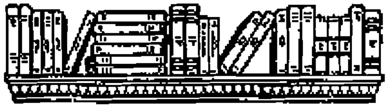

COMPLEXITY THEORY FOR A SUSTAINABLE FUTURE

Edited by Jon Norberg and Graeme S. Cumming

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ENVIRONMENTAL ASYMMETRIES

Graeme S. Cumming, Grenville Barnes, Jane Southworth

THE WORLD IS essentially uneven. We exist in an environment that continually presents us with change and variation in multiple manifestations; sunlight and shadow, day and night, hills and valleys, town and country. Such systematic unevenness is an important property of complex systems, from the large to the small. In this chapter we explore the idea of environmental symmetry and its converse, environmental asymmetry. We start by defining what we mean by symmetry and demonstrating how symmetry concepts in a variety of guises have been widely applied in the biological and social sciences. We then consider the mechanisms that produce environmental asymmetry, the consequences of asymmetry, and the potential for interactions between different kinds of asymmetries in landscapes. We argue throughout that asymmetries are integral to self-organization in complex systems and are consequently of high importance for understanding complex system dynamics.

DEFINING ENVIRONMENTAL SYMMETRY

Although it is widely applied in physics, the current scientific usage of symmetry is unfamiliar to many people in other disciplines. We use symmetry in its modern group-theoretic sense to mean invariance of group members under a set of specified rotations or reflections (Brading and Castellani 2003). This definition includes the traditional concept of symmetry that most of us were taught at school; for example, a highly symmetrical human face is invariant under reflection in the vertical plane and an unblemished daisy can be considered invariant under rotation on the axis of its stem. However, the group-theoretic definition also extends the traditional concept of symmetry by including other kinds of transformation. Symmetry in this broader context is associated with equality of the parts with respect to the whole in the sense of an interchangeability of parts; it implies 'a unity of different and equal elements' (Brading and Castellani 2003).

Symmetries can be exact, approximate, or broken (Castellani 2003). Exact symmetries are unconditionally valid; approximate symmetries are only valid under certain conditions; and broken symmetry in our context implies a deviation from some theoretically plausible or expected symmetrical state. Symmetry breaking does not imply that no symmetry remains in the system, but rather that the state of the system is characterized by a lower symmetry than would be present where symmetry has not been broken (Castellani 2003). We use the term *asymmetry* to describe situations in which symmetry has been broken, making no distinction between asymmetry and alternative terms such as *nonsymmetry* and *dissymmetry*. In group-theoretic terms, symmetry breaking means that the initial symmetry group is broken into one (or several) of its subgroups. Asymmetries thus arise from symmetries rather than the other way around. In a system that contained absolute symmetry, nothing would exist; absolute symmetry means a complete lack of differentiation (Castellani 2003). Simon (1962) distinguished between hierarchical systems that are 'decomposable' (i.e., into discrete levels and subunits) and those that are not; highly symmetrical systems are generally more decomposable than highly asymmetrical systems and hence tend to be easier to model and to understand analytically. Nonetheless, many real-world hierarchical systems in which symmetry has been broken fall into Simon's 'nearly decomposable' category, implying that reasonable mathematical approximations of system dynamics can be achieved.

Since the beginnings of modern science, the homogeneity and isotropy of physical space and time have been taken for granted in most areas of research (Brading and Castellani 2003). A representation of space that uses a grid of coordinates or cells without attaching attributes to any location is symmetrical; a cell in any one location could be interchanged with any other. In a typical neutral landscape model in which cells are assigned a value of 0 or 1 using a random number generator, the resulting landscape is symmetrical in the sense that the overall properties of the landscape are invariant to spatial transforms. A landscape consisting of patches of three different types can be considered approximately symmetrical if random interchanges of patches between locations have little or no effect on the overall properties of interest within the landscape. By contrast, a landscape in which patches of the same three types are arranged along a gradient is asymmetrical. Note that the patches themselves are, by definition, expected to be symmetrical at a finer scale of analysis; when defining a patch, we assume that areas within the patch are interchangeable.

Symmetry questions come to the fore in the consideration of scale. Under a scaling transformation, symmetrical systems will be those that are fully or approximately scale invariant. For example, the relationship between log body mass and log metabolic rate in mammals is largely symmetrical; it can be described using a straight line (Peters 1983). Spatial analyses also use scaling relationships to assess how system properties change with changes in dimension. For example, the fractal dimension of a stream network can be described as the scaling function of the slope of the relationship between the number of cells containing part of the network and the dimension of the cells (Tarboton, Bras, and Rodriguez-Iturbe 1988). A straight line with a constant slope (and hence an isotropic fractal dimension) indicates symmetry in scale. Unsurprisingly, most real-world patterns are not self-similar across multiple scales, and hence can be termed asymmetrical. Scale in complex systems is discussed further in chapter 9.

Heterogeneity refers to the differentiation of landscape elements (at any given scale) in space. Variation, in its commonest usage, is effectively heterogeneity in time. Asymmetry has much in common with heterogeneity but is not identical to it. Heterogeneity implies differentiation of system components but not necessarily asymmetry. Asymmetry refers only to systematic differentiation—so in thinking about landscape asymmetry we focus on the role of nonrandom spatial and temporal differentiation (heterogeneity, variation) in ecological systems. The importance of differentiation of individual system components is discussed in more detail in the next chapter. Classical examples of landscape asymmetry include such things as the systematic arrangement of different vegetation types down an elevation gradient (spatial asymmetry), successional change in a mosaic of abandoned fields (temporal asymmetry), and continental rainfall patterns over a decade (spatial and temporal asymmetry).

Although we may appear to be proposing a novel application of the term *asymmetry* in relation to social-ecological systems, we are simply recognizing previous research on asymmetries and recasting it in a slightly more general framework. As we now demonstrate, symmetry concepts have a long history of application in many disciplines, including ecology, medicine, and economics.

APPLICATIONS OF SYMMETRY CONCEPTS IN THE STUDY OF COMPLEX SYSTEMS

Assumptions about symmetry and symmetry breaking are widely applied outside of physics, even though the philosophical basis for these assumptions is not always made transparent. We have grouped the applications of symmetry-related concepts into three different categories.

ASYMMETRY AS A CONSEQUENCE OR A RESPONSE

Asymmetry is often seen as a consequence of nonrandom variation or a form of environmental response to process variation. In this context it is used consistently with the definitions given earlier in this chapter; an implicit assumption that symmetry is to be expected means that asymmetries demand explanation. For example, historical variations in the formation of oceanic crusts and the movements of tectonic plates produce asymmetries in bathymetry and elevation (Borisova and Kazmin 1993; Pushcharovsky and Neprochnov 2003; Toomey et al. 2002). Historical changes in the local environment and historical measurement inaccuracies can produce asymmetries in buildings and consequently are of interest to architects (Cummings, Jones, and Watson 2002; Lemoine 1986; Middleton 1989; Wilson Jones 2001). In studies of plant communities, attempts have been made to explain asymmetry in vegetative structures that include leaf canopies and branch structures ('crown asymmetry') as well as root systems (Logli and Joffre 2001; Rajaniemi 2003; Schwinning and Weiner 1998; vanderMeer and Bongers 1996). Asymmetries in the paired wing and tail feathers of birds and the organs or body sizes of other animals are used as indicators of quality or malfunction in studies of sexual selection and nutrition (Ahtiainen et al. 2003; Buyanovsky 1996; Van Dongen, Lens, and Molenberghs 1999; Vollestad, Hindar, and Moller 1999). Asymmetries in foraging patterns may be a response to environmental heterogeneity or a consequence of self-organization (Portha, Deneubourg, and Detrain 2002). In businesses asymmetries in returns may result from differences in past activity and the ensuing difference in activity costs (Acemoglu and Scott 1997). And in studies of the human brain, asymmetry in neuron activity has been suggested as a diagnostic feature of schizophrenia (Gruzelier et al. 1999). Asymmetry is referred to less explicitly in scaling studies, but deviations from expected scaling relationships typically demand explanation. For example, in the highly symmetrical relationship between the hoof area and the body mass of ungulates, the larger than expected hoof size of the camel is explained as an adaptation to walking on sand (Cumming and Cumming 2003) and in studies of urban boundaries, changes in fractal dimension have been proposed as indicators of societal mechanisms (Brown and Witschey 2003; Chen and Zhou 2003; White and Engelen 1993; Yizhaq, Portnov, and Meron 2004). Asymmetry may also be seen as an integral part of scale-independent processes, as described in studies of fractal branching patterns in arteries (Schreiner et al. 1997; van Beek 1997).

SYMMETRY AND ASYMMETRY AS EMERGENT PROPERTIES OF COMPLEX SYSTEMS

Both asymmetry and symmetry have been viewed as emergent properties of complex systems. In bee and ant colonies, asymmetries arise in the division of labor; symmetry breaking occurs when the numbers of foragers visiting two equally profitable food sources diverge (de Vries and Biesmeijer 2002; Portha, Deneubourg, and Detrain 2002). In mathematical models of the process of evolution, accumulated random changes ('noise') may generate system bifurcations and, hence, sympatric speciation (Stewart 2003). A similar symmetry-breaking response is visible in the difference in oil demand between developed and less developed countries (Dargay and Gately 1995).

