Chapter 5

WHAT IS THE SCOPE OF "HISTORY" IN HISTORICAL ECOLOGY? ISSUES OF SCALE IN MANAGEMENT AND CONSERVATION

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5.1 INTRODUCTION

Understanding and applying concepts such as historical range of variation (HRV) in management and conservation requires a specification of what is "history" and what is "variation." Both are matters of scale. Depending on one's perspective, history is what happened yesterday, last week, a month ago, or years, decades, centuries, millennia, or even longer in the past. Variation in any factor of interest depends on the timescale as well. Because variation is often expressed as a departure from some average condition, whether that condition remains stable or itself varies depends on the time frame adopted. Spatial scale is also important: both history and variation are likely to differ between a small, local area and a larger, regional area. Whether historical variation is used to guide management (e.g. Landres et al. 1999), assess recovery from environmental disturbances (e.g. Wiens 1995), or set targets for restoration actions (e.g. White & Walker 1997), determining appropriate scales should be a central concern.

More often than not, however, the scales of investigation or management are determined arbitrarily, on the basis of factors related more to logistics, the time frame of human perception, or the availability of data than to the dynamics of the system of interest. Consider just temporal scale. Much of the information used to test the ecological theories on which management and conservation are based, for example, comes from 1- to 3-year studies constrained by academic degree requirements or grant-funding cycles. Such studies can provide only a snapshot of variation, so in order to generalize the results, one must assume that system dynamics are in equilibrium. Long-term studies (10–40 years or more) can document variation within the specified time window, but such studies have been conducted for only a handful of species or ecosystems and are likewise limited by the duration of funding support or the interest or persistence of the investigator (Likens 1989; Irland et al. 2006). In the management arena, US National Forest Land Management Plans generally consider a 10- to 15-year planning horizon (as established by the National Forest Management Act), and strategic plans of agencies such as the US Geological Survey or US Fish and Wildlife Service are cast in terms of 5-year periods covering a decade or two.

More to the point of this book, the timescales used to define HRV differ depending on the attributes used to characterize variation, the availability of data, the particular management directives or policies, and an often-unstated perception of what past time period is relevant to the present (Millar & Woolfenden 1999a). In North America, the period of relevant history is often considered to be the two to three centuries before the arrival of European colonists, when disturbance dynamics are assumed to have been "natural," and the beginnings of the transformation of the continent (Whitney 1994) (although this excludes the previous effects of indigenous Native Americans on the landscape; Denevan 1992; but see Barrett et al. 2005). The comparable demarcation points for history are quite different in Europe or, for that matter, Australia or parts of Africa or South America. Paleoecologists think of timescales in yet different ways (e.g. Schoonmaker 1998; Jackson, Chapter 7, this book).

There are two points to be made. First, the scales used to define time periods over which historical variation is considered cover a broad range, in part reflecting different purposes, objectives, constraints, perceptions, and attributes of interest. Second, no matter which scale is used, the patterns and magnitude of variation observed will be dictated and circumscribed by that scale, and any management or conservation practices that are guided by historical variation will be similarly constrained.

Our objective in this chapter is to delve more deeply into some of the issues related to scale and historical variation and the implications for incorporating historical ecology into resource management and conservation. These issues complicate applications of historical ecology, and the specter of rapid changes in ecological systems wrought by climate change and land-use change only adds to the difficulty. Our perspective is that, despite these difficulties, historical ecology is fundamental to understanding the current and likely future status of the ecosystems we manage and value, because it provides insight into the temporal and spatial mechanisms by which ecosystems respond to global change. At the very least, historical information can inform resource managers about the level of departure of current from past conditions, which can assist in articulating goals and desired conditions and identifying appropriate management options. Regardless of how the future plays out, planning for it requires knowing where we are today, and knowing where we are today requires knowing how we got here.

5.2 SCALE IN ECOLOGY

First, some background on what scale means and how it has been used in ecology. Although ecologists use "scale" or "scaling" in a variety of ways (Peterson & Parker 1998; Wu 2007), scale generally refers to the dimensions in space or time in which a study is conducted or a concept or theory is intended to apply. Saying that a study area is 10 ha or was conducted over 2 years specifies the spatial or temporal scale of the study.

There are two components of scale: *grain* and *extent* (Wiens et al. 1993; Fortin & Dale 2005). In a spatial context, grain refers to the resolution of a study or analysis or the finest unit of observation (e.g. the smallest grid-cell size), while extent defines the overall area in which a study or analysis is conducted. For example, an investigator might study the distribution and survival of oak (*Quercus* spp.) seedlings in a 100-ha woodlot (the extent) by sampling several dozen quadrats of 1 m^2 (the grain). The temporal analog might be conducting the study over 3 years (the extent) by sampling every month (the grain). Considerations of grain and extent, as components of scale, relate closely to the definition of both history and variation in determination of the HRV. Extent defines the span of history considered, and grain determines what one sees of the variation that actually occurs.

Grain and extent are selected by an investigator or manager as part of a study design or management application. Beyond this, however, natural phenomena often vary nonlinearly in relation to scale. Scale domains (Wiens 1989) define ranges of scale within which the linkages between ecological processes (causes) and patterns (effects) remain relatively stable before shifting to some different process–pattern relationship as the scale is changed and a "scaling threshold" is passed (Fig. 5.1). Such scale-dependent domains and thresholds are well-known in population dynamics (May 1974) and chaos theory (Gleick 1987), where they represent transitions to a different state space (Gunderson & Holling 2002).

