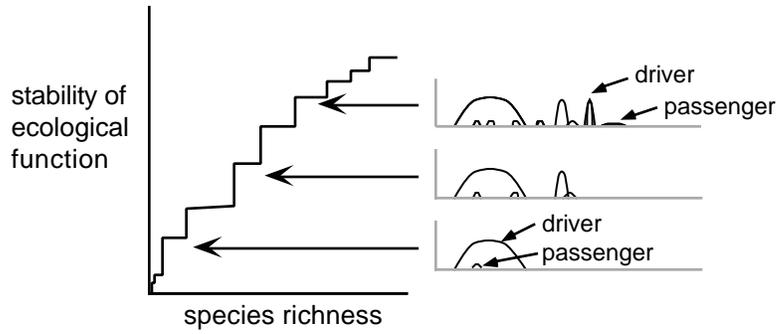


Figure 7-4 Walker's 'drivers and passengers' model of redundant ecological function (Walker 1992, Walker 1995), proposes that ecological function is unevenly distributed among species. Drivers have a large ecological impact, while passengers have a minimal impact. The addition of drivers increases the stability of the system, while passengers have little or no effect.

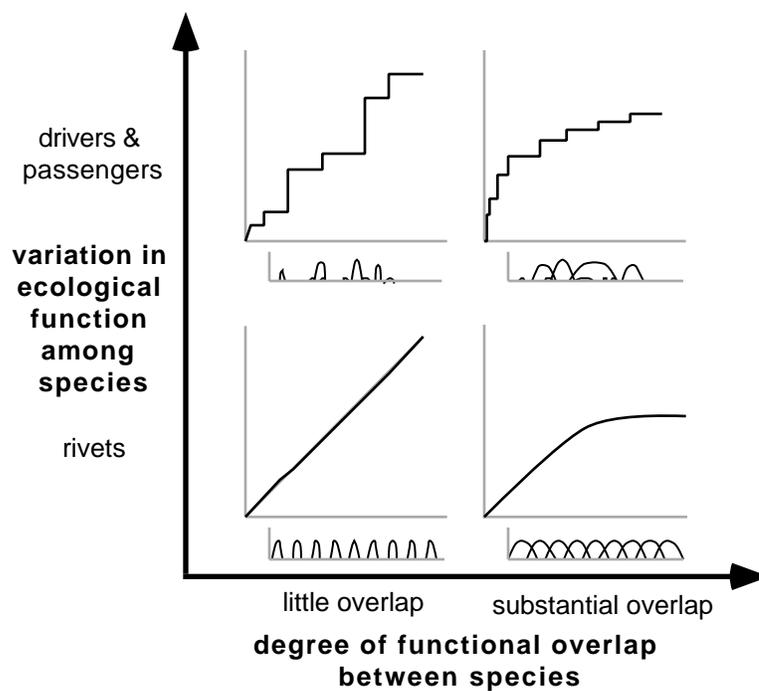


Figure 7-5. The relationship between stability and species richness varies with the degree of overlap that exists among the ecological function of different species, and the amount of variation in the ecological impact of species ecological function. Overlap in ecological function leads to ecological redundancy. If the ecological impact of different species is similar they are 'rivets', while if some species have relatively large ecological impact they are 'drivers' and others are 'passengers'.

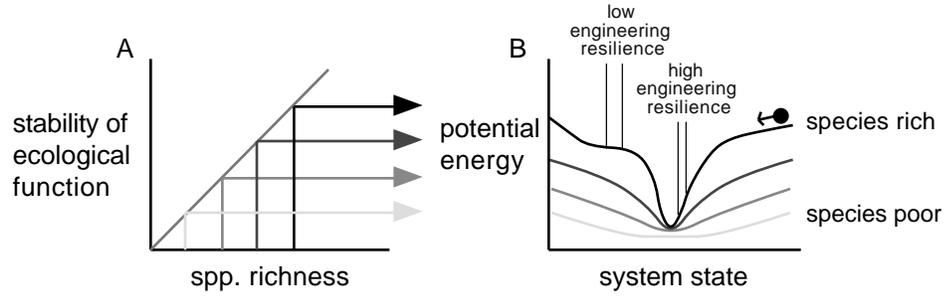


Figure 7-6. The relationship between stability and species richness can be represented by a set of stability landscapes. The dynamics of a system are expressed by a landscape, and its 'state' is represented by a ball that is pulled into pits. Different landscape topographies may exist at different levels of species richness. In this model, the stability of a state increases with the depth of a pit. Zones of the stability surface that have low slopes have less engineering resilience than areas that have steep slopes.