ASYMMETRY AS A CAUSE OR DRIVER OF PATTERN

Asymmetry has been portrayed as a driver of pattern in a number of different contexts. In business the role of asymmetries of information and other resources in determining business success has received considerable attention (Amir and Wooders 1998; Cooper, Downs, and Patterson 2000; Miller 2003). For example, asymmetries in brand switching may explain aspects of purchasing behavior (Wedel et al. 1995). Similarly, asymmetries in the colony sizes of ants can be key drivers of the outcome of competition (Palmer 2003). While the generation of asymmetries by landscape processes has been relatively well explored (e.g., Turner, Gardner, and O'Neill 2001), the converse (i.e., the feedback from pattern to process) is considered less frequently.

As this categorization shows, the relevance of asymmetry in complex systems can vary; asymmetry may be an integral component of a process, an emergent property that arises through the action of one or more processes, or an inevitable (and possibly trivial) response to a process. In each of these cases, however, asymmetry provides us with useful information about the relationship between pattern and process in the system of interest.

THE RELEVANCE OF ENVIRONMENTAL ASYMMETRY FOR STUDIES OF COMPLEX SYSTEMS

Landscapes at any scale are composed of numerous locations in space. These locations can usually be considered as a distinct group or set, even if the sole commonality that they share is their proximity to one another. Consideration of landscapes as symmetrical or asymmetrical groups leads to an interesting perspective on the relationships between structure and function. Pierre Curie, working on symmetry and symmetry breaking in crystals in the year 1894, initiated the empirical study of asymmetry by asking which phenomena can occur in a physical medium that has specified symmetry properties. What is the importance of the relationship between the symmetry of a physical medium and the symmetry of the phenomenon occuring within it? Investigating this question led Curie to the conclusion that if a phenomenon is to occur in a medium, the symmetry of the medium must be lowered to the symmetry of the phenomenon by the action of some cause. Curie's conclusion implies strongly that symmetry breaking, or the formation of asymmetry, is what "creates the phenomenon" (Castellani 2003).

Our central argument through the rest of this chapter is that Curie's conclusion has a broad and general application in complex systems; environmental asymmetry is essential for the maintenance of the majority of ecological, sociological, and economic processes that are of interest in understanding sustainability. To demonstrate the importance of asymmetry in complex systems, we discuss a number of specific, detailed examples. These examples are intended to explore the proximate causes of environmental asymmetry, some of its consequences, and the ways in which different kinds of asymmetries (spatial, temporal, and scale related) may interact to affect system dynamics.

CAUSES OF ENVIRONMENTAL ASYMMETRY

Environmental asymmetry arises from processes that break environmental symmetry. If the degree of environmental symmetry is a description of pattern, symmetry is altered by the action of process. Phrased differently, we can say that systematic variation in the environment arises from three main sources: 1. processes that occur at different rates, frequencies or magnitudes in different locations (e.g., deposition of sand on coastlines), 2. processes that are constrained by existing environmental variation (e.g., fire will only burn where the fuel load is sufficient), and 3. processes of equivalent rates and magnitudes that occur out of spatial or temporal synchrony with one another (e.g., succession in a patch mosaic). Note that this summary is similar to, but slightly different from, Levin's (1976) classification of the causes of spatial heterogeneity in ecosystems as local uniqueness, phase differences, and dispersal. We assume that in the absence of differential process action, environments would remain symmetrical; environmental asymmetry demands explanation, environmental symmetry does not.

Broadly speaking, the processes that break symmetry in the environment may come from one of three causes: abiotic drivers (including geology, climate, or other purely physical processes), biotic nonhuman drivers (including interactions between organisms or between organisms and the abiotic environment), or anthropogenic drivers (including humans and the social and economic systems that they create). Asymmetries can also be explained as consequences of disturbances (such as fires, floods, and hurricanes) and historical variation in symmetry-breaking processes.

A considerable amount has been written on the causes of asymmetry in landscapes (reviewed in Turner, Gardner, and O'Neill 2001). Indeed, this has been one of the central themes of ecology. There have been innumerable studies of the relationship between the abiotic environment and the biotic environment, including the degree to which ecological communities are determined by their abiotic environment, the role of biotic processes in modifying or moderating the abiotic environment, and the variables that maintain spatial patterns in the environment. Consideration of spatiotemporal scaling relationships has long been considered one of the more important challenges facing ecology (Levin 1999). The relationships between anthropogenic, biotic, and abiotic variables have also been widely studied. The study of primarily anthropogenic causes of asymmetries in landscapes (such as political ecology and tenure systems) has been less extensive, but is a rapidly growing field.

As these comments should make clear, a thorough summary of the causes of asymmetry in landscapes would require book-length treatment. In this chapter we are more interested in the consequences of environmental asymmetry, to which we now turn, and the interactions and feedbacks between different kinds of environmental asymmetries.

CONSEQUENCES OF ENVIRONMENTAL ASYMMETRY

Environmental asymmetries are central to a large number of ecological processes. They may cause changes in community structure and create gradients and edges that drive the movements of water, minerals, and organisms through landscapes. By generating potential differences between areas they effectively create flows and act as channels that regulate flows once they are in motion. The influence of environmental asymmetries on movement is obvious in the case of a weary hiker traversing a mountainous landscape, trying to select the safest route that offers little resistance to her movements. Just as she skirts the rocky peaks of hills and follows the river in the valley until a suitable crossing point is reached, so the edges created by systematic variation in the environment can constrain and direct movement patterns of a multitude of species.

One of the most important environmental asymmetries in the abiotic environment is the change in available energy with changing latitude from the equator to the poles. This gradient is associated with systematic variation in rainfall and temperature and has been implicated as a major driver of patterns of biodiversity in ecosystems (Allen, Brown, and Gillooly 2002; Brown 1995). At a finer scale the elevation gradient that ranges from hills to lowlands has a profound structuring effect on plant and animal communities through its influences on local climate, substrate, and the availability of water. The communities of many organisms, from trees to rodents and birds, are stratified according to the elevation at which they occur (Lomolino 2001; Whittaker 1960). Streams and rivers in temperate environments show predictable transitions of substrates and biota from highlands to lowlands (Vannote et al. 1980); coastal vegetation composition and structure are largely determined by the environmental gradients imposed by dune formation (or erosion) and the influence of winds and mists from the sea; and, in the Sahel, distinct banding patterns in stands of shrubs and trees (the so-called tiger bush) arise in arid areas as a consequence of asymmetries in subsurface water flows (HilleRisLambers et al. 2001; Rietkirk et al. 2000).

Asymmetries in the social environment are also important. As societies have shifted from a basis of agriculture to industry to information, there has been a growing recognition of the importance of information as a resource (Toffler 1980). Information is the basic ingredient in decision making related to planning, conservation, development, and a host of daily decisions made by individuals. In developing countries, characterized by large asymmetries in wealth distribution, there are corresponding information asymmetries. For example, people with wealth and power have access to information on land markets, prices, and land regulations, while the poor do not have the resources to obtain this information. Solutions to the problem of inequity in some nations have given rise to the advancement of transparent and accessible property systems where all sectors of society have equal access. In this sense, information may be regarded as a public good (Deininger 2003) that promotes greater economic and social symmetry among rich and poor.

Environmental asymmetries occur in both space and time. In variable environments, such as African savannas, the spatial distribution of resources varies in a predictable manner through the course of a single year. The biomass of large herbivores in a given area is strongly correlated with rainfall (Coe, Cumming, and Phillipson 1976). Du Toit (1995) states that 'the primary ecological determinants of large mammal communities in African savannas are rainfall and soil nutrients, since these determine the quantity and quality of food available to large herbivores.' Among the notable consequences of asymmetrical seasonal and spatial variation in resources are the broad-scale migrations of a wide range of animals. Migratory species in Africa include birds, ungulates, carnivores, insects, fishes, and fruit bats (e.g., Berger 2004; Thirgood et al. 2004; Thomas 1983; Trinkel et al. 2004; Walther, Wisz, and Rahbek 2004; Ward et al. 2003). Many human societies, particularly those in arid environments, have also developed behavioral patterns (such as migration and food storage) that help them to cope with spatiotemporal asymmetries in the environment.