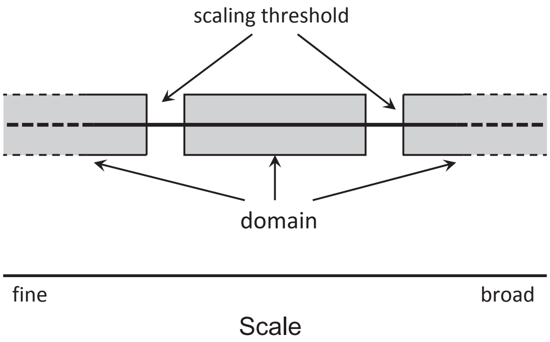

Fig. 5.1 Domains of scale define regions of the scale spectrum within which ecological attributes (e.g. organisms, processes, spatial patterns) and pattern–process relationships remain relatively consistent. Adjacent domains are separated by transitional zones or thresholds in which system dynamics may be unpredictable. If the focus is on phenomena within a given scale domain, studies conducted at finer scales may fail to include critical components, whereas studies conducted at broader scales may fail to reveal the pattern or causal relationships because such linkages are averaged out or are characteristic only of the given domain.

In addition to drawing attention to the importance of grain and extent and threshold dynamics, the last two decades of research and thinking about scaling in ecology have led to several insights about the factors that influence the choice of appropriate scales. These are not new or novel insights, but they bear on how history can inform management and conservation practice.

- The inherent dynamics of the ecological system determine in part the appropriate scale of investigation or management. These dynamics (e.g. population fluctuations, frequency of disturbances) are what produce the ecologically relevant variations. The scale(s) on which a system is viewed will determine how or whether these dynamics and variations are revealed. A single-year study with monthly observations will not capture variations associated with multiyear droughts or El Niño Southern Oscillation (ENSO) oceanographic cycles.
- Different system attributes, such as weather, climate, fire, or the life-history strategies of different species, vary in their characteristic scale domains in space and time (Fig. 5.2). The appropriate scale(s) for assessing variation in these attributes will therefore differ. There is no "one size fits all" scale.
- The appropriate scale will also differ depending on the question asked and the focus of the question. A study of the physiology of an individual tree, for example, will require a different scale in space and time to capture critical cause–effect relationships than one focused on the controls of nitrogen cycling in forest ecosystems (Fig. 5.2).
- Policies that govern the protection or management of natural resources are frequently implemented opportunistically, often at the scales of administrative units (e.g. individual Wildlife Refuges, US Forest Service Regions) or budget cycles. The implicit nature of scale in these instances often makes it difficult to learn why some policies succeed and others fail. Permeating all of

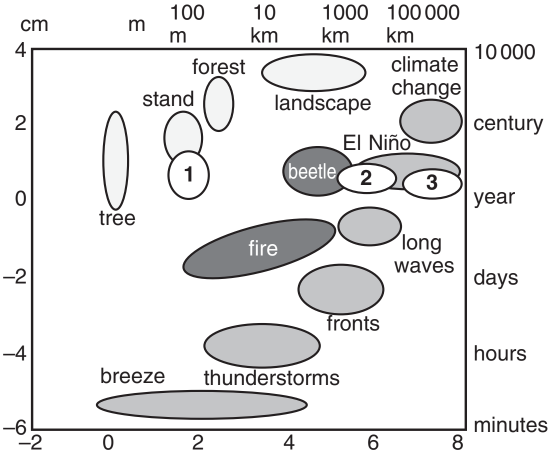

Fig. 5.2 Generalized space-timescale domains of features of forests, disturbances associated with fire or beetle outbreaks, and atmospheric factors (after Holling et al. 2002). The scale domains for different forest-management approaches are also shown (1 = forest thinning or prescribed burning; 2 = regional forest plan; 3 = National Forest policy). (From *Panarchy* edited by Lance H. Gunderson and C.S. Holling. Copyright © 2002 Island Press. Reproduced by permission of Island Press, Washington, DC, USA.)

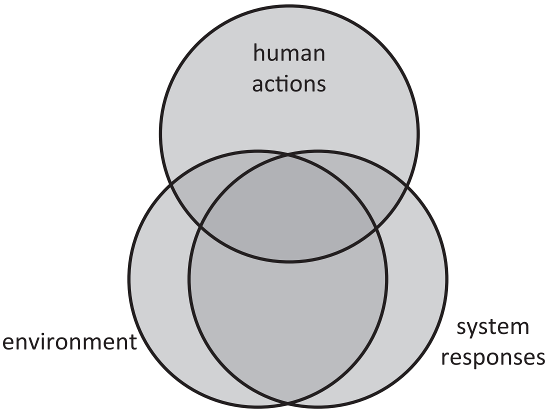

Fig. 5.3 Venn diagram of the relationships between the scales (areas of the circles) of variation in the environment, in the responses of ecological systems to the environment, and in the application of human actions (e.g. management, conservation, resource extraction, policy). The scales only partially overlap because some variations in the environment occur at scales to which ecological systems do not respond or some attributes of ecological systems occur at scales too fine or too broad for management or conservation actions. The areas of overlap indicate matching of scales. The large overlap between the scales of environmental variation and responses of ecological systems reflect the general tendency of organisms or biological processes to be adjusted to environmental variations, either through short-term responses or evolutionary adaptation. The lesser overlap between these scales and that of human actions reflects the general practice of determining the scale of these actions on the basis of the size of management units, the prevue of policy, duration of funding, and so on, rather than the inherent scaling of environmental variation and ecological responses.

this are the scales of human perception. Most people view the things that affect their lives (and over which they have some control) at local spatial scales or short-term temporal scales. They tend to be more detached from international (or even national) affairs or things that may affect them a decade or two hence. There is an important asymmetry here, in that most people have a short-term view of the future but a much longer, even nostalgic, view of the past. This is one reason why it is so difficult to generate public concern over the potential impacts that climate change may have in 2050. Like it or not, our perceptual scaling is often imposed on the natural systems we study or attempt to manage or conserve.