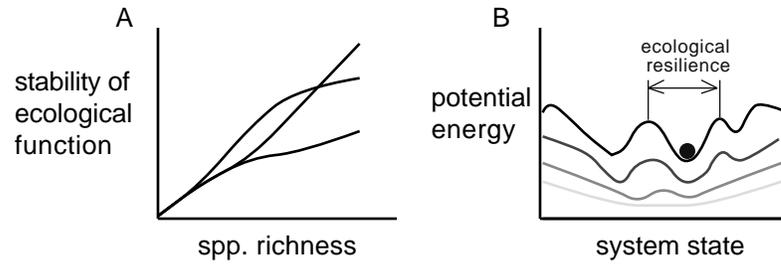


Figure 7-7. A system may be locally stable in a number of different states. Disturbance which moves the system across the landscape, or slow systemic changes which alter the shape of the landscape both drive the movement of a system between states. The stability of a state is a local measure. It is determined by the slope of the landscape at its present position. The resilience of a state is a large-scale measure, as it corresponds to the width of the pit the system is currently within.

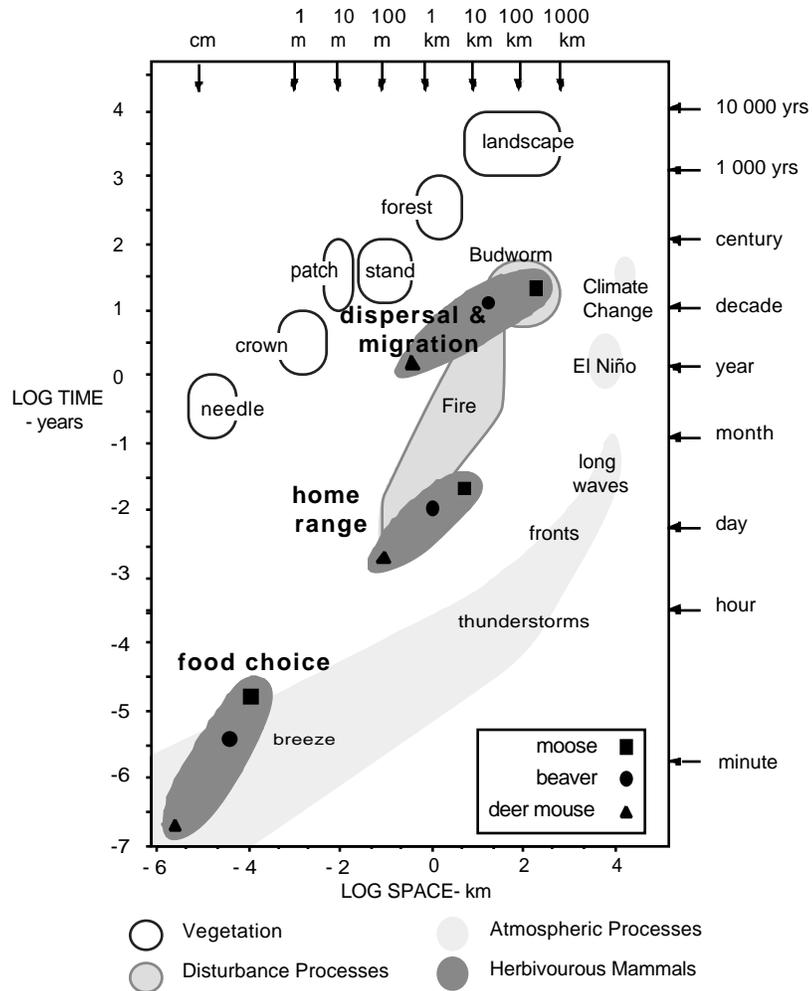


Figure 7-8. Time and space scales of the boreal forest (Holling 1986), and their relationship to some of the processes which structure the forest. These processes include insect outbreaks, fire, atmospheric processes, and the rapid CO₂ increase in modern times (Clark 1985). Contagious meso-scale disturbance processes provide a linkage between macro-scale atmospheric processes and micro-scale landscape processes. Scales