Practical Approaches to the Conservation of Biological Diversity

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ISLAND PRESS
Washington, D.C. • Covelo, California

Library of Congress Cataloging-in-Publication Data
Practical approaches to the conservation of biological diversity /
edited by Richard K. Baydack, Henry Campa III, Jonathan B. Haufler.
p. cm.
Includes bibliographical references and index.
ISBN 1-55963-543-6 (cloth : alk. paper). — ISBN 1-55963-544-4
(pbk. : alk. paper)
1. Biological diversity conservation—Congresses. I. Baydack, Richard K. II. Campa, Henry. III. Haufler, Jonathan B.
QH75.A1P735 1999 98-25753
333.95'16—dc21 CIP

Printed on recycled, acid-free paper

Manufactured in the United States of America
10 9 8 7 6 5 4 3 2 1

Chapter 5

Application of Historical Range of Variability Concepts to Biodiversity Conservation

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In the age of ecosystem management, no single theme has dominated the conservation of biological diversity more than the role of disturbance in maintaining ecosystem composition, structure, and function. The relationship between ecosystem complexity and dynamic processes is not an entirely new topic in ecology; succession, the changes that occur in ecological communities after disturbance, has been a central focus of ecology since the advent of the science (Clements 1916; Watt 1947), and the role that fire plays in maintaining natural ecosystems has been acknowledged for decades (see review by Parsons 1981). Nevertheless, the ubiquity of disturbance as an organizing force in ecosystems has only recently become widely appreciated (Pickett and White 1985; Botkin 1990). It is now understood that ecosystem conditions change over time as they are affected by disturbance; when disturbances act with a characteristic behavior, ecosystems exhibit a characteristic behavior and complexity. When humans act to alter disturbance patterns, such as through traditional logging or fire suppression, ecosystems change. As Pickett et al. (1992) noted, "Human-generated changes must be constrained because nature has functional, historical, and evolutionary limits. Nature has a range of ways to be, but there is a limit to those ways, and therefore human changes must be within those limits." The attempt to understand and apply these limits to sustain the complexity and dynamics of ecosystems is the subject of this chapter.

What Is Historical Range of Variability?

All ecosystems may be described in terms of composition, structure, and function (Landres et al. 1998). "Composition" refers to the abundance, or relative abundance, of components, such as water, nutrients, and species, that make up the ecosystem. "Structure" refers to their physical arrangement in space, and "function" refers to the processes through which composition and structure interact, including predation, decomposition, and disturbances, such as fire and floods. Because ecosystems are dynamic, these attributes are constantly changing, but composition, structure, and function are constrained within limits. The bounded behavior of an ecosystem can be called its "range of variability."

Figure 5.1 provides a simplistic illustration of range of variability, a hypothetical fluctuation of old-growth acreage within a watershed. Over time, old-growth acreage increases as stands mature until a large, catastrophic disturbance event, such as fire, consumes some old growth and the acreage declines. The dynamics of old growth in this system describe the range of variability of this ecosystem component.

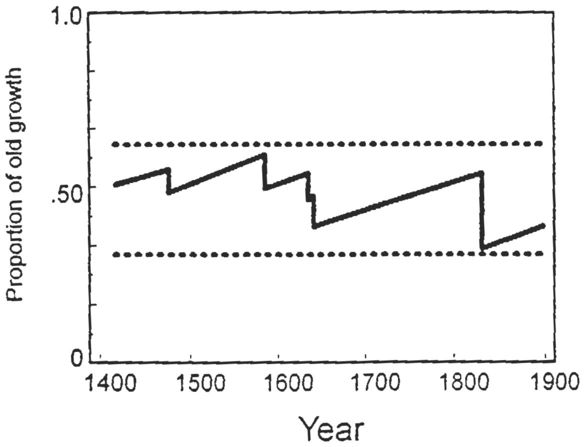

Figure 5.1. Graphical representation of historical range of variability showing fluctuation in the area of old growth in a hypothetical watershed.

The phrase "range of variability" has been justly criticized for failing to communicate important aspects of ecosystem behavior (Rhodes et al. 1994; Frissell and Bayles 1996), and some authors have concerned themselves only with the range of, or difference between, high and low values of ecosystem attributes (Caraher et al. 1992). However, most authors who have explored the meaning and utility of the concept have agreed with Morgan et al. (1994) that "the rate of change in ecosystem characteristics is as important to the concept of historical range of variability as is the magnitude of historical fluctuations." In other words, the phrase "range of variability" conveys much more than extreme values; it also describes rates of change and duration of states represented by the fluctuations (Swanson et al. 1994; Morgan et al. 1994; Landres et al. 1998). The range of variability is thus a portrait of the dynamic behavior of an ecosystem.