The upshot of these multiple layers of scaling is that what one perceives about natural systems – their dynamics, history, and variations – is filtered by scale. Roughly speaking, there are three dimensions of scale filtering that must be considered: the scales at which the environment varies, the scales at which the system operates and responds to environmental variations, and the scales at which we observe and manipulate these dynamics (Fig. 5.3). The first two scaling filters are usually functionally intermeshed: through either short-term or evolutionary adaptation, ecological systems tend to adjust to the scales of relevant variation in environmental factors. The third scaling filter, however, involves human scalings that are often detached from those of the environment and the natural systems. As a result, the scales of both academic studies of these systems and the actions taken to manage or conserve them may be mismatched to the natural scaling of the systems. Management may go astray when there is a lack of congruence between the scale of management actions and the scales of variation in the environment and in the dynamics of the natural system. For example, treatments to protect western conifer forests from losses to bark beetles (*Scotylus, Dendroctonus,* and *Ips* spp., among others) typically are conducted at the scale of individual trees (applying insecticides) or stands (thinning to reduce tree-to-tree competition and stress), and important research has been conducted to support management at this spatial scale (e.g. Amman & Logan 1998; Schmid & Mata 2005). However, the bark beetle outbreaks now occurring across much of western North America are being driven primarily by changing climatic conditions (warmer temperatures) occurring at a continental or global scale (Raffa et al. 2008), which are overwhelming the effects of stand-level forest treatments.

5.3 SOME IMPLICATIONS OF SCALE IN HISTORICAL ECOLOGY

The perception of system dynamics

What one sees of the dynamics of an ecological system is a function of the scale on which the system is viewed. Consider, for example, the three hypothetical scenarios of system dynamics depicted in Fig. 5.4. These scenarios represent distinctly different forms of system dynamics. In "A" the system is in a dynamic equilibrium in which variation occurs within limits about an average condition that does not change over a long time period. This is what is envisioned in the concept of stationarity (Milly et al. 2008). In "B" the system is undergoing a long-term, continuous change; variation occurs about an average condition that shows a trend over time. In "C" the system exhibits sudden, discontinuous changes as the dynamics pass thresholds or tipping points. Threshold dynamics are well known in many ecological systems (Beisner et al. 2003; Bestelmeyer 2006; Groffman et al. 2006), and they have spawned an array of state-and-transition models (Westoby et al. 1989; Bestelmeyer et al. 2009) that deal with the nonlinear dynamics of complex systems. If these systems were to be viewed only over a short timescale (a in Fig. 5.4), their dynamics and variations would appear to be much the same. Expanding the temporal scale (b in Fig. 5.4) might enable one to distinguish between the long-term stability of scenario A and the trend of scenario B, but the dynamics of scenario C would be indistinguishable from those of scenario A. Only over a long temporal scale (relative to the dynamics of the system; c in Fig. 5.4) would one detect the abrupt shifts in system state that accompany thresholds.

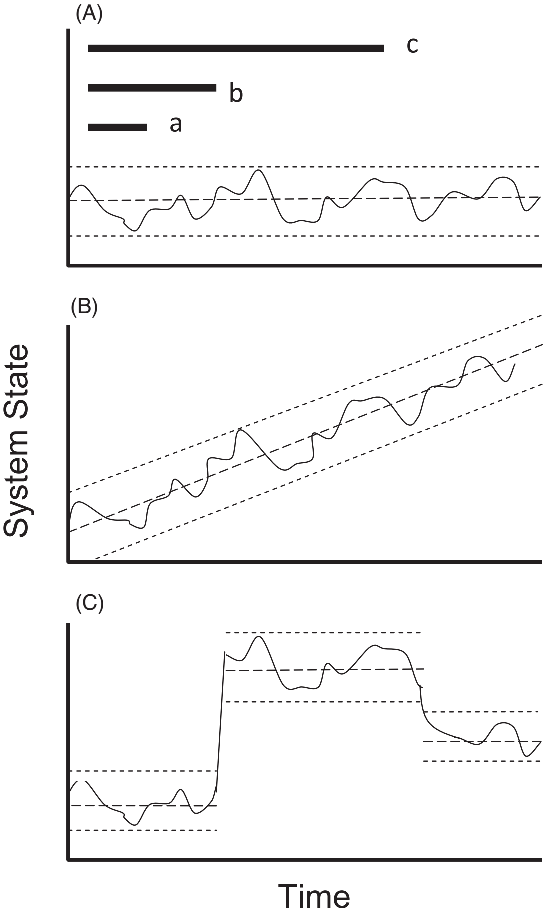

Fig. 5.4 Three hypothetical examples of the temporal variation in a system property. A = dynamic equilibrium; B = continuous trend over time; C = system dynamics characterized by thresholds and shifts in system state. The dashed line indicates the long-term mean; the dotted lines envelope the range of variation. Bars a, b, and c illustrate different scales on which the system dynamics might be observed. Although the magnitude of variation is shown as unchanging over time in these examples, it is more likely to change, perhaps especially as a system approaches a threshold in system dynamics (see text).

As the recognition of nonequilibrium dynamics has become more widespread in ecology (Wiens 1984; Rohde 2005), it has become evident that the equilibrium envisioned in scenario A of Fig. 5.4 may be unlikely except over short time spans in ecosystems that recover rapidly from disturbances or that are intensively managed to maintain the dynamics within a restricted envelope of variation. Scenario B may typify ecosystems undergoing recovery, restoration, or succession after disturbances such as forest fires (Turner et al. 2003; Hobbs & Suding 2009), but it is often coupled with the presumption that, absent recurrent disturbance, system dynamics will eventually stabilize and thereafter resemble scenario A. If the disturbances are large and frequent (relative to recovery times), however, the system may resemble scenario C, changing suddenly to a different configuration and different dynamics when a threshold is passed. Such changes have been documented where severe grazing and/or changes in fire frequency fostered the establishment of invasive plants, resulting in the replacement of a shrub-dominated community by grassland or vice versa (Bestelmeyer et al. 2004; Chambers et al. 2007). Systems with dynamics such as in scenarios A, B, or C are likely to require different management, even if the management objectives are the same. Use of an inappropriate scale can lead to a misinterpretation of system dynamics, resulting in management that is ineffective or worse (Cumming et al. 2006).