at which deer mouse, beaver and moose choose food items, occupy a home range, and disperse to locate suitable home ranges vary with their body size (Holling 1992a, Macdonald 1985, Nowak and Paradiso 1983). These processes link meso- and micro-scales.

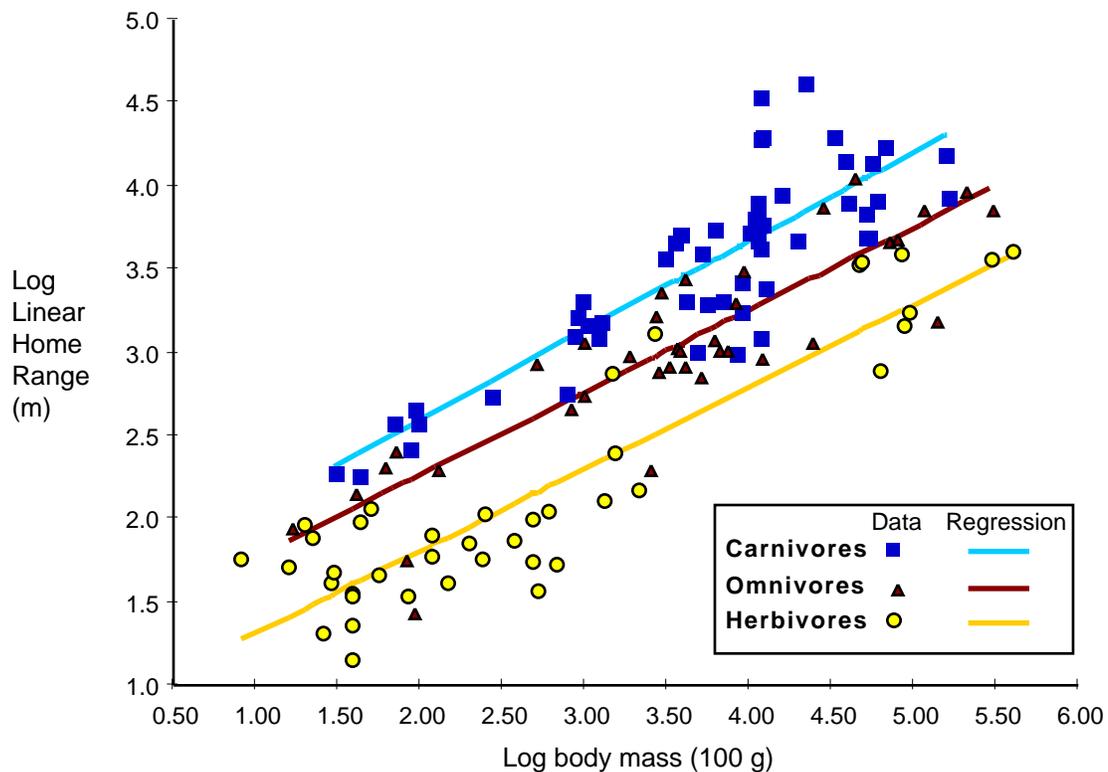


Figure 7-10. Regression of log body mass against linearized home range area (the square root of home range area), for several carnivore, omnivore, and herbivore species. Data from Holling (1992). The regression line for the carnivores was $\text{Log}(\text{HR}^{1/2}) = 0.535 \cdot \text{Log}(\text{BodyMass}) + 1.515$ ($n=53$, $R^2 = .724$). The regression line for the omnivores was $\text{Log}(\text{HR}^{1/2}) = 0.496 \cdot \text{Log}(\text{BodyMass}) + 1.262$ ($n=37$, $R^2 = .766$). The regression line for the herbivores was $\text{Log}(\text{HR}^{1/2}) = 0.493 \cdot \text{Log}(\text{BodyMass}) + 0.810$ ($n=40$, $R^2 = .820$). The slopes of the regression lines are not significantly different.