The range of variability concept can also be thought of as a dynamic version of a well-established model in ecology. Over a forty-year period, Jenny (1941, 1980) refined a model of ecosystem development that he called the "state factor model." According to the state factor model, the state of any ecosystem, *e*, is a function of a relatively small number of "state factors," including local climate (*cl*), the organisms available to colonize the site (*o*), topographic relief (*r*), soil parent material (*p*), time since the last disturbance (*t*), and additional, unspecified factors. (Jenny represented this model as $e = f(cl, o, r, p, t \ldots)$, thus, the model is sometimes known as the "clorpt model.") Recent developments in disturbance ecology have shown that other factors besides time since the last disturbance are important (White and Pickett 1985), so *t* is probably better thought of as describing a multifactor "disturbance regime." In dynamic ecosystems, the behavior of ecosystems should remain bounded as long as the state factors controlling ecosystem behavior are themselves bounded.

"Historical range of variability" (HRV) describes the bounded behavior of ecosystems prior to the dramatic changes in state factors that accompanied the settlement of North America, beginning with the discovery of the "New World." For several thousand years prior to colonization, topographic relief and parent material remained relatively constant. Climate fluctuated but narrowly, relative to the Quaternary or even the entire Holocene (Johnson et al. 1994; Woolfenden 1996). Rates of extinction and species arrival were relatively low (OTA 1993), and disturbance operated according to characteristic regimes (Mooney et al. 1981). Population levels and technologies of indigenous people may have had widespread ecological impacts, which were severe in some localized cases (Betancourt and Van Devender 1981), but as those impacts were relatively consistent across the landscape over several thousand years (see, for example, Anderson and Moratto 1996). Resulting ecosystems were likewise bounded in their behavior; they maintained characteristic species composition, pattern, and behavior.

Since European settlement, many ecosystems have changed dramatically as a result of changes in state factors. The organism state factor has been altered as some species have become extinct and many others have been introduced from other continents (OTA 1993). The disturbance state factor has been even more dramatically changed. Through forest clearing, agriculture, timber harvest, fire suppression, and other effects, the composition, structure, and function of entire regions have changed (Thomas 1956; Whitney 1994). While Native Americans manipulated the landscape for thousands of years, their technologies were far different from those employed by European settlers (Cronon 1983; Anderson and Moratto 1996). The recent colonization of North America may be thought of not as a biological invasion, but as a technological invasion—with devastating effects on biodiversity and ecosystem integrity. The concept of HRV is useful in describing ecosystem dynamics prior to these dramatic changes—the ecosystem dynamics that had sustained biodiversity and ecosystem integrity over the thousands of years before the devastating changes of the last few hundred years.

This bounded ecosystem behavior goes by a number of different names, including "range of natural variability" (Caraher et al. 1992; Landres et al. 1998), "natural variability" (Swanson et al. 1994), and "reference variability" (Manley et al. 1995). "Historical range of variability" differs from the others by conveying a sense of time, an essential quality of the concept (Morgan et al. 1994), and it avoids use of the term "natural," which has been criticized because of the ubiquity of human impacts in ecosystems, the changing nature of ecosystems over time, and the imprecision of descriptions of communities and ecosystems in ecological literature (Schrader-Frechette and McCoy 1995; Hunter 1996). By explicitly acknowledging the time frame of observation and the role of humans in shaping ecosystems, HRV can provide an approximate description of "natural conditions" that addresses these criticisms (Comer 1997). Though we prefer the use of "historical," we intend that HRV be interpreted as a description of "natural conditions."

The assumption behind the use of HRV in management is that "restoring and maintaining landscape conditions within distributions that organisms have adapted to over evolutionary time is the management approach most likely to produce sustainable ecosystems" (Manley et al. 1995). According to this approach, if landscapes can be maintained within HRV, or a socially preferred range based on HRV, those landscapes stand a good chance of maintaining their biodiversity and integrity over time. Sustainable management employs historical information as a reference for restoring and maintaining the patterns and processes characteristic of North American landscapes prior to recent alteration.