Scales a, b, and c in Fig. 5.4 indicate the temporal scale extent. This is the span of "history" included in assessments of HRV. But the grain of temporal observation may also be important, since this is what determines the variation component. By definition, variations that occur at a scale finer than the observation grain cannot be detected. As the grain becomes coarser, more of the inherent variation in a system may be filtered out. Use of a 10-year running mean to portray annual precipitation, for example, smoothes out the peaks and troughs of wet and dry years. Such extreme events can have disproportionate effects on ecological systems, particularly if the physiological tolerances of organisms are exceeded. For example, bark beetle outbreaks may be terminated by a short period (a week or so) of extreme cold (below ca. −20°C), which kills the beetle larvae within the trees, especially if the cold spell occurs in early or late winter (Logan & Powell 2001; Logan et al. 2003). Daily or weekly temperature data are required to detect this key ecological event; average monthly or annual temperature values would be unlikely to capture the critical short-duration cold period that terminated an outbreak. These points emphasize the importance of assessing what scales are relevant to the ecological system of interest and the conservation or management objectives. We are not interested in documenting variation simply because it is there, but rather because it affects properties of interest. The art of dealing with scale involves "getting it just right." If the grain is too fine, we may be overwhelmed by a deluge of extraneous detail and fail to see the important factors, but if the scale is too coarse, we may average away critical dynamics and likewise fail to see the important factors. If the extent is too brief or small, we may fail to capture the true historical or spatial dynamics of the system, but if it is too broad, we may confound our understanding of the system (and thus management effectiveness) by including the effects of factors that no longer operate or that are not amenable to management. It is perhaps trite, but also necessary, to emphasize the importance of a deep understanding of the system – Barbara McClintock's "feeling for the organism" (Keller 1983) – if one is to use a scale (grain and extent) that will capture the relevant variations over a relevant span of history.

Nonlinearities in history

Some years ago, Harold Blum (1951) published a book entitled *Time's Arrow and Evolution* in which, drawing from arguments in physics and cosmology, he addressed the irreversibility of temporally chronological processes such as evolution. Although history may sometimes appear to repeat itself, in reality, there is no going back – time's arrow points only forward. But this does not mean that history follows linear pathways. Father Time does not shoot straight. History follows a convoluted pathway, in which particular events at particular time may have decisive impacts on the future trajectories of history. This is the "butterfly effect" of chaos theory and quantum physics, in which the temporal trajectory of complex systems is sensitive to initial conditions (Gleick 1987). In fact, any historical trajectory represents a series of possible branch points stemming from critical events (or even seemingly benign events) at particular points in time (Fig. 5.5). The characteristics of an ecological system are affected by what has come before. Knowing what has come before is perhaps the most compelling reason for paying attention to historical variation when we attempt to manage or conserve a system.

Sudden shifts or tipping points in the wandering trajectory of history may define the boundaries of domains of scale (Wiens 1989). Patterns and variations within scale domains may be governed by a common set of processes. This consistency in process–pattern rela-

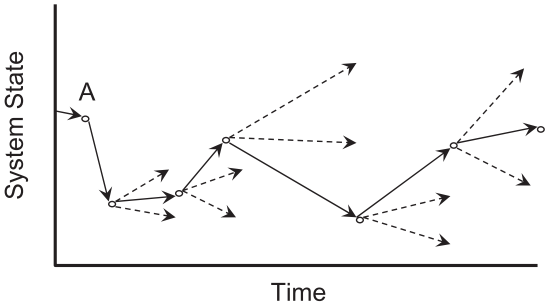

Fig. 5.5 Alternative trajectories of change in system state over time. Following a disturbance event (A), the system at subsequent points might follow any of several trajectories; which trajectory is followed determines the subsequent system state. Over time, a series of potential branching points may create the potential for the system to display a wandering trajectory. History is a sequence of such branch points and alternative trajectories of change.

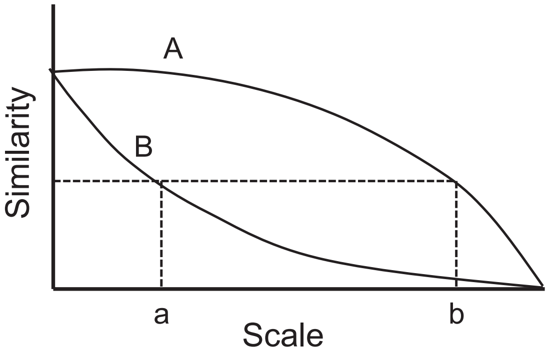

Fig. 5.6 The similarity of a system to its condition at some initial point tends to decrease as the space or timescale over which similarity is calculated increases. Different systems (or different components of the same system) may follow different similarity-decay functions (A and B). In this hypothetical example, the two systems exhibit the same level of similarity to the initial point at quite different scales (a and b).

tionships engenders similarity, which means that there is a reasonable likelihood that causes and effects that have operated in the past will continue to operate now and in the future. This is the premise of using HRV to guide management and conservation actions. Changing scale, however, may increase the likelihood of encountering and crossing thresholds between different sets of factors that control ecological dynamics (e.g. Fig. 5.2). Thus, as we go farther back in time (or a greater distance in space), similarity diminishes – there is a distance-decay function to scale (Nekola & White 1999). Depending on the decay rate, the scale domains of history that may encompass sufficiently similar conditions to inform present practices will differ (Fig. 5.6). In some instances, these scale domains may be lengthy. For example, Millar and Woolfenden (1999b) argue that the major ecosystem components and processes in the Sierra Nevada of California have remained broadly similar over the last ca. 4000 years.

Within these domains, system dynamics may be inherently resilient to disturbance: the systems are able to absorb the potentially disruptive effects of disturbances without being forced out of the "comfort zone" of variation (Beisner et al. 2003). Resilience acts through feedback mechanisms to maintain the composition or functioning of ecological systems within limits despite environmental stresses, disturbances, and disruptions (Peterson et al. 1998). Consequently, resilience is a much talked-about trait of ecological systems, and some approaches to conservation and management are explicitly focusing on enhancing the resilience of ecological systems, particularly in the context of climate change (Millar et al. 2007). If ecological systems are more resilient to change within scaling domains, then aligning the scale used to define historical variation for management with the scale of such domains may be particularly effective.