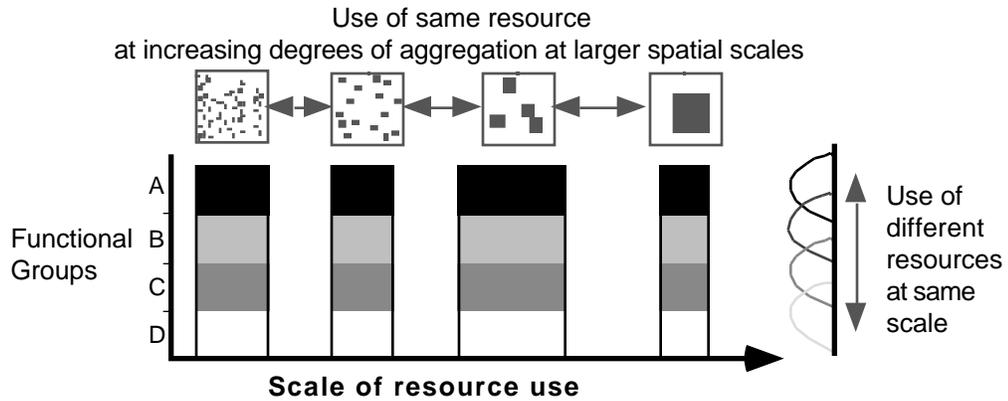


Figure 7-10. The relationship between species' scale and membership in a functional group proposed by the cross-scale resilience model. Different species use resources at different spatial and temporal scales. Members of a functional group use similar resources, but species that operate at larger scales require those resources to more aggregated in space than species that operate at smaller scales. Within scales the presence of different functional groups provides robust ecological functioning, while replication of function across scales reinforces ecological function. The combination of a diversity of ecological function at specific scales, and the replication of function across at a diversity of scales, produces resilient ecological function.