Of course, no management approach can be expected to provide a "silver bullet," and HRV has sustained its share of criticism. Obtaining historical information for many important aspects of ecosystems is difficult, variation in ecosystem conditions (especially climate) limits its usefulness, HRV is scale dependent, and presettlement conditions have been criticized as an arbitrary model for the future (Rhodes et al. 1994; Hunter 1996; Millar 1997). Nevertheless, historical information can be very helpful in understanding and illustrating the dynamic nature of ecosystems, the processes that sustain and change ecosystems, the current state of the system in relation to the past, and the possible ranges of conditions that are feasible to maintain (Morgan et al. 1994). To ignore historical information because of the difficulties it presents "would be to throw the baby out with the bathwater" (Millar 1997).

In theory, there is no limit to the number of ecosystem variables that can be used to describe HRV. HRV can describe changes in soil conditions, animal population sizes, composition of the plant community, stream sediment loads, air quality, human communities, or any other aspect of ecosystems that can be quantified. Indicators of ecosystem condition can be characterized with respect to HRV to help understand management impacts and preferred directions for the future. Manley et al. (1995) compiled over three dozen "key ecosystem elements" for which historical ranges can guide management. In practice, however, historical information is very difficult to obtain for most aspects of ecosystems (Rhodes et al. 1994; Millar 1997). In most cases, HRV should be limited to those few aspects of ecosystem condition for which historical information is available or can be confidently inferred. Some of the best sources of historical information include tree rings, fire scars, and pollen cores, which can divulge information about species composition and disturbance regimes hundreds or even thousands of years ago. If changes in conditions can be understood in terms of processes, historical information can be used in conjunction with simulation models to infer HRV (Baker 1992), though investigators must be careful not to "pile inference upon inference" (Millar 1997).

In general, the ecosystem attribute for which we seem to have the most historical information is vegetation, particularly forests; thus, HRV is often described, appropriately, in terms of forest composition (e.g., hectares of old growth), structure (e.g., patch size distribution), and function (e.g., fire frequency). While there is much more to the description of ecosystem composition, structure, and function than vegetation, this one feature can provide insights into a broad range of ecosystem attributes, including wildlife habitat, aquatic systems, visitor experience, and fire behavior. As Manley et al. (1995) noted, "The vegetation mosaic is a Key Ecosystem Element when determining habitat suitability for all biological species and individuals."

Application of HRV to the Conservation of Biodiversity

The objective behind the application of HRV to biodiversity conservation is to sustain into the future the ecosystem conditions that sustained biodiversity prior to the dramatic changes of the recent past. Fundamental to this approach is the concept of "representation" (Noss and Cooperrider 1994), which aims to maintain on the landscape conditions that represent all of the variety extant in nature. Historically, representation has been used to help identify lands (for example, vegetation types) that should be included in a conservation reserve system (see Chapters 2 and 3). This is the same approach to conservation advocated in the 1920s by the Committee on the Preservation of Natural Conditions of the Ecological Society of America (Shelford 1926) and later by The Nature Conservancy (1982). Representation was also used by the USDA Forest Service in its evaluation of the wilderness potential of roadless areas (RARE II) in the 1970s (Foreman 1995–96). Alternatively, representation can be achieved by maintaining the historical range of variability across the landscape, both in reserved and nonreserved lands.

Application of HRV to Improve Coarse-Filter Conservation

As a basis for determination of a reserve system, representation is certainly a key concept, but it is insufficient. Representation addresses only the question of what to protect, not how much or in what arrangement or how to sustain it in a dynamic ecosystem. Understanding the historical ecosystem behavior implicit in the concept of HRV can help improve reserve-based conservation by providing insights into the kinds and amounts of ecological elements that should be included in a coarse-filter reserve system (see Chapter 2) and what processes are necessary to sustain them into the future.

Because both HRV and coarse-filter conservation generally involve descriptions of vegetation, insights derived from HRV analysis can be readily applied to improve the coarse-filter approach. For example, coarse filters have been criticized for employing vegetation classification systems that fail to account for the dynamic nature of vegetation (Hunter 1991). Analysis of HRV can help identify dynamic stages of vegetation within vegetation types, and coarse-filter protection can be applied to those dynamic stages. Also, coarse filters are traditionally applied to existing vegetation evenly, without regard to the historical importance of vegetation classes. By describing the bounded abundance of vegetation types and seral stages, HRV can help identify the appropriate amount of each vegetation class that should be included in a reserve, and it can help identify for protection those vegetation elements that were important historically but that are rare or absent today (Haufler 1994).