If only we knew how to define scaling domains *a priori*! Ah, there's the rub. Although it has been suggested that the magnitude and frequency of variations in system properties may increase as an ecological system approaches a threshold (Wiens 1992; Carpenter & Brock 2006; Scheffer et al. 2009), it is in the nature of thresholds that there is often no warning that they are about to be crossed. Once a system is pushed over a threshold or beyond a tipping point, however, the composition and functioning of the system may be so altered that it is fundamentally changed – it is a different system. Returning the system to its former condition may not be possible, even with massive management efforts. For example, cheatgrass (*Bromus tectorum*), a nonnative annual, has invaded shrubsteppe vegetation in much of the Great Basin of western North America, where it has profoundly altered the historical disturbance regime and caused widespread ecological degradation (Mack 1981; D'Antonio & Vitousek 1992). Widely spreading fires formerly were infrequent in the shrubsteppe, largely because bare ground between individual shrubs and bunchgrasses created a discontinuous fuel bed. However, cheatgrass is a winter annual grass that senesces in early spring, creating a continuous fuel bed of easily ignited fuel. Fires within cheatgrass-dominated areas can spread rapidly over large areas. A positive feedback becomes established, in which more frequent fire promotes more abundant cheatgrass, which in turn promotes more frequent fire. As a result, the historical fire-return interval (30–110 years) has been drastically shortened to 1–5 years. The fire-intolerant native flora eventually may be extirpated, at which point the system is converted to annual grassland. Once established, cheatgrass is very difficult to eradicate; as long as it is abundant, attempts to reestablish the native shrubs and bunchgrasses will not likely succeed because of recurrent cheatgrass-fueled fires (Whisenant 1990; Chambers et al. 2007). Peterson (in Holling & Gunderson 2002) gives several examples of other systems displaying such alternative stable states.

5.4 SCALES IN TIME AND SPACE INTERACT

So far we have emphasized temporal scaling because of its close relationship with historical variation. But a glance at Fig. 5.2 reveals that there are parallels in the characteristic temporal and spatial scale domains for many factors. Some, such as weather or individual reproduction, operate at “small-fast” scales where biophysical processes that control physiology or behavior dominate, while others, such as landscape or biome composition and structure, may be dictated largely by climatic, geomorphological, or biogeographical processes that operate at “large-slow” scales (Holling et al. 2002). Obviously, holding the temporal scale (i.e. history) constant while changing the spatial scale (or vice versa) will alter the factors controlling the dynamics of a system, confounding attempts to understand what produces the historical variation and compromising the applicability of historical information to current or future management.

The magnitude and pattern of temporal variation in a system may also be influenced by the form of spatial variation, and this interaction may determine whether one sees high or low variance in system attributes (and manages accordingly). For example, many populations of plants and animals have a patchy population structure. Local subpopulations may be loosely connected by dispersal and immigration, with the result that their dynamics are partially but not entirely independent of one another, as envisioned in metapopulation or source-sink theory (Hanski & Gaggiotti 2004; Liu et al. 2011). The similar concept of shifting-mosaic steady-state dynamics (Bormann & Likens 1995) has been developed to explain the high variation in successional state among patches in a forested landscape while the landscape as a whole appears to be much more stable. If the spatial scale on which these dynamics are viewed is fine, one will see the variation among the patches or subpopulations, whereas a broader scale perspective will reveal the relative stability of the landscape or metapopulation (Turner et al. 1993). Whether one sees the forest or the trees is a matter of scale, and it affects the variation component of historical variation.

When one defines a time period in which to assess historical variation, there is also an implicit presumption that the spatial scaling of important factors or processes has remained much the same over that period. We know that this is not often the case. Over the past two centuries, for example, forest clearing and subsequent afforestation have reduced and then increased forest cover in the northeastern United States (Irland 1999), whereas in much of the midwestern and western United States, land-use conversion has led to a progressive loss and isolation of both forests and native grasslands (Curtis 1956; Sharpe et al. 1987; George & Dobkin 2002). These changes would have altered the size and frequency of forest and grassland disturbance due to fire even without the additional effects of a century of fire suppression. As a result of these spatial changes, the temporal dynamics of these systems have also changed. As the spatial extent of forested areas has shrunken over time, the scale of the temporal domain over which variation is gauged for management application should also become smaller, at least if our interest is in historical variations that are similar enough to contemporary conditions to be relevant. Of course, there continue to be valid reasons to understand ecosystem dynamics from before fragmentation, but the contemporary applicability of such knowledge may be limited. Either way, history is a function of spatial as well as temporal scale.

The lingering effects of past history

History, of course, is not something that is nicely partitioned off wherever we decide to place our scale boundaries. History also leaves its legacies, elements that reflect conditions at some past time but which no longer hold. The oldest trees in an old-growth sequoia (*Sequoiadendron giganteum*) forest, for example, germinated as seedlings thousands of years ago, when the climate was different and the imprint of humans on the landscape was still light, and they grew and aged through periods in which fire frequencies varied substantially from one century to another. Their dominance in the overstory of a contemporary forest may have little to do with current environmental conditions or disturbance regimes. Another example: Lost Forest is an isolated stand of ponderosa pine (*Pinus ponderosa*) in central Oregon that is a relict of a more extensive forest that contracted during a hot dry period thousands of years ago (Chadwick & Eglitis 2007). Although annual precipitation is now less than what is usually required to maintain a ponderosa pine forest, Lost Forest persists because of unusual soil properties that retain sufficient water (Moir et al. 1973). The biota of every region on earth is the result of the complex intermingling of travelers who came at different times under different conditions.