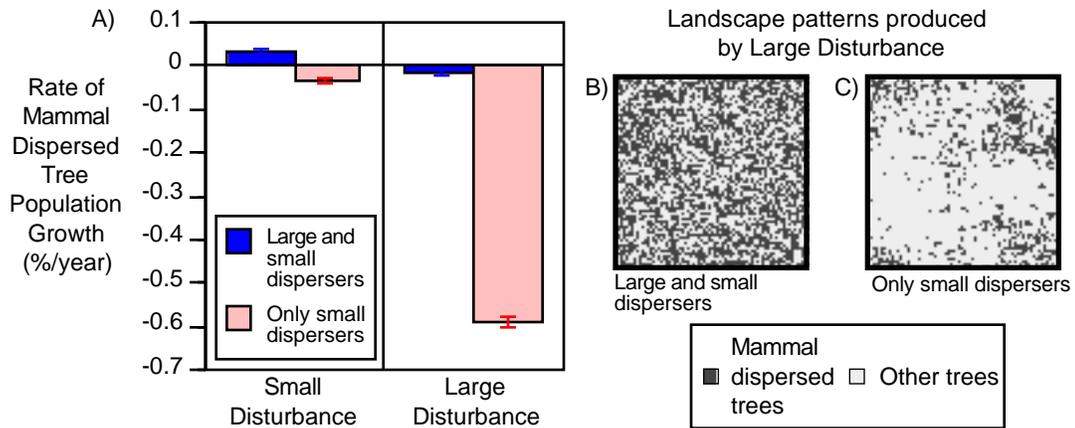


Figure 7-11. Results from a simple model of forest dynamics and seed dispersal by mammalian frugivores in Kibale National Park, Uganda. A) Forest disturbance size interacts with the disperser community to determine the success of mammal-dispersed trees. When both large and small seed dispersers are present the mammal-dispersed trees are resilient to both small and large disturbance events. When large dispersers are absent, mammal-dispersed trees slowly decline following small disturbances, but rapidly decline following large disturbances. Large differences in landscape pattern can be seen after 200 years when the forest is subjected to large disturbances, between (B) a forest containing both large and small seed dispersers, and (C) a forest with only small seed dispersers. The model demonstrates that seed dispersal at a diversity of scales is more resilient to disturbance than seed dispersal over small scales. The model assumes lottery colonization of disturbed sites (Hubbell 1979) by either mammal-dispersed or other tree species (Chapman and Chapman 1996). Mammal dispersal is assumed to be constant with the proportion performed by various animals varying. Dispersal range was estimated for large mammals (1010 m for *Cercocebus albigena*, and 1930 m for *Pan troglodytes*), and small mammals (355 m for *Cercopithecus mitis*, 245 m for *Cercopithecus ascanius*, and 30 m for various Rodentia) (Chapman, unpublished data). The disturbance rate was held constant at 1.5%/yr in the model, with only the spatial scale of disturbance varying between the small (0.04 ha) and large (10.24 ha) disturbance regimes.

SUMMARY

Earlier, I argued that anthropogenic global change appears to be of the same magnitude as Earth's previous periods of revolutionary ecological change. However, the biosphere and humanity are probably in a more vulnerable state during this transition than during past transitions, due to the increasing proportion of the Earth's biosphere that is used by humanity. The likelihood that humanity's domination of the biosphere is reducing the resilience of the Earth to anthropogenic global changes underscores the importance of analyzing the resilience of Earth's biosphere.

Translating Across Scales

Assessing the impact of change on ecosystems requires the use of scaling methods, but these scaling methods may not apply in an altered world. Translating either data or understanding across scales is often difficult, because dynamic hierarchical ecological organization emerges from ecological interactions. The resilience of ecological organization to changes in key processes determines the situations in which scaling methods apply, require adjustment, and break down. Ecological change that alters the resilience of an ecosystem may modify its scaling relationships, reducing or expanding the scale range over which a relationship applies, as shown by the analysis of changes in avian predation on budworm.

By focusing upon the cross-scale processes that create, maintain, and destroy ecological organization a richer set of scaling relationships can be explored. By analyzing the cross-scale organization of ecosystems, methods for translating across scales can be developed. These scaling methods can be improved by considering the dynamics of cross-

scale organization. By perturbing dynamic ecological models, the effects of change on scaling methods can be calculated, and the limits of a system's resilience predicted.

Floridan Fire Management

I used the concept of ecological resilience to construct a set of alternative models of fire dominated longleaf pine savanna that were used to explore the ecological behavior of the managed forest of Eglin Air Force Base in northwest Florida. I developed an empirically based, technique for assessing ecological resilience in response to specific disturbance regimes, or in this case, managed disturbance regimes. This work illustrated the importance of spatial dynamics in shaping a landscape. It also illustrated that management of such heterogeneous, scale variant ecosystems, that does not adapt to temporal and spatial heterogeneity, will fail. However, when management adapts to landscape pattern, it increases the number and diversity of management strategies that can be utilized.

Boreal Forest Fires and Forest Resilience

Severe frequent fires are the dominant processes determining the landscape structure the boreal forest. Topography, vegetation, and climate interact with fire to determine the frequency and spatial configuration of fires. However, when the fire-forest system possesses 'memory' it is possible for fire and forest interactions to produce a forest landscape characterized by semi-persistent, self-maintaining, homogenous patches that are renewed rather than destroyed by fire, in the absence of any external heterogeneity.

The self-organizing forest landscape that emerges from the interaction of forest processes and fire provides the forest landscape with an ability to adapt to change while maintaining its organization. The landscape heterogeneity tends to constrain fire to the inside of patches. This constraint causes landscape change to occur in local asynchronous lurches of landscape transformation. However, if the limits of landscape resilience are

exceeded the self-organized pattern of the landscape is broken down by many large fires. The breakdown of resilience occurs abruptly and regionally. Large fires disrupt existing forest processes, such as seed dispersal and inter-species relationships, while also providing opportunities for the emergence of new forest structuring processes, such as insect outbreaks.