Other aspects of reserve design not adequately addressed by traditional coarse-filter approaches are habitat arrangement and patch size. Representation fails to account for the juxtaposition of vegetation patches and its influence on ecosystem function (Chapel et al. 1995). For example, species that forage at the boundary between two vegetation types will find no suitable habitat if the two types are protected on separate tracts of the coarse-filter reserve system. Also, distance between patches can affect dispersal and colonization and limit reserve effectiveness (Soulé and Simberloff 1986). Patch *size* is also an important variable determining the suitability of habitat for many species (Robbins et al. 1989; Thomas et al. 1990). The effectiveness of a reserve system may be improved if vegetation patch size and arrangement are informed by historical analysis of the landscape. Reconstruction of historical patch dynamics (see, for example, Morrison and Swanson 1990) can reveal insights into these important variables. Ultimately, the goal of reserve design is to identify an area in which natural disturbance processes will maintain these characteristics over time.

The application of historical dynamics to reserve design is not entirely new. Pickett and Thompson (1978) introduced the phrase "minimum dynamic area" to describe "the smallest area with a natural disturbance regime, which maintains internal recolonization sources, and hence minimizes extinction." These authors recognized that disturbances would inevitably change the very conditions for which a reserve was established unless the reserve were large enough to "absorb" characteristic disturbances. Such a reserve would be in a state of "dynamic equilibrium"; the proportion of vegetation patches would remain constant, though the location of patches in various stages of development would change over time (Shugart and West 1981). The advantage of setting reserve size above the minimum dynamic area based on HRV is that natural disturbance can continually refresh the appropriate amount of habitat and maintain appropriate patch-size and juxtaposition, provided that the disturbance regime has not been fundamentally altered.

Application of HRV to Achieve Representation across the Landscape

To summarize the above discussion, the coarse-filter approach to conservation attempts to sustain biodiversity by protecting examples of plant communities over time. These reserves must be large enough to sustain viable populations of constituent species and be capable of sustaining their character in the face of disturbance. Where species have minimal habitat requirements and disturbances are small and infrequent, this can be accomplished on relatively small areas. Where territories and disturbances are large, reserves must be carefully planned to provide adequate habitat and endure inevitable disturbance.

It is increasingly clear, however, that even the very largest reserves are insufficient to meet the conservation requirements of a coarse-filter system. Populations of grizzly bears, bison, and elk rely upon the millions of hectares of wilderness and roadless areas outside Yellowstone National Park to meet their habitat needs (Harting and Glick 1994). Eight hundred and ten thousand hectares were not enough to protect half of the reserve from being consumed by fire in 1988. The conservation of late-successional forest ecosystems in the Pacific Northwest required approximately 3 million hectares of reserves distributed around the region, but even these reserves were insufficient to conserve the ecosystem without riparian reserves and management guidelines for the intervening lands (FEMAT 1993). It is now also clear that conservation cannot be accomplished on reserves alone; reserves must be integrated with management guidance on the rest of the landscape to stitch together a functional landscape ecosystem.

Analysis of HRV can help identify the elements of biodiversity to be protected in reserves and can help develop prescriptions for intervening lands that will sustain the landscape. Instead of protecting some of everything, the coarse filter should sift out those rare, valuable, or slowly changing portions of the landscape ecosystem identified through analysis of historical ecosystem behavior. As an example, old growth may exist in places that are refugia from fire (Camp 1995); these settings can be identified for protection in reserves. In addition to plant communities, rare elements of landscape diversity, such as roadless areas, and biodiversity hotspots are worthy candidates for protection even if they are relatively dynamic. Large blocks of land with high ecological integrity are likewise outstanding candidates for inclusion in a coarse-filter reserve network as they retain the highest likelihood of continued integrity in the absence of human intervention. Protecting large blocks with high integrity and smaller tracts supporting key elements of biodiversity recognizes the hierarchical nature of ecosystems by employing a structured system that spans multiple spatial scales (Sullivan and Shaffer 1975; Noss and Cooperrider 1994).