Such legacies complicate attempts to understand why a particular set of species occurs in a particular area. They also make it difficult to define an appropriate scale for assessing historical variation. No matter how time is sliced, the period selected to represent variation that is relevant to current conditions will be tainted by interlopers from previous periods. Extending the timescale back four centuries would include the effects of the "Little Ice Age"; a millennium would include the Medieval Warm Period. Some of the trees still present in Wytham Woods in England would have germinated and grown under those conditions (see Kirby, Chapter 20, this book). The shorter the timescale considered, the more likely that legacies will be present. What is "short," however, must be measured relative to the longevity of the organisms: a short time to an oak may be an infinity to a caterpillar feeding upon its leaves.

5.5 CONCLUSIONS: DEALING WITH SCALE

Everything about ecology is scale dependent at some level. Individuals, populations, communities, and ecosystems of different types operate on characteristic domains of scale. These domains differ for different ecological processes such as feeding, reproduction, habitat selection, trophic flows, nitrogen cycling, and so on. What one attempts to manage or conserve at a particular place and time is a compilation of the multiple scales on which the components of the system function and respond to the environment, with some broader scale elements (e.g. landscape effects, historical legacies) thrown in. And overriding all of it are filters of human perceptions and societal mandates, which are also scale dependent. There is great potential for mismatching the scales of management with the scales most relevant to the biology and ecology of the systems of interest.

So what messages should a manager or conservationist take away from our musings about scale, particularly as they relate to the use of historical variation to guide their actions? Here are some:

- Avoid arbitrary definitions of the scale of history. The appropriate scales depend on the targets of management and the biology and ecology of those targets, the management objectives or questions asked, and the policy and societal imperatives and constraints.
- Be open to management at multiple scales. Because the above factors all operate within different scale domains, there is no single best scale for management; managers and conservationists will need to adopt a much broader, multiscale perspective than they have in the past.
- Consider the scales of the dominant disturbance processes as a starting point for determining appropriate scales for management. Ecological insight, based on an understanding of natural history, can help to identify those ecological processes that most clearly determine the status of the focal ecosystem features. These disturbance processes can be used to establish provisional scales for management or conservation.
- Recognize that the size of a management unit profoundly influences our perception of the inherent dynamics of the system. A land unit may appear as a dynamic, steady-state system or as an unstable, nonequilibrium system, depending on the spatial and temporal scales at which the natural disturbance regime operates relative to the size of the unit and the time frame over which the dynamics of the system are observed. Thus, an extensive forested landscape in which the natural-disturbance regime is dominated by frequent small tree-fall gaps that fill in quickly will appear to be in a state of equilibrium, whereas a small protected area within a landscape where the natural fire regime is one of infrequent but large stand-replacing fires may be perceived as destroyed by the first large fire that occurs.

- Be diligent in consulting the historical record – as far back as information is available – before developing resource-management plans. There are many examples of misguided management actions and restoration plans that did not properly account for the full range of ecosystem variability or its connection to exogenous drivers like climate, raising questions about the current or future effectiveness of the actions or plans.

5.6 CODA: SCALING CONSERVATION AND MANAGEMENT IN A CHANGING WORLD

Although the future is by definition uncertain, the one thing that does seem certain is that the future will be different from the past. The accelerating pace of climate change and land-use change will see to that. There is more to it than changes occurring more rapidly than in the past, however. As species shift distributions, disappear, or evolve in response to the changing environment, existing assemblages will be torn apart and reassembled into new, novel configurations that have not been seen before (Hobbs et al. 2006; Williams et al. 2007; Stralberg et al. 2009).

We have discussed above the multiple factors that make it difficult to define appropriate scales of time or space to inform contemporary conservation and management. How can we then hope to avoid compounding mismatches of scale in the future, when the dynamics of populations, communities, and ecosystems shift to different scales or pass thresholds into new, unexplored domains of scale?

We can begin with some speculations about how future environmental changes might affect the scaling of the elements of Fig. 5.2. Although the scales of forest units from conifer needles to landscapes may remain much the same, the scales on which the "slow-broad" weather and climate factors (e.g. long waves, El Niño Southern Oscillation, climate change) operate are likely to shift toward faster but even broader scales. For example, model projections suggest that episodes of extreme temperatures, rainfall, or droughts may become more frequent, longer lasting, and more widespread (Climate Change Science Program 2008). In response to changes in regional climates, outbreaks of insects such as spruce budworm (*Choristoneura* spp.) may become more widespread and more persistent and forest fires may become more frequent. To be effective, management and conservation must anticipate how the biological elements or disturbance processes of ecosystems will shift in their time-space scaling dimensions.

The challenge is exacerbated because future environmental change will be driven by a combination of land-use change and climate change (Pielke et al. 2002; Jetz et al. 2007). These forces operate across multiple scales. Changes in land use are responsive to broadscale policies, such as farm policies that encourage uniformly intensive agricultural practices over large regions or the fire-exclusion policies that were applied to almost all federal lands. Such policies are usually implemented, however, at a local scale of tens of hectares to a few hundred square kilometers. On the other hand, changes in climate are driven by broadscale continental or global atmospheric and oceanographic dynamics, which percolate down to affect regional climate and local weather (or, in marine systems, sea level, salinity, and alkalinity). As land use continues to fragment landscapes, the spatial scale of management may shrink (to focus on the smaller remnant patches) or expand (to focus on entire landscape mosaics). The global drivers of climate change may also necessitate a broadening of scale, especially if one is to consider the causes as well as the consequences of change. The fragmentation of landscapes due to land use and the reshuffling of biological communities resulting from climate change may reduce the distance in time or space over which systems display similar composition or dynamics; the distance-decay functions in Fig. 5.6 will shift from A toward B.