In each instance people and animals follow a gradient of resource availability that coincides with the timing of rainfall and related vegetation patterns. Asymmetries in vegetation and rainfall patterns in the Sahel can result in outbreaks of migratory locusts (Despland, Rosenberg, and Simpson 2004); in the Serengeti and Kalahari systems wildebeeste and other ungulates travel long distances each year to find water and grazing (Fryxell, Wilmshurst, and Sinclair 2004); and spatiotemporal variations in forest fruit abundance are thought to drive the annual migration of the straw-colored fruit bat *Eidolon helvum* from the Congo forests south into Zambia (Richter and Cumming 2006). Many birds migrate between Africa and Europe, including wading birds, raptors, and songbirds (Meyburg, Paillat, and Meyburg 2003; Walther, Wisz, and Rahbek 2004). In other parts of the world the seasonal migrations of wading birds, caribou, fruit bats, and monarch butterflies are all driven largely by environmental asymmetries, supporting our contention that symmetry breaking is an important driver of processes in terrestrial landscapes. The same principle is applicable in the oceans; whales, manatees, and turtles undertake seasonal migrations along resource and temperature gradients, and many fish species respond to temporary 'loopholes' of high resource availability and/or low predator abundance in the ocean, using these ephemeral resource asymmetries to boost recruitment in a given year (Bakun and Broad 2003; Best and Schell 1996). Migrant workers and refugees respond to their social-ecological environment in much the same way, finding secure or resource-rich pockets and escaping bad conditions through movement.

In addition to regulating communities and driving movements of animals, environmental asymmetries can cause particular areas to become net exporters or importers of organisms, water, or other substances such as minerals and wastes. In many cases ecological and human communities are maintained by subsidies or flows of substances that have their origin in other areas (Polis, Power, and Huxel 2004). Source and sink areas, defined as net importers or exporters of organisms respectively, are largely determined by asymmetries in environmental quality. In other instances environmental asymmetries lead to a continual flow of resources from one area to another. A classic example is the dependence of many large cities on processes that occur in the upper catchments of their water sources. For instance, the town of Melbourne in Australia obtains its drinking water from the Murray-Darling basin. Water salinity in many catchment areas is increasing as a consequence of salty groundwater and the rise in the water table that has resulted from clearing of native vegetation for sheep production (Keating et al. 2002; MDBC 1999). The state government has been forced to impose a salt credit system on smaller municipalities upstream, where the farmers in each subcatchment can only export a certain amount of salt and must modify their agricultural activities accordingly.

Depending on their nature and their context, environmental asymmetries will play a central role in creating edges and channels within landscapes. Edges occur where two distinct habitat types meet; for example, at the interfaces between forest and grassland, water and land, road and grassland, or rock and soil. The proportion of edge habitat in a landscape may be increased by anthropogenic activities (Cadenasso et al. 2003). Edges will often occur where strong environmental asymmetries exist, because edges are created by processes that show the kind of differential localization or concentration that is anticipated in an asymmetrical landscape. For example, the actions of weathering and subsurface processes on asymmetries in rock formations create cliff edges; water concentrates in the lower parts of landscapes to create the land-water edge; and fires burn only in areas with adequate fuel loads, creating patches in different successional stages. Once created, edges may serve as channels or corridors for the movements of organisms and their propagules (e.g., Machtans, Villard, and Hannon 1996).

INTERACTIONS AND FEEDBACKS BETWEEN ASYMMETRIES

In most environments multiple processes act to create multiple asymmetries. Different asymmetries will not necessarily follow the same gradient in space and time. For example, soil properties are influenced by weathering processes, and the climate that produces weather changes systematically with latitude. Some areas have been glaciated; other areas have not. Where weathering processes act to make poor soils poorer or rich soils richer, climatic and soil fertility asymmetries will align; where weathering makes poor soils richer or rich soils poorer, they will be antagonistic.

Asymmetry in land tenure regimes can have profound consequences for related social, economic, and political processes. Flying over the continental United States for the first time, one is immediately struck by the unusual symmetry in the landscape (figure 1.1).

The landscape resembles a quilt composed of square patches (one mile by one mile) bounded by county and state roads all running east-west or north-south. This symmetry reflects the fundamental principles on which the U.S. was built. The public land survey system that originally divided the public domain into these squares was designed by Thomas Jefferson around 1780. He believed that a democracy could only be built through dividing the land equally and creating a large middle class of yeoman farmers (Linklater 2002). Only through such symmetry would the social and economic asymmetries of feudal Europe be avoided. Where land distribution was and continues to be extremely asymmetrical, such as Latin America (figure 1.1b),

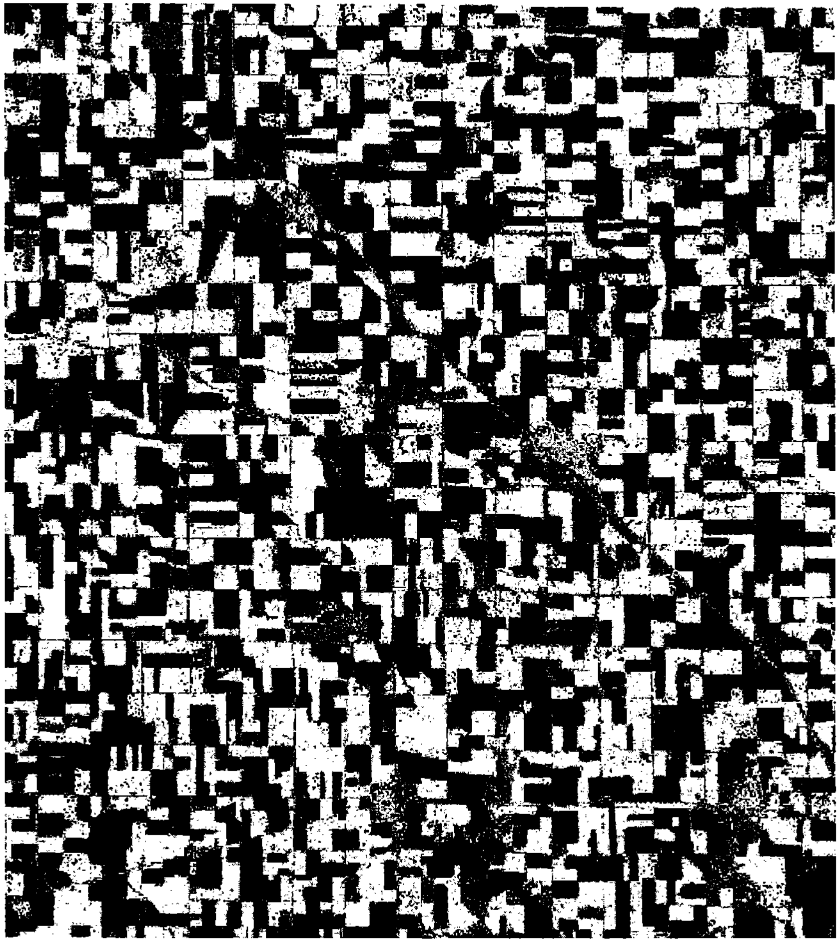

FIGURE 1.1. Two landscapes with very different levels of symmetry in land development patterns. (a) A relatively symmetrical landscape in the United States Midwest (Indiana). Note how, in this classification scheme, the different elements of this landscape are highly interchangeable; random rearrangements of patches would have little effect on its overall structure or function. (b) Asymmetrical land development patterns in Latin America (Bolivia).

there can be severe political, social, and economic consequences (Thiesenhusen 1995). The Jeffersonian ideals contrasted with the experience in Latin America illustrate the strong correlation between symmetry in land distribution, on the one hand, and political, social, and economic symmetry on the other hand.

Although many of the classical examples of landscape asymmetries are passive, in the sense that gradients are perceived to exist in the environment