On lands outside of reserves, HRV can help identify the communities, patterns, and processes necessary to sustain the integrity of the landscape ecosystem. It is on these "matrix" lands that HRV has its greatest potential as a model for sustainable management. Franklin (1993) identified three critical roles for nonreserve matrix lands in conserving biodiversity: (1) providing habitat at smaller spatial scales, (2) increasing the effectiveness (buffering) of reserved areas, and (3) providing for connectivity. All three of these roles can be enhanced by application of historical information to matrix management.

Just as an understanding of historical ecosystem behavior can be used to guide the identification of reserves, that same information can be used to derive objectives for vegetation management in the matrix. Under this approach, the overarching goal of matrix management would have to change from maximizing production to sustaining biodiversity. Production of fiber and forage would remain appropriate uses of the matrix, but the objective of management would be to sustain historically appropriate seral patches across the landscape.

Managing the matrix as a dynamic mosaic allows for both the harvesting of materials and the production of key habitats away from reserves. It also addresses one of the principal shortcomings of reserve-based biodiversity conservation: the inevitable loss of habitat from disturbance (Keeton and Aplet 1997). Maintaining HRV in the matrix ensures the availability of a continuous supply of replacement habitat to replenish that lost from reserves (provided that both reserves and matrix lands have the same potential to provide habitat).

Managing the matrix within HRV also extends the effectiveness of biodiversity reserves. As already discussed, many reserves are of insufficient size to conserve viable populations of constituent species. Managing the landscape within HRV effectively increases the size of the landscape that can support native biodiversity. Advocates of the "core reserve approach" to conserving biodiversity (Noss and Cooperrider 1994; DellaSala et al. 1996) often describe a "multiple-use buffer zone" that is managed to increase the effective size of a reserve. Managing the matrix to sustain historical ecosystem conditions, rather than for maximum production, would serve the purpose of extending the effectiveness of reserves without requiring the explicit designation of a buffer zone (Franklin 1993).

Finally, maintaining the matrix within HRV would provide a level of connectivity across the landscape consistent with historical ecosystem function and the needs of constituent species. Many reserve-based conservation strategies rely on habitat corridors to maintain connectivity across the landscape (Noss and Cooperrider 1994). However, the effectiveness of corridors has been challenged because of a lack of evidence that itinerant or dispersing species will actually use them (Simberloff et al. 1992). Maintaining the landscape mosaic within historical conditions would provide the habitat distribution similar to that which dispersing species historically encountered, rather than requiring them to follow predetermined habitat corridors.

It should be noted that applying HRV to land management in the absence of reserves is not advocated here. In a perfect world, the landscape might have been managed to maintain historical conditions without interim protection for lands of high ecological integrity. Unfortunately, the world we have inherited has suffered decades to centuries of human impacts that now threaten its integrity. Restoring healthy ecosystems is not simply a matter of managing within the "free space" (Frissell and Bayles 1996) or "slop" (Aplet et al. 1993) that we hope exists in natural ecosystems. Instead, we must protect ecosystem integrity where it remains high and work on the degraded lands to restore HRV to the whole landscape (Keeton and Aplet 1997). Only once ecosystem health has been restored to the broader landscape can we turn our attention toward harvesting the redundancy or "free space" in ecosystems. As Frissell and Bayles (1996) have said, "[I]f there ever was a free lunch, we already ate it."

Viewing the landscape as an integrated complex of reserve and matrix, with each designed and managed to sustain historical pattern and process, requires a change in the way we think about the land. Traditionally, wilderness areas have been "set aside" and protected for natural values. By implication, lands outside wilderness have been the object of management and are not meant to be natural. But ecosystem research is showing that ecosystems do not end at the borders of reserves. Sustaining ecosystems requires attention to the whole landscape. It is this integrated, whole landscape of reserves and matrix lands that must become the object of management (Franklin 1993). Reserves, including wilderness, can no longer be thought of as "protected from management." Management practices in and out of reserves will differ, but the land must be seen as one.

Barriers to the Application of HRV

Unfortunately, as is so often the case in natural resource management, what appears simple in concept is quite complex in practice. One factor complicating application of HRV is how to translate fluctuation into a management objective. Research in disturbance-prone ecosystems has demonstrated that variability itself can be important to the life histories of many organisms. Managing ecosystem attributes at a constant level, even if it is within HRV, fails to produce the heterogeneity important to ecosystem function (Christensen 1988; Baker 1992; Rhodes et al. 1994). For instance, short-term fluctuations in habitat availability and corresponding fluctuations in population sizes do not necessarily jeopardize species or populations in a dynamic system; however, long-term persistence of population sizes at low historical thresholds can create problems through inbreeding, genetic drift, and increased susceptibility to random environmental and demographic events (Shaffer 1981). Christensen (1988) concluded, "In many ecosystems, one of the most important consequences of fire (or natural disturbance in general) is to maintain landscape heterogeneity. The simulation and maintenance of that heterogeneity is one of the most significant challenges to natural landscape managers."