As a result of these environmental changes, there may be shrinkage in the size of the scale domains over which one can assume some degree of uniformity in ecological process–pattern relationships, and thus expect historical variation to be relevant. Moreover, the likelihood that more and more "no-analog" assemblages and ecosystems will emerge may suggest that past history is no longer sufficient to adequately inform future conservation and management practices. Yet history is not dead. We may no longer be able to expect historical variation to prescribe the domain of future variation, but there is still much to be learned from an examination of how environments have varied in the past and how ecological systems have responded to these variations through adaptation, movements and reassembly of communities, or, in some cases, extinction (see Chapter 7, this book). These lessons can be learned from the many scales of history discussed elsewhere in this book. Paleoecology can indicate how large-magnitude environmental changes in the distant past affect biotas, although the temporal grain of this perspective is limited by the available data. Historical ecology can use fine-grain information from the past decades or centuries to assess responses to environmental variations in greater detail, although the range of variation encompassed by these records tends to be inversely related to the time span of the data. Despite such limitations, information on historical variation at multiple scales, combined with the projections of models of climate change, fire dynamics, species distributions, and the like, may provide a foundation for scenario analyses of possible future trajectories of ecosystem change. Just as landscape ecology provided new insights into ecological processes at a range of spatial scales, historical ecology provides a means for understanding the temporal dynamics of systems more clearly and, through that understanding, obtaining sharper insights into the potential characteristics of ecosystems in the future.

REFERENCES

Amman, G.D. & Logan, J.A. (1998). Silvicultural control of mountain pine beetle: prescriptions and the influence of microclimate. *American Entomologist*, **44**, 166–177.

Barrett, S.W., Swetnam, T.W., & Baker, W.L. (2005). Indian fire use: deflating the legend. *Fire Management Today*, **65**(3), 31–34.

Beisner, B.E., Haydon, D., & Cuddington, K.L. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, **1**, 376–382.

Bestelmeyer, B.T. (2006). Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology*, **14**, 325–329.

Bestelmeyer, B.T., Hedrick, J.E., Brown, J.R., Trujillo, D.A., & Havstad, K.M. (2004). Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. *Environmental Management*, **34**, 38–51.

Bestelmeyer, B.T., Tugel, A.J., Peacock, G.L., et al. (2009). State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management*, **62**, 1–15.

Blum, H.F. (1951). *Time's Arrow and Evolution*. Princeton University Press, Princeton, NJ, USA.

Bormann, F.H. & Likens, G.E. (1995). *Pattern and Process in a Forested Ecosystem*. 2nd ed. Springer-Verlag, New York, USA.

Carpenter, S.R. & Brock, W.A. (2006). Rising variance: a leading indicator of ecological transition. *Ecology Letters*, **9**, 308–315.

Chadwick, K.L. & Eglitis, A. (2007). Health assessment of the Lost Forest Research Natural Area. USDA Forest Service, Bend, OR, USA. http://www.fs.fed.us/r6/nr/fid/pubsweb/lost-forest.pdf.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., & Whittaker, A. (2007). What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, **77**, 117–145.

Climate Change Science Program. (2008). Abrupt climate change. A report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research (P.U. Clark and A.J. Weaver, coordinating lead authors; E. Brook, E.R. Cook, T.L. Delworth, and K. Steffen, chapter lead authors), 244 pp. U.S. Geological Survey, Reston, VA, USA. http://web.mac.com/dannysatterfield/climatechange/Resources_files/sap3-4-final-report-all.pdf.

Cumming, G.S., Cumming, D.H.M., & Redman, C.L. (2006). Scale mismatches in social-ecological systems: causes, consequences, and solutions. *Ecology and Society*, **11**(1), 14. http://www/ecologyandsociety.org/vol11/iss1/art14/.

Curtis, J.T. (1956). The modification of mid-latitude grasslands and forests by man. In *Man's Role in Changing the Face of the Earth* (ed. L. Thom Jr.), pp. 721–736. University of Chicago Press, Chicago, IL, USA.

D'Antonio, C.M. & Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Denevan, W.M. (1992). The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers*, **82**, 369–385.

Fortin, M.-J. & Dale, M.R.T. (2005). *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.

George, T.L. & Dobkin, D. (eds.). (2002). The effects of habitat fragmentation on western bird populations. *Studies in Avian Biology*, **25**, 4–7.

Gleick, J. (1987). Chaos: making a new science. Vintage, New York, USA.

Groffman, P.M., Baron, J.S., Blett, T., et al. (2006). Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, **9**, 1–13.

Gunderson, L.H. & Holling, C.S. (2002). *Panarchy: Understanding Transformations in Human and Natural Systems*. Island Press, Washington, DC, USA.

Hanski, I. & Gaggiotti, O.E. (eds.). (2004). *Ecology, Genetics, and Evolution of Metapopulations*. Elsevier, Amsterdam, The Netherlands.

Hobbs, R.J., & Suding, K.N. (2009). *New Models for Ecosystem Dynamics and Restoration*. Island Press, Washington, DC, USA.

Hobbs, R.J., Arico, S., Aronson, J., et al. (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holling, C.S. & Gunderson, L.H. (2002). Resilience and adaptive cycles. In *Panarchy: Understanding Transformations in Human and Natural Systems* (ed. L.H. Gunderson and C.S. Holling), pp. 25–62. Island Press, Washington, DC, USA.

Holling, C.S., Gunderson, L.H., & Peterson, G.D. (2002). Sustainability and panarchies. In *Panarchy: Understanding Transformations in Human and Natural Systems*. In (ed. L.H. Gunderson and C.S. Holling), pp. 63–102. Island Press, Washington, DC, USA.

Irland, L.C. (1999). *The Northeast's Changing Forest*. Harvard University Press, Cambridge, MA, USA.

Irland, L.C., Camp, A.E., Brissette, J.C., & Donohew, Z.R. (2006). Long-term silvicultural and ecological studies: results for science and management. GISF Research Paper 005. Yale University, Global Institute of Sustainable Forestry, New Haven, CT, USA.

Jetz, W., Wilcove, D.S., & Dobson, A.P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**(6), e157. doi: 10.1371/journal.pbio.0050157.

Keller, E.F. (1983). *A Feeling for the Organism*. W.H. Freeman and Company, New York, USA.