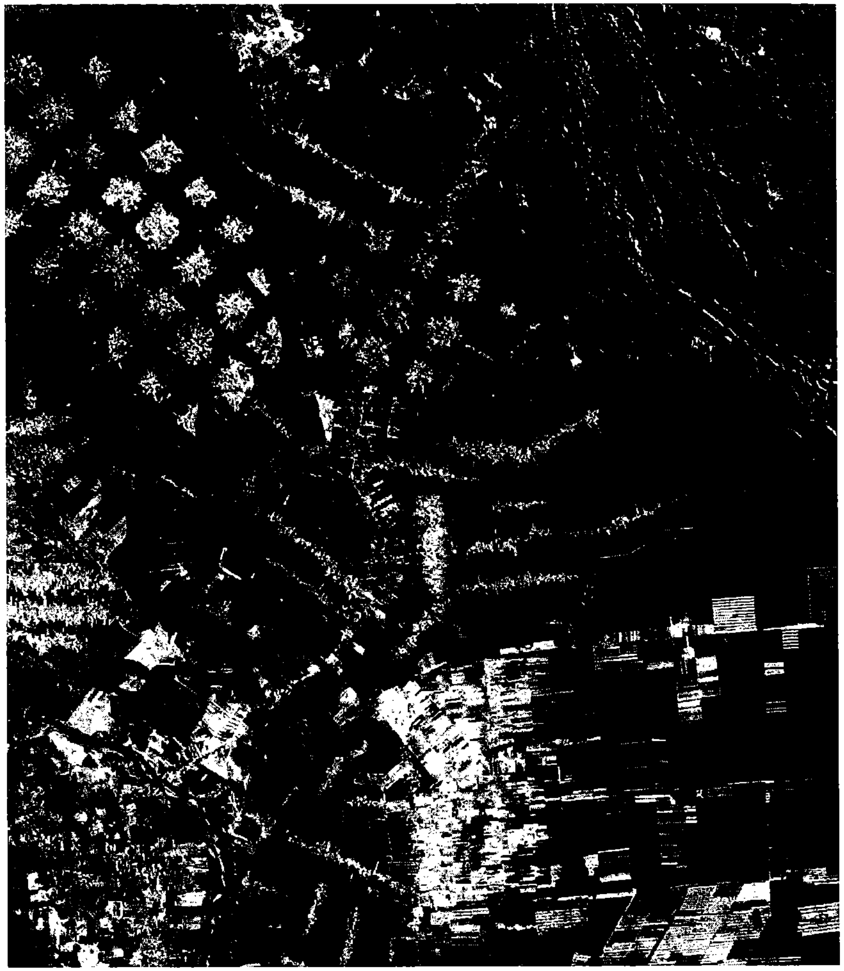

FIGURE 1.1. *continued.*

but to play a relatively static ecological role, asymmetries may be dynamic and variable. Dynamic analysis of landscape asymmetries is relatively recent in ecology, and there are few well-documented case studies to draw on in this context. In theory, however, some of the most interesting dynamics associated with asymmetries could occur if asymmetrical patterns and related processes are self-organizing through space and time. In this context, we take self-organization to mean that landscape patterns might influence the processes that produce or sustain them, resulting in a dynamic feedback between pattern and process. For example, fire is an essential component of vegetation dynamics in Alaska (Kasischke, Christiansen, and Stocks 1995). The different albedos (reflectance values) of spruce forests (fire susceptible) and tundra (fire sustained) in Alaska result in different temperature balances and air circulation patterns over forests and tundra respectively. Circulation patterns influence the formation of clouds and the incidence of thunderstorms. Thunderstorms in turn produce lightning, which is the main cause of fires in these areas. A situation thus exists in which the properties of the landscape can become self-maintaining; the fire-dependent, reflective tundra experiences a higher incidence of lightning strikes than the fire-susceptible, more absorptive spruce forest (Bonan, Chapin, and Thompson 1995; Higgins, Mastrandrea, and Schneider 2002; Kasischke, Christiansen, and Stocks 1995; Lafleur and Rouse 1995). Both habitat types influence the local disturbance regime in such a way as to maintain beneficial conditions for their own continuation. A similar kind of feedback between vegetation and fire, although with a different underlying mechanism, has been documented in Florida (Peterson 2002).

In other cases there will be feedbacks between different sets of asymmetries in the same environment. Feedbacks occur when an effect influences the magnitude or rate of its cause. For instance, asymmetries in fruit production can drive the movements of seed dispersing animals; and the movements of seed dispersers will influence the spatial distribution of fruit production. If fruit production and seed dispersal are both asymmetrical and enhance one another, then local amplifications of asymmetries may make existing environmental gradients steeper. In practice this dynamic could lead to a clustered distribution of fruiting trees and the formation of a fruit-based spatial network, with clusters of fruit trees as nodes and its edges defined by the pathways traveled by seed dispersing agents as they move along paths or flyways between nodes. Asymmetries in spatial patterns and plant-animal interactions will also occur at different scales within the same system (e.g., Jordano 1994; Olesen and Jordano 2002) and may interact with one another across scales, resulting in complex hierarchical dynamics. For example, rainfall and elevation asymmetries may influence seed dispersers directly through their effects on energy expenditure and ease of movement or indirectly via their effects on fruit and other resources.

In general, the potential for landscape self-organization (including, but not limited to, bifurcations and the formation of alternate stable states) arises whenever asymmetries exist in a linked pattern-process relationship. This observation suggests that there may be a relationship between spatial and temporal variation. If the action of a given process varies in both space and time in response to asymmetries, then areas of higher spatial heterogeneity may be more variable in time than areas of lower spatial heterogeneity. In other words, habitats that show higher local heterogeneity may also exhibit faster turnover times in such things as vegetation types and nutrient cycling. To return to the fire example, areas in which fuel loads build up in a more variable manner will experience spatial differences in the intensity and duration of fires, resulting in an even more heterogeneous postfire landscape that may be prone to a second fire a few years later and a resulting shift in the patch mosaic of grassland, shrubs, and forest. By contrast, where fuel

TABLE 1.1. Some Examples of Self-Organizing Environmental Asymmetries

PATTERN ASYMMETRY	SELF-ORGANIZING PROCESS OR MECHANISM.
Fuel load	Hotter fires in areas with higher fuel loads favor rapidly regenerating/pyrophilic species; heterogeneity begets further heterogeneity.
Edge effects	Edges facilitate edge-specific processes that create further edges, as in subdivision of properties or ramification of a road network.
Fruit production	Frugivory and seed dispersal by frugivores. High local abundance of fruit attracts more seed dispersers to region.
Frequency of lightning-ignited fires	Differing albedos between adjacent dark and light vegetation types result in differential, self-sustaining lightning and fire regimes.
Property sizes and associated income differences	Ownership of more resources generates greater wealth and allows purchase of more land.
Rainfall, transpiration, and vegetation	Higher rainfall leads to more vegetation, greater transpiration, water vapor, rainfall; reduced transpiration leads to reduced water vapor and rainfall.
Grazing lawns	Dung deposition favors production of high-nutrient grasses, which in turn attract large herbivores that deposit more dung.
Access to information	Individuals or firms who have access to more and better information have a competitive advantage over those lacking such information, which allows them to generate further information more easily than their competitors.
Elevation	Erosion. Steeper areas erode more rapidly, sediment is deposited in lower areas, the earth's surface becomes flatter, and asymmetry is reduced over time.

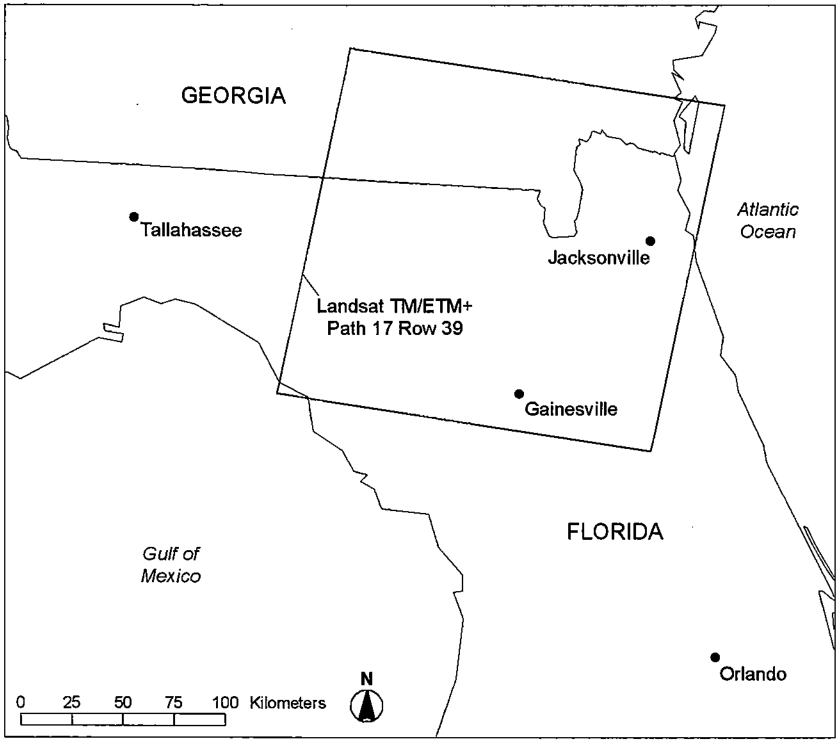

FIGURE 1.2. Location of our study site in north central Florida. The black square indicates the footprint of the Landsat images used in the analysis.

loads are homogeneous, a single hot fire will reset a successional state in such a way that rates of landscape change will be slow for decades.

To the best of our knowledge, the question of causal feedbacks between spatial and temporal variation in landscapes has not been explicitly considered. We have recently undertaken a study of interactions between spatial and temporal asymmetries in the landscape of north central Florida (Southworth et al. 2006). We discuss this analysis in some detail because it provides an interesting example of how the interactions between spatial and temporal asymmetries can be considered across multiple scales.

The analysis used six Landsat images (1985, 1989, 1992, 1997, 2001, 2003) of a study area centered around Gainesville, Florida (figure 1.2). After applying standard processing methods, Normalized Difference Vegetation Index (NDVI) images (Jensen 1996) were created for each year to provide a continuous vegetation/land cover data set that varies in both space and time. NDVI is an index of primary production. For the analysis of asymmetries, the continuous nature of NDVI data offers an appealing alternative to the categorical data sets that are used in standard land cover maps (Southworth, Munroe, and Nagendra 2004). NDVI images were created for all image dates. To obtain images that showed the change through time at each location, we simply subtracted the earlier images from the later images. For example, subtraction of NDVI values for the year 2001 from NDVI values for the year 2003 produces a difference image for the period 2001 to 2003. Difference images were calculated for each of the lag times in the data set. We then used a moving window of different sizes (3 × 3, 10 × 10, 25 × 25, 50 × 50, 100 × 100, and 250 × 250 pixels) to calculate local spatial variation in both the original data and the difference images. The variance (sigma) of all NDVI values in the window is assigned to the central pixel; as the window moves through the data set, each location in the image is assigned a variance value.