Aquatic systems present a special challenge in this regard. Riparian and aquatic ecosystems are highly dependent on disturbance for rejuvenation and inputs of resources. Often, natural disturbances are quite violent, exceeding the perturbations caused by humans (Frissell and Bayles 1996). Instead, human impacts tend to be chronic, arising "from the cumulative and persistent effects of thousands of miles of roads, thousands of dams, and century of logging, grazing, mining, cropland farming, channelization, and irrigation diversion" (Frissell and Bayles 1996). Simply managing "within the range of natural variability" will not maintain the temporal heterogeneity necessary to sustain the natural function of these ecosystems. The 1996 release of floodwaters from Glen Canyon Dam through the Grand Canyon was an explicit attempt to reintroduce a dramatic perturbation to a disturbance-dependent ecosystem that had experienced too little fluctuation (Wegner 1996). Developing similar prescriptions to sustain disturbance processes and heterogeneity presents a tremendous challenge.

Another factor complicating application of HRV is scale (Morgan et al. 1994). It is now widely recognized that ecosystems occur at a variety of spatial scales, with smaller systems nested in larger systems in a hierarchical fashion. Properties of large ecosystems are the product of the properties of smaller constituent ecosystems. For example, the forest vegetation of the central Rockies may be thought of as occurring in three zones: ponderosa pine at the low elevations, lodgepole pine at mid-elevations, and spruce-fir forest in the subalpine zone. At a smaller scale, say the subalpine zone of Rocky Mountain National Park, one finds that lodgepole and spruce-fir forests are often found on adjacent slopes, depending on aspect. At the scale of a small watershed, vegetation may vary dramatically, depending on time since catastrophic fire. Different processes operate at each scale to produce the observed patterns. Observations of ecosystem phenomena are thus scale dependent. How we characterize pattern is a function of the scale of observation.

HRV is no different. Observed fluctuations in, for instance, old-growth acreage are going to be very different, depending on whether that observation is made at the scale of a watershed, a national forest, or a region (Figure 5.2). In a small watershed subject to large disturbance, old-growth acreage may fluctuate widely but infrequently, as

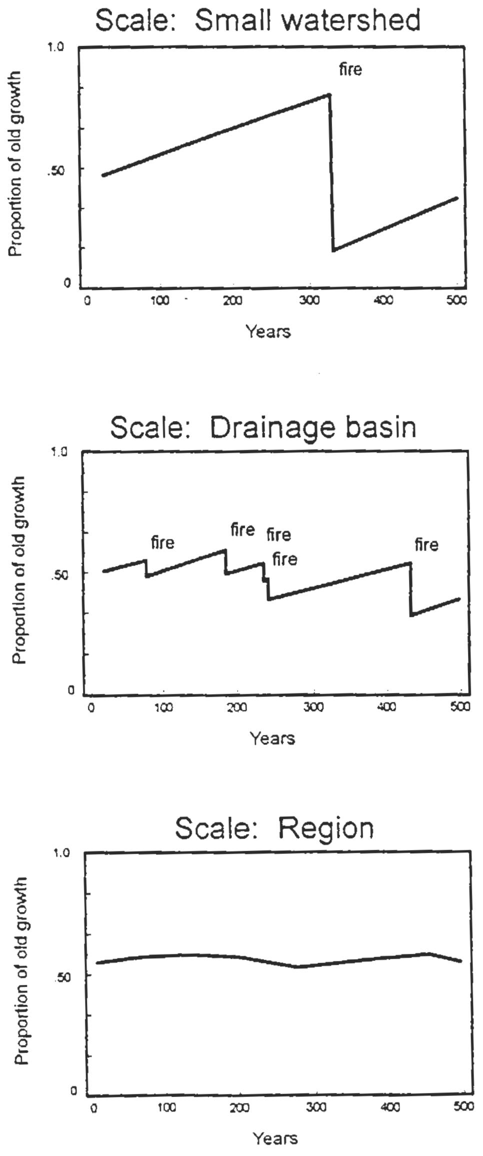

Figure 5.2. The historical range of variability for any given variable is a function of the scale of observation.