Landres, P., Morgan, P., & Swanson, F.J. (1999). Overview and use of natural variability concepts in managing ecological systems. *Ecological Applications*, **9**, 1179–1188.

Likens, G.E. (ed.). (1989). *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, New York, USA.

Liu, J., Hull, V., Morzillo, A., & Wiens, J. (eds.). (2011). *Sources, Sinks, and Sustainability*. Cambridge University Press, Cambridge, UK.

Logan, J.A. & Powell, J.A. (2001). Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, **47**, 160–173.

Logan, J.A., Régnière, J., & Powell, J.A. (2003). Assessing the impacts of global climate change on forest pests. *Frontiers in Ecology and the Environment*, **1**, 130–137.

Mack, R.N. (1981). Invasion of Bromus tectorum L. into Western North America: an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.

May, R.M. (1974). Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science*, **186**, 645–647.

Millar, C.I. & Woolfenden, W.B. (1999a). The role of climate change in interpreting historical variability. *Ecological Applications*, **9**, 1207–1216.

Millar, C.I. & Woolfenden, W.B. (1999b). Sierra Nevada forests: where did they come from? Where are they going? What does it mean? In *Transactions of the 64th North American Wildlife and Natural Resources Conference*. pp. 206–236.

Millar, C.I., Stephenson, N.L., & Stephens, S.L. (2007). Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, **17**, 2145–2151.

Milly, P.C.D., Betancourt, J., Falkenmark, M., Hirsch, R.M., Kundzewicz, Z.W., Lettenmaier, D.P., & Stouffer, R.J. (2008). Stationarity is dead: whither water management? *Science*, **319**, 573–574.

Moir, W.H., Franklin, J.F., & Maser, C. (1973). Lost forest research natural area: supplement 3 to Federal research natural areas in Oregon and Washington, a guidebook for scientists and educators. Miscellaneous publication 271. USDA Forest Service, Portland, OR, USA.

Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.

Peterson, D.L. & Parker, V.T. (eds.). (1998). *Ecological Scale: Theory and Applications*. Columbia University Press, New York.

Peterson, G., Allen, C., & Holling, C.S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.

Pielke, R.A., Sr., Marland, G., Betts, R.A., et al. (2002). The influence of land-use change and landscape dynamics on the climate system: relevance to climate-change policy beyond the radiative effect of greenhouse gases. *Philosophical Transactions of the Royal Society of London A*, **15**(360), 1705–1719.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., & Romme, W.H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*, **58**, 501–517.

Rohde, K. (2005). *Nonequilibrium Ecology*. Cambridge University Press, Cambridge, UK.

Scheffer, M., Bascompte, J., Brock, W.A., et al. (2009). Early-warning signals for critical transitions. *Nature*, **461**, 53–59.

Schmid, J.M., & Mata, S.A. (2005). Mountain pine beetle-caused tree mortality in partially cut plots surrounded by unmanaged stands. Research Paper RMRS-RP-54. USDA Forest Service, Fort Collins, CO, USA.

Schoonmaker, P.K. (1998). Paleoecological perspectives on ecological scale. In *Ecological Scale: Theory and Applications* (ed. D.L. Peterson and V.T. Parker), pp. 79–103. Columbia University Press, New York.

Sharpe, D.M., Guntenspergen, G.R., Dunn, C., Leitner, L.A., & Stearns, F. (1987). Vegetation dynamics in a southern Wisconsin agricultural landscape. In *Landscape Heterogeneity and Disturbance. Ecological Studies*, Vol. 64 (ed. M.G. Turner), pp. 137–155. Springer-Verlag, New York.

Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., Alexander, J.D., & Wiens, J.A. (2009). Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE*, **4**(9), e6825. doi: 10.1371/journal.pone.0006825.

Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V., & Kratz, T.K. (1993). A revised concept of landscape equilibrium: disturbance and stability in scaled landscapes. *Landscape Ecology*, **8**, 213–227.

Turner, M.G., Romme, W.H., & Tinker, D.B. (2003). Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.

Whisenant, S.G. (1990). Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In *Proceedings: Symposium on Cheatgrass Invasion, Shrub Die-off and Other Aspects of Shrub Biology and Management*. (E.D. McArthur, E.M. Romney, S.D. Smith, and P.T. Tueller, compilers), pp. 4–10. General Technical Report GTR-INT-276. USDA Forest Service, Ogden, UT, USA.

White, P.S., & Walker, J.L. (1997). Approximating nature's variation: Selecting and using reference information in restoration ecology. *Restoration Ecology*, **5**, 338–349.

Whitney, G.G. (1994). *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America 1500 to the Present*. Cambridge University Press, New York, USA.

Wiens, J.A. (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological Communities: Conceptual Issues and the Evidence* (ed. D.R. Strong Jr., D. Simberloff, L.G. Abele, and A.B. Thistle), pp. 439–457. Princeton University Press, Princeton, NJ, USA.

Wiens, J.A. (1989). Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Wiens, J.A. (1992). Ecological flows across landscape boundaries: a conceptual overview. In *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows* (ed. A.J. Hansen and F. di Castri), pp. 217–235. Springer-Verlag, New York, USA.

Wiens, J.A. (1995). Recovery of seabirds following the Exxon Valdez oil spill: an overview. In *Exxon Valdez Oil Spill: Fate and Effects in Alaskan Waters*. ASTM Special Technical Publication 1219 (ed. P.G. Wells, J.N. Butler, and J.S. Hughes), pp. 854–893. American Society for Testing and Materials, Philadelphia, PA, USA.

Wiens, J.A., Stenseth, N.C., Van Horne, B., & Ims, R.A. (1993). Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369–380.

Williams, J.W., Jackson, S.T., & Kutzbacht, J.E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA*, **104**, 5738–5742.

Wu, J. (2007). Scale and scaling: a cross-disciplinary perspective. In *Key Topics in Landscape Ecology* (ed. J. Wu and R.J. Hobbs), pp. 115–142. Cambridge University Press, Cambridge, UK.