To summarize, by this point in the analysis the imagery-derived measures represent the spatial variation in primary production (at a single time) and the change in spatial variation through time, at multiple spatial scales. The next step in the analysis is to regress our data for spatial variation (termed *S* for variation through Space) on our values for the change in spatial variation (termed *T* for spatial variation through Time) at multiple scales. If spatial and temporal variation are interacting in a landscape, we would expect to see a predictable relationship between *S* and *T*. For example, greater values of *S* would lead to greater values of *T* if pattern-process amplification occurs, resulting in a significant regression with a positive slope.

The regression analysis was undertaken for each window size and each pair of image dates. As a null model, we randomized the 1997 and 2001 images and repeated the analysis for these data and the difference image 2001–1997. The data were randomized in such a way as to maintain the same statistical properties as the original images while destroying any spatial asymmetries inherent in the data by rearranging the locations of data points. The values of the regression parameters for the S-T relationship change with scale, and there is no single ‘correct’ scale for this analysis, so a scaling component is integral to the study. Of particular interest was the question of whether there were predictable, scale-related changes in the slope and intercept of the regressions. Somewhat to our surprise, we found that several predictable relationships emerged. The strength of the relationship between spatial variance and temporal variance was parabolic, peaking

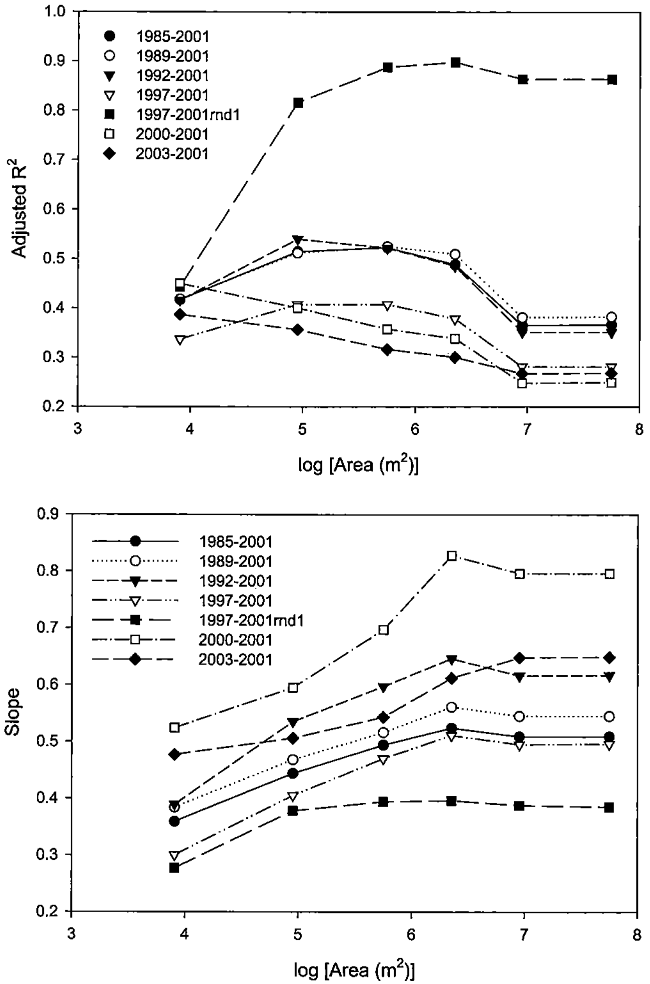

FIGURE 1.3. Scatterplots showing (a) the strength of the relationships and (b) the slope of a linear regression of temporal variation on spatial variation for a time series of NDVI data for north central Florida.

at a window size of 10x10 pixels (350 × 350m or 12.25ha; figure 1.3). The slope of the relationship between spatial variance and temporal variance was highest at a kernel size of 50x50 pixels (1750 × 1750m or 306.25ha). The ratio of temporal variance to spatial variance increased with the spatial scale of analysis. At smaller spatial scales, the spatial variation was greater than the temporal variation. With increasing spatial scale we also found increasing temporal variance. As the scale of analysis increased, the difference between the actual and random data increased, and so spatial variation explained less and less temporal variation than the null model (figure 1.3).

This analysis begs the question of mechanism, but it does demonstrate that spatial and temporal variation are closely related to one another in the landscape of northern Florida and that consideration of interacting asymmetries across multiple scales may ultimately allow us to derive relationships that have predictive power for landscape change. Many remote sensing studies are critiqued on the basis of a lack of transferability across space and time and a lack of consistent relationships (Foody and Atkinson 2003). This kind of research, in which general system properties such as heterogeneity and asymmetry are considered, has the potential to generate relationships that are both useful and transferable between different landscapes.

To what extent are the same methods applicable to the study of asymmetries in social systems? We applied our approach to a land tenure data set that showed ownership in a small subset of the same north Florida landscape. Ownership was recorded every five years over a thirty-year time horizon (figure 1.4; Barnes et al. [2003]).

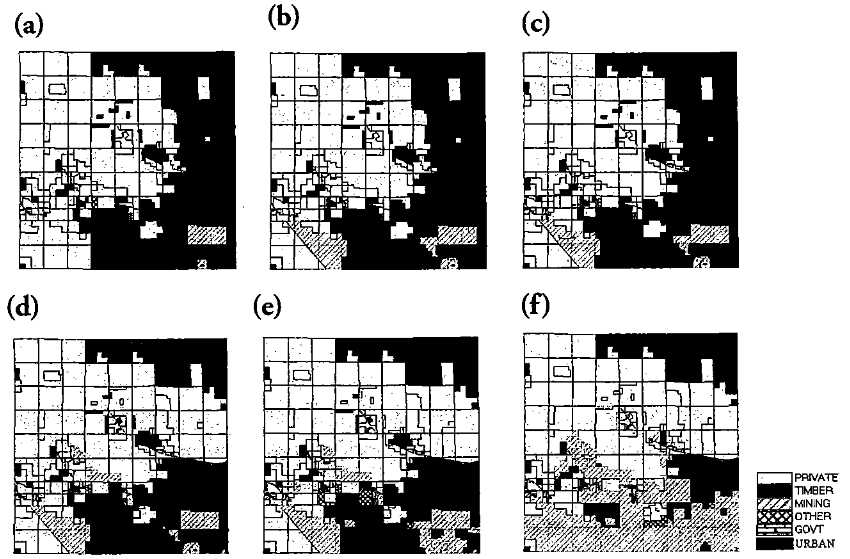

FIGURE 1.4. Maps showing changes in land ownership for Hamilton area. Each square (section) is approximately one square mile.

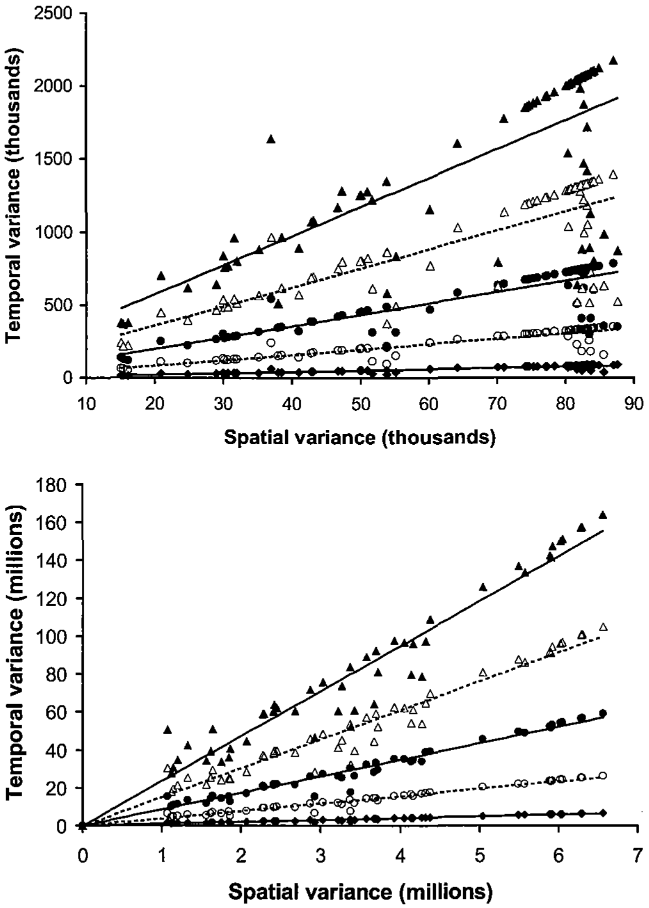

FIGURE 1.5. Plots showing the relationship between spatial and temporal variation in the Hamilton data in moving windows at different scales. (a) 1 × 1 section, (b) 3 × 3 sections, (c) 5 × 5 sections, (d) 7 × 7 sections. In each case the slope of the line increases with time relative to a 1974 baseline. Filled diamond, 1975–1980; hollow circle, 1975–1985; filled circle, 1970–1990; hollow triangle, 1975–1995; filled triangle, 1975–2000.