The results of this research have several implications for a world facing potential climate change. Firstly, it is important to understand the relationship between the speed of climate change and forest processes. Gradual climate change will produce gradual forest change through small spatially distributed fires. However if climate changes rapidly, large fires could produce abrupt change across broad regions of the boreal forest. Secondly, if large fires do occur it is possible that new ecological communities will emerge from their ashes. These new communities may be structured by unexpected sets of ecological processes.

Contagious Disturbance

Based upon the empirical models of chapters 4 and 5, I developed a general model of contagious disturbance and defined disturbance agents, stress accumulation and release, chain reactions and evolutionary epidemics as four key sub-types of contagious disturbance. I have identified initiation, reproduction, contagion, virulence, and recovery as the five key properties of a contagious disturbance regime, and shown how a change in the relationship of these variables alters the behavior of contagious disturbances. These models provide general insights into the consequences of specific ecological organizations, allowing qualitative predictions to be made about the behavior of a poorly understood disturbance process. Such disturbances can be classified based upon the relationships among their defining rates. These models can provide Null models for the investigation of contagious disturbances in specific ecosystems. In addition these models provide a

framework for constructing more realistic alternative models of specific disturbance processes.

Cross-scale Resilience

In chapter 7 I develop a model of cross-scale resilience. I propose that ecological resilience is generated by diverse, but overlapping, function within a scale and by apparently redundant species that operate at different scales. The distribution of functional diversity within and across scales allows regeneration and renewal to occur following ecological disruption over a wide range of scales. The consequences of species loss may not be immediately visible, but species loss decreases ecological resilience to disturbance or disruption. It produces ecosystems that are more vulnerable to ecological collapse, and reduces the variety of possible alternative ecological organizations. Ecological resilience must be understood if humanity is to anticipate and cope with the ecological crises and surprises that accelerated global change will bring.

The model of cross-scale resilience has several consequences for ecological policy. The history of resource exploitation and development reveals that ecological crisis and surprises often emerge from unexpected cross-scale interactions. Management of natural resources often produces high short-term yields and, either purposefully or unintentionally, creates ecosystems that are less variable and diverse over space and time. Management channels ecological productivity into a reduced number of ecological functions and eliminating ecological functions at many scales. This simplification reduces cross-scale resilience, leaving systems increasingly vulnerable to biophysical, economic or social events that otherwise could have been absorbed – disease, weather anomalies, or market fluctuations. To avoid repeating the ecological management disasters of the past, it is necessary that ecologists understand how the scale-dependent organization of ecosystems and functional reinforcement across scales combine to produce ecological resilience.

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BIOGRAPHICAL SKETCH

Garry Peterson was born in 1969 in Vancouver, British Columbia, Canada. He lived in Lions Bay, a small village on the coast of Howe Sound just north of Vancouver, and grew up in the temperate rainforest that covers the mountains north of Vancouver, and along the rocky coasts of its fjords. While, he attended school in the south of England for one year, he spent the vast majority of his early years living in Lions Bay and attending school at Gleneagles Community School and Hillside Secondary School in West Vancouver.

In 1986, he moved to Ontario to study Systems Design Engineering at the University of Waterloo. During this time at Waterloo, he worked as a co-op student at several Canadian high technology companies. In 1989, he was an exchange program with Tottori University in Japan. The study of systems theory lead Garry to attempt to model the adaptive behavior of animals and the dynamic organization of ecosystems. These activities combined with a number of courses in Environmental Science convinced Garry that after he received a first class honors B.A.Sc. in Engineering in 1991, he would attend graduate school to study theoretical applied ecology. This interest lead Garry to move south to the University of Florida to work with H.T. Odum and C.S. Holling, two scientists who combine a strong systems theoretical approach to ecology with an equal devotion to focus on applied questions

Garry entered the Masters program of Environmental Engineering Sciences in 1991 and in 1994 he completed his Masters thesis on spatial forest-fire interactions in the boreal forest, and then entered the Ph.D. program in the department of Zoology to continue and expand upon his work with C.S. Holling.