In this instance there were even stronger relationships between spatial and temporal variation, particularly over long time horizons (figures 1.5 and 1.6). The slope of the regression relationship becomes steeper over longer time horizons and shows no indication of leveling off, suggesting that the temporal scale at which land ownership changes is longer than the thirty-year scale of this data set. Taken in context, the results imply that changes in ownership are most likely to occur in areas where there are already multiple owners. These areas will often be at the edges of existing properties. This conclusion makes sense in light of the mechanisms that are likely to lead to subdivision of a property; it is considerably more likely that someone will sell land that is at the periphery of their existing plot than in the center, and it is also more likely that an owner who is interested in expanding their property in a rural setting will focus their attention on purchasing blocks of land that are adjacent to their current holdings.

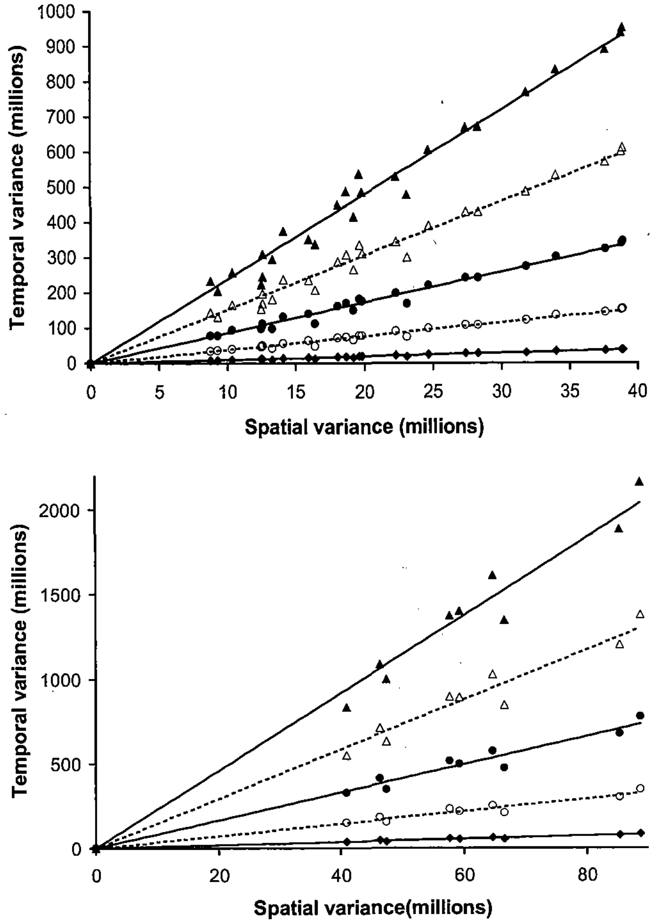

FIGURE 1.5. *continued.*

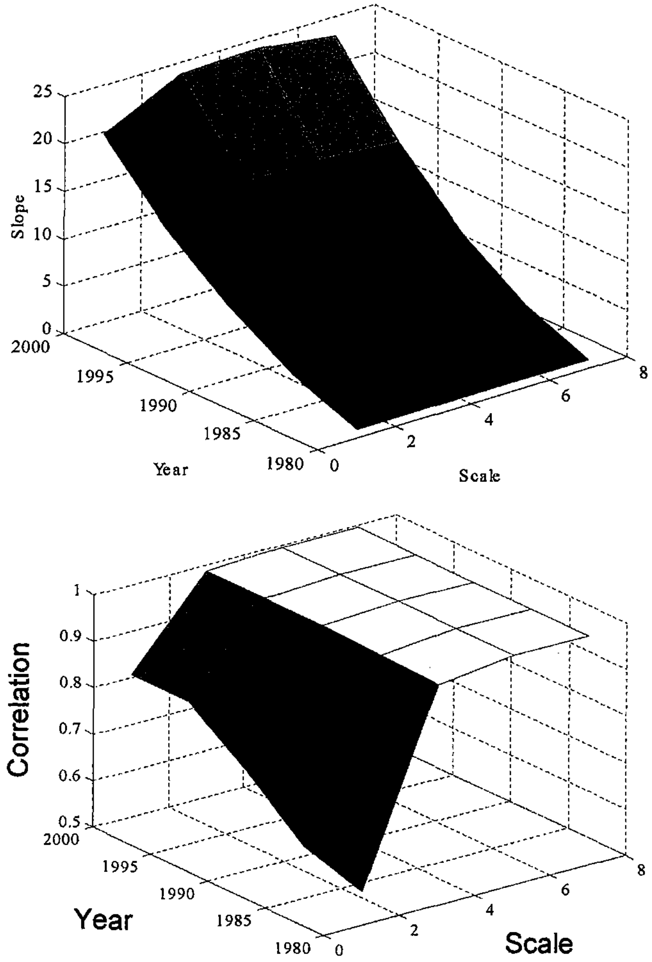

FIGURE 1.6. Three-dimensional plots showing the relationship between scale, time step relative to a 1975 baseline, and (a) slope of the linear regression of temporal variation on spatial variation or (b) the strength of the correlation between spatial and temporal variation, as measured by the r^2 statistic.

Land tenure data are often considered using GINI indices. The classical GINI index is defined as

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}|x_i^n - x_j|}{2n^2\bar{x}}$$

where x is an observed value, n is the number of values observed, and x bar is the mean value of all x. The GINI index is a simple measure of asymmetry for a particular data set. It has been widely used in national-level analyses of poverty and human health. The index in formula 1 is often depicted as a Lorenz curve, in which the cumulative proportional increase in income (or other quantity of interest) per person, sorted from smallest to largest, is plotted against the number of people. A straight diagonal line (x = y) for the Lorenz curve indicates a completely equitable distribution of resources, because each additional person adds an equivalent amount of wealth, health, or land. The area under the Lorenz curve is the GINI index, which ranges from 0 to 1 and is highest when equity is lowest. In this particular example we considered GINI indices for the areas of different parcel sizes. Land parcels were grouped together into one of six different ownership types (private, timber, mining, government, urban, other; see figure 1.5) at each of five different scales (subparcel, parcel, 3 × 3 parcels, 5 × 5 parcels, and 7 × 7 parcels), and GINI indices were calculated for the resulting area data. Although there is little change in the GINI index for the study area over the time period of this study, the scale-dependency of the GINI index is quite obvious (figure 1.7). If land ownership were a contentious issues in this system, we could easily envisage that asymmetries in parcel size could drive social or economic processes (such as stock theft, the formation of lobby or special interest groups, or price wars in the local market) at some scales but not at others, depending on the alignment between the scales at which land tenure occurs and the scales at which socioeconomic processes occur.

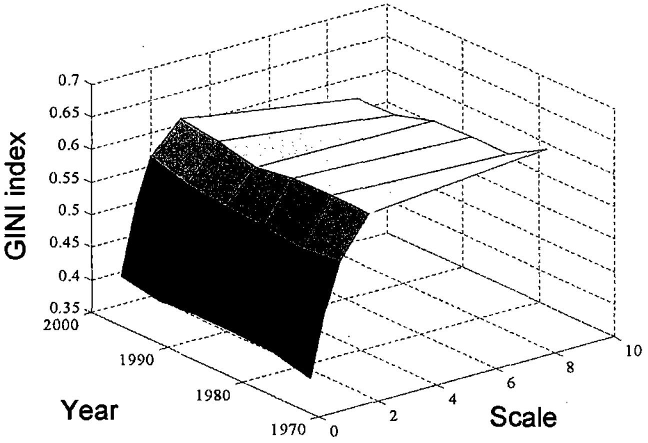

FIGURE 1.7. Three-dimensional plot showing the scale dependency (*x*) of the GINI index (*z*), a simple measure of asymmetry, at different time steps (*y*).

GENERAL DISCUSSION AND CONCLUSIONS

Asymmetries in landscapes arise from a number of different processes across a wide range of different scales. Once asymmetries have arisen, they may either facilitate their own continuation or may gradually disappear. Many kinds of landscape asymmetry have arisen from slowly-acting, broad-scale processes and patterns such as continental drift and the size and shape of the earth. Other kinds of landscape asymmetry have been generated relatively recently by organisms and their interactions with their environment. Landscapes provide the context for evolution, and organisms have shaped their environments as they have evolved (Levin 1999). More recently, and more rapidly, humans have had a huge and disproportionate effect on landscape pattern and process. Each of these different drivers of change has created its own set of feedbacks and influences on the arrangement of heterogeneity within landscapes. To fully understand the consequences of landscape asymmetries, we thus need to understand not only the ways in which organisms and human societies respond to slowly changing asymmetries (such as elevation and rainfall gradients or cultural norms) but also the different kinds of feedback that serve to stabilize system dynamics or propel them along novel trajectories.

Levin (1999) argues that some kind of selection process, by which individual system components are removed or enhanced, is a central attribute of complex adaptive systems. Landscape asymmetries can be considered as gradients that serve to drive such processes, as discussed in later chapters in this volume. However, it is important to note that asymmetries themselves may also be the subject of selection or enhancement by both internal and external processes. Although the broader landscape can be viewed as a passive and fairly constant context in which other ecological and sociological processes occur, it is also in constant flux at one scale or more.

Research on the role of landscape asymmetries in CASs is currently in its infancy. Most ecological research has focused on organismal responses to asymmetries. A small but growing body of research exists on the dynamics of complex systems, particularly in regard to the broadscale feedbacks between different kinds of system components (e.g., Higgins, Mastrandrea, and Schneider 2002; Scheffer et al. 2001). One of the steps that will be necessary to relate this research to environmental asymmetries is to make it more explicitly spatial so that we can understand the context dependence of different kinds of environment-organism feedbacks. Further analysis of land tenure regimes and how these change through time is also a fertile area for expanding our understanding of complex social-ecological systems, as is the study of self-organization and the mechanisms that lead to landscape change. The growing fields of metapopulation and metacommunity analysis may contribute usefully to this agenda, particularly if synergies can be found between metacommunity studies, land use/land cover studies, and studies of the higher-level properties of landscapes (such as landscape diversity, permeability, and fractal dimension). It seems to us that the concept of environmental asymmetry, as defined in this chapter, has much to offer the further theoretical and empirical development of complex systems theory and its applications to real-world problems.

REFERENCES

Acemoglu, D., and A. Scott. 1997. "Asymmetric Business Cycles: Theory and Time-Series Evidence." *Journal of Monetary Economics* 40:501–533.

Ahtiainen, J.J., R.V. Alataio, J. Mappes, and L. Vertainen. 2003. "Fluctuating Asymmetry and Sexual Performance in the Drumming Wolf Spider Hygrolycosa Rubrofasciata." *Annales Zoologici Fennici* 40:281–292.

Allen, A.P., J.H. Brown, and J.F. Gillooly. 2002. "Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule." *Science* 297:1545–1548.

Amir, R., and J. Wooders. 1998. "Cooperation vs. Competition in R and D: The role of stability of Equilibrium." *Journal of Economics-Zeitschrift Fur Nationalokonomie* 67:63–73.

Bakun, A., and K. Broad. 2003. "Environmental 'Loopholes' and Fish Population Dynamics: Comparative Pattern Recognition with Focus on El Nino Effects in the Pacific." *Fisheries Oceanography* 12:458–473.

Barnes, G., A. Agrawal, L. Genc, B. Ramachandran, V. Sivaraman, B. Pudi, M. Binford, and S. Smith. 2003. "Developing a Spatio-temporal Cadastral Database Using County Appraisal Data from Northern Florida." *Surveying and Land Information Science* (special cadastral issue) 63:243–251.

Berger, J. 2004. "The Last Mile: How to Sustain Long-Distance Migration in Mammals." *Conservation Biology* 18:320–331.

Best, P.B., and D.M. Schell. 1996. "Stable Isotopes in Southern Right Whale (Eubalaena Australis) Baleen as Indicators of Seasonal Movements, Feeding and Growth." *Marine Biology* 124:483–494.

Bonan, G.B., F.S. Chapin, and S.L. Thompson. 1995. "Boreal Forest and Tundra Ecosystems as Components of the Climate System." *Climatic Change* 29:145–167.

Borisova, I.A., and V.G. Kazmin. 1993. "Dependence of the Ocean Depth on the Age of the Sea-Floor in the North-Atlantic in Connection with History of Continental Break-Up." *Okeanologiya* 33:915–923.

Brading, K., and E. Castellani. 2003. "Introduction." In K. Brading, and E. Castellani, eds., *Symmetries in Physics: Philosophical Reflections*, 1–18. Cambridge: Cambridge University Press.

Brown, C.T., and W.R.T. Witschey. 2003. "The Fractal Geometry of Ancient Maya Settlement." *Journal of Archaeological Science* 30:1619–1632.

Brown, J.H. 1995. *Macroecology*. Chicago: University of Chicago Press.

Buyanovsky, A.I. 1996. "Bimodality and Asymmetry in Size-Frequency Distribution of the Young Mussels Mytilus Trossulus (Bivalvia, Mytilidae)." *Zoologichesky Zhurnal* 75:978–984.

Cadenasso, M.L., S.T.A. Pickett, K.C. Weathers, S.S. Bell, T.L. Benning, M.M. Carreiro, and T.E. Dawson. 2003. "An Interdisciplinary and Synthetic Approach to Ecological Boundaries." *BioScience* 53:717–722.

Castellani, E. 2003. "On the Meaning of Symmetry Breaking." In K. Brading and E. Castellani, eds., *Symmetries in Physics: Philosophical Reflections*, pp. 321–334. Cambridge: Cambridge University Press.

Chen, Y.G., and Y.X. Zhou. 2003. "The Rank-Size Rule and Fractal Hierarchies of Cities: Mathematical Models and Empirical Analyses." *Environment and Planning B—Planning and Design* 30:799–818.

Coe, M.J., D.H. Cumming, and J. Phillipson. 1976. "Biomass and Production of Large African Herbivores in Relation to Rainfall and Primary Production." *Oecologia* 22:341–354.

Cooper, M., D.H. Downs, and G.A. Patterson. 2000. "Asymmetric Information and the Predictability of Real Estate Returns." *Journal of Real Estate Finance and Economics* 20:225–244.

Cumming, D.H.M., and G.S. Cumming. 2003. "Ungulate Community Structure and Ecological Processes: Body Size, Hoof Area and Trampling in African Savannas." *Oecologia* 134:560–568.

Cummings, V., A. Jones, and A. Watson. 2002. "Divided Places: Phenomenology and Asymmetry in the Monuments of the Black Mountains, Southeast Wales." *Cambridge Archaeological Journal* 12:57–70.

Dargay, J., and D. Gately. 1995. "The Response of World-Energy and Oil Demand to Income Growth and Changes in Oil Prices." *Annual Review of Energy and the Environment* 20:145–178.

de Vries, H., and J.C. Biesmeijer. 2002. "Self-organization in Collective Honeybee Foraging: Emergence of Symmetry Breaking, Cross Inhibition and Equal Harvest-Rate Distribution." *Behavioral Ecology and Sociobiology* 51:557–569.

Deininger, K. 2003. *Land Policies for Growth and Poverty Reduction*. Washington, DC: World Bank and Oxford University Press

Despland, E., J. Rosenberg, and S.J. Simpson. 2004. "Landscape Structure and Locust Swarming: A Satellite's Eye View." *Ecography* 27:381–391.

Du Toit, J. T. 1995. "Determinants of the Composition and Distribution of Wildlife Communities in Southern Africa." *Ambio* 24:2–6.

Foody, G., and P. Atkinson 2003. *Uncertainty in Remote Sensing and GIS*. London: Wiley.

Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. "Predictive Models of Movement by Serengeti Grazers." *Ecology* 85:2429–2435.

Gruzelier, J. H., L. Wilson, D. Liddiard, E. Peters, and L. Pusavat. 1999. "Cognitive Asymmetry Patterns in Schizophrenia: Active and Withdrawn Syndromes and Sex Differences as Moderators." *Schizophrenia Bulletin* 25:349–362.

Higgins, P. A. T., M. D. Mastrandrea, and S. H. Schneider. 2002. "Dynamics of Climate and Ecosystem Coupling: Abrupt Changes and Multiple Equilibria." *Philosophical Transactions of the Royal Society: Biological Sciences* 357: 647–655.

HilleRisLambers, R., M. Rietkirk, F. Van Den Bosch, H. H. T. Prins, and H. De Kroon. 2001. "Vegetation Pattern Formation in Semi-arid Grazing Systems." *Ecology* 82:50–61.

Jensen, J. R. 1996. *Introductory Digital Image Processing: A Remote Sensing Perspective*. Saddle River, NJ: Prentice-Hall.

Jordano, P. 1994. "Spatial and Temporal Variation in the Avian-Frugivore Assemblage of *Prunus Mahaleb*: Patterns and Consequences." *Oikos* 71:479–491.

Kasischke, E. S., N. L. Christiansen, and B. J. Stocks. 1995. "Fire, Global Warming, and Carbon Balance of Boreal Forests." *Ecological Applications* 5:437–451.

Keating, B. A., D. Gaydon, N. I. Huth, M. E. Probert, K. Verburg, C. J. Smith, and W. Bond. 2002. "Use of Modelling to Explore the Water Balance of Dryland Farming Systems in the Murray-Darling Basin, Australia." *European Journal of Agronomy* 18:159–169.

Lafleur, P.M., and W. R. Rouse. 1995. "Energy Partitioning at Treeline Forest and Tundra Sites and Its Sensitivity to Climate Change." *Atmosphere-Ocean* 33:121–133.

Lemoine, B. 1986. "Symmetry, Form and Character in Architecture—French—Szambien,W." *Architecture D'Aujourdhui* 246:R47–R47.

Levin, S. A. 1976. "Spatial Patterning and the Structure of Ecological Communities," pp. 1–36. In S. A. Levin, ed., *Lectures on Mathematics in the Life Sciences*. Vol. 8: *Some Mathematical Questions in Biology VII*. Providence, R. I., American Mathematical Society.

Levin, S. A. 1999. *Fragile Dominion: Complexity and the Commons*. Cambridge: Perseus.

Linklater, A. 2002. *Measuring America: How an Untamed Wilderness Shaped the United States and Fulfilled the Promise of Democracy*. New York: Walker.

Logli, F., and R. Joffre. 2001. "Individual Variability as Related to Stand Structure and Soil Condition in a Mediterranean Oak Coppice." *Forest Ecology and Management* 142:53–63.

Lomolino, M.V. 2001. "Elevation Gradients of Species-Density: Historical and Prospective Views." *Global Ecology and Biogeography* 10:3–13.

Machtans, C. S., M.-A.Villard, and S. J. Hannon. 1996. "Use of Riparian Buffer Strips as Movement Corridors by Forest Birds." *Conservation Biology* 10:1366–1379.

MDBC. 1999. *The Salinity Audit of the Murray-Darling Basin*. Canberra: Murray-Darling Basin Commission. http://www.mdbc.gov.au/salinity/salinity_audit_1999.

Meyburg, B. U., P. Paillat, and C. Meyburg. 2003. "Migration Routes of Steppe Eagles Between Asia and Africa: A Study by Means of Satellite Telemetry." *Condor* 105:219–227.

Middleton, R. 1989. "Symmetry, Taste, Character: Theory and Terminology of Classical-Age Architecture, 1500–1800." *Burlington Magazine* 131:44–45.

Miller, D. 2003. "An Asymmetry-Based View of Advantage: Towards an Attainable Sustainability." *Strategic Management Journal* 24:961–976.

Olesen, J., and P. Jordano. 2002. "Geographic Patterns in Plant-Pollinator Mutualistic Networks." *Ecology* 83:2416–2424.

Palmer, T. M. 2003. "Spatial Habitat Heterogeneity Influences Competition and Coexistence in an African Acacia Ant Guild." *Ecology* 84:2843–2855.

Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Peterson, G. D. 2002. "Estimating Resilience Across Landscapes." *Conservation Ecology* 6:17. http://www.consecol.org/vol16/iss11/art17.

Polis, G. A., M. E. Power, and G. R. Huxel 2004. *Food Webs at the Landscape Scale*. Chicago: University of Chicago Press.

Portha, S., J. L. Deneubourg, and C. Detrain. 2002. "Self-organized Asymmetries in Ant Foraging: A Functional Response to Food Type and Colony Needs." *Behavioral Ecology* 13:776–781.

Pushcharovsky, Y. M., and Y. P. Neprochnov. 2003. "Tectonics and Deep Structure of Deep-Sea Basins in the North of the Central Atlantic Ocean." *Geotectonics* 37:95–106.

Rajaniemi, T. K. 2003. "Evidence for Size Asymmetry of Belowground Competition." *Basic and Applied Ecology* 4:239–247.

Richter, H. V., and G. S. Cumming. 2006. "Food Availability and the Annual Migration of the Straw-Coloured Fruit Bat (*Eidolon helvum*) at Kasanka National Park, Zambia." *Journal of Zoology, London* 268:35–44.

Rietkirk, M., P. Ketner, J. Burger, B. Hoorens, and H. Olff. 2000. "Multiscale Soil and Vegetation Patchiness Along a Gradient of Herbivore Impact in a Semi-arid Grazing System in West Africa." *Plant Ecology* 148:207–224.

Scheffer, M., S. R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. "Catastrophic Shifts in Ecosystems." *Nature* 413:591–596.

Schreiner, W., F. Neumann, M. Neumann, R. Karch, A. End, and S. M. Roedler. 1997. "Limited Bifurcation Asymmetry in Coronary Arterial Tree Models

Generated by Constrained Constructive Optimization." *Journal of General Physiology* 109:129–140.

Schwinning, S., and J. Weiner. 1998. "Mechanisms Determining the Degree of Size Asymmetry in Competition Among Plants." *Oecologia* 113:447–455.

Simon, H.A. 1962. "The Architecture of Complexity." *Proceedings of the American Philosophical Society* 106:467–482.

Southworth, J., G.S. Cumming, M. Marsik, and M. Binford. 2006. "Linking Spatial and Temporal Variation at Multiple Scales in a Heterogeneous Landscape." *Annals of Geography* 58:406–420.

Southworth, J., D. Munroe, and H. Nagendra. 2004. "Land Cover Change and Landscape Fragmentation—Comparing the Utility of Continuous and Discrete Analyses for a Western Honduras Region." *Agriculture, Ecosystems and Environment* 101:185–205.

Stewart, I. 2003. "Self-organization in Evolution: A Mathematical Perspective." *Philosophical Transactions of the Royal Society of London, Series A* 361: 1101–1123.

Tarboton, D.G., R.L. Bras, and I. Rodriguez-Iturbe. 1988. "The Fractal Nature of River Networks." *Water Resources Research* 24:1317–1322.

Thiesenhusen, W. 1995. *Broken Promises: Agrarian Reform and the Latin American Campesino.* Boulder: Westview.

Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A.R.E. Sinclair, and M. Borner. 2004. "Can Parks Protect Migratory Ungulates? The Case of the Serengeti Wildebeest." *Animal Conservation* 7:113–120.

Thomas, D.W. 1983. "The Annual Migrations of Three Species of West-African Fruit Bats (Chiroptera, Pteropodidae)." *Canadian Journal of Zoology* 61:2266–2272.

Toffler, A. 1980. *The Third Wave.* New York: Morrow.

Toomey, D.R., W.S.D. Wilcock, J.A. Conder, D.W. Forsyth, J.D. Blundy, E.M. Parmentier, and W.C. Hammond. 2002. "Asymmetric Mantle Dynamics in the MELT Region of the East Pacific Rise." *Earth and Planetary Science Letters* 200:287–295.

Trinkel, M., P.H. Fleischmann, A.F. Steindorfer, and G. Kastberger. 2004. "Spotted Hyenas (Crocuta Crocuta) Follow Migratory Prey. Seasonal Expansion of a Clan Territory in Etosha, Namibia." *Journal of Zoology* 264:125–133.

Turner, M.G., R.H. Gardner, and R.V. O'Neill 2001. *Landscape Ecology in Theory and Practice: Pattern and Process.* New York: Springer.

van Beek, J. 1997. "Is Local Metabolism the Basis of the Fractal Vascular Structure in the Heart?" *International Journal of Microcirculation-Clinical and Experimental* 17:337–345.

Van Dongen, S., L. Lens, and G. Molenberghs. 1999. "Mixture Analysis of Asymmetry: Modelling Directional Asymmetry, Antisymmetry and Heterogeneity in Fluctuating Asymmetry." *Ecology Letters* 2:387–396.

vanderMeer, P.J., and F. Bongers. 1996. "Formation and Closure of Canopy Gaps in the Rain Forest at Nouragues, French Guiana." *Vegetatio* 126:167–179.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. "The River Continuum Concept." *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.

Vollestad, L.A., K. Hindar, and A.P. Moller. 1999. "A Meta-analysis of Fluctuating Asymmetry in Relation to Heterozygosity." *Heredity* 83:206–218.

Walther, B.A., M.S. Wisz, and C. Rahbek. 2004. "Known and Predicted African Winter Distributions and Habitat Use of the Endangered Basra Reed Warbler (Acrocephalus Griseldis) and the Near-Threatened Cinereous Bunting (Emberiza Cineracea)." *Journal of Ornithology* 145:287–299.

Ward, T.M., J. Staunton-Smith, S. Hoyle, and I.A. Halliday. 2003. "Spawning Patterns of Four Species of Predominantly Temperate Pelagic Fishes in the Subtropical Waters of Southern Queensland." *Estuarine Coastal and Shelf Science* 56:1125–1140.

Wedel, M., W.A. Kamakura, W.S. Desarbo, and F. Terhofstede. 1995. "Implications for Asymmetry, Nonproportionality, and Heterogeneity in Brand Switching from Piece-Wise Exponential Mixture Hazard Models." *Journal of Marketing Research* 32:457–462.

White, R., and G. Engelen. 1993. "Cellular-Automata and Fractal Urban Form—A Cellular Modeling Approach to the Evolution of Urban Land-Use Patterns." *Environment and Planning A* 25:1175–1199.

Whittaker, R.H. 1960. "Vegetation of the Siskiyou Mountains, Oregon and California." *Ecological Monographs* 30:279–338.

Wilson Jones, M. 2001. "Doric Measure And Architectural Design 2: A Modular Reading of the Classical Temples." *American Journal of Archaeology* 105:675–713.

Yizhaq, H., B.A. Portnov, and E. Meron. 2004. A mathematical model of segregation patterns in residential neighbourhoods. *Environment and Planning A* 36:149–172.