in the case of the rare catastrophic fire killing trees over a large area. However, at the scale of the national forest, fire resulting in the loss of old growth somewhere in the forest is a more frequent phenomenon, ensuring that old growth remains somewhere on the forest but never at the high proportion occurring in a single watershed. At the scale of the region, catastrophic fire somewhere in the region is virtually guaranteed on an annual basis, but the amount is small relative to the total, thereby dampening fluctuations. Variability in old-growth acreage reflects cyclic variability in regional fire weather (climate). Thus, HRV is very different, depending on the scale of observation.

The issue of scale dependence of HRV is important because misapplication of the concept to management may lead to inappropriate conclusions. For example, a watershed composed mostly of old growth may be targeted for harvest because it is "outside of HRV," according to the estimate of old-growth HRV derived at the regional scale. Such misapplication might lead to further loss of old growth from a region already drastically below HRV. The proper application of HRV would lead to conservation of watersheds with abundant old growth until old-growth HRV is restored at the landscape or regional scale. HRV should be assessed at the broadest scale first, then stepped down to the next level, reassessed, and so on down to the site level.

Another factor complicating the application of HRV is that disturbance itself is multidimensional. Not all patches are created equal. It sounds quite simple to say that the proper distribution of patch ages should be maintained in the managed forest. But the frequency of patch creation is not the only relevant factor. The disturbance regime that creates new patches can be characterized according to type of disturbance, frequency, predictability, size and shape of patches, intensity or severity, and seasonality (Pickett and White 1985; Agee 1993). Each of these factors can have long-lasting effects on the ecosystem. For example, studies in the Pacific Northwest have found that the effects of catastrophic or stand-replacing fires were extremely heterogeneous, creating a diversity of patch sizes, shapes, and configurations, with long-lasting consequences (Morrison and Swanson 1990). Not only does the distribution of patch *ages* need to be maintained within HRV, but so does patch *character*. It is not the creation of even-aged patches through management, per se, that has altered the character of Pacific Northwest forests to their current degraded state, but the frequency, intensity, and dispersion of 16-hectare clearcut blocks (Hansen et al. 1991). The cumulative effect of changing all these disturbance variables has been the loss of ecosystem integrity. A forest managed within HRV would not only contain significant older forest with the proper configuration, but it would also contain young patches with size, shape, composition, and structure within the HRV of young patches.

HRV is only applicable to management if changes in the factors controlling ecosystems have not permanently altered ecosystem conditions. In some places, fire suppression, grazing, and logging have transformed disturbance regimes. Simply reintroducing disturbance may produce effects outside of any historical precedent, driving the system farther from, rather than closer to, HRV. Likewise, biological invasions have changed the function of whole ecosystems (Vitousek 1986). Our ability to restore historical composition may be seriously constrained by cost, even where we know what we need to do. Finally, the application of HRV may lose all utility under a dramatically altered climate. Where future conditions are not at all like the past, historical behavior is of little use as a management guide.

Summary and Conclusions

Historical range of variability can be a useful tool for thinking about the characteristics of dynamic ecosystems. It can provide a basis for a reserve system and for the management of the intervening matrix if it properly reflects scale dependence and the complexity of the post-disturbance environment. But the application of HRV to conservation is truly a coarse filter. Follow-up fine-filter assessment and conservation measures are absolutely essential to account for biological diversity at all hierarchical levels of organization. The HRV approach may have little utility in the conservation of rare or locally endemic species and assemblages. Used in tandem with a fine-filter approach, HRV provides a scientifically sound rationale for the construction of a comprehensive approach to conservation.

Nevertheless, we must be cautious in developing management prescriptions that ostensibly mimic conditions within HRV. Using the HRV approach means providing a full diversity of structural elements in variable configurations and quantities, with the ultimate objective being maintenance of dynamic patterns and processes that are integral to healthy ecosystems. But we are just beginning to comprehend the complexity of ecosystems; developing prescriptions to sustain that complexity presents a formidable challenge.

Finally, we close with a thought that turns the HRV/coarse-filter relation on its head. That is, not only can HRV be used to develop a coarse filter for land protection, but land protection is also needed as a coarse filter for HRV. Describing HRV requires protection of the remaining areas of high ecological integrity from which we can derive historical conditions. This is not a new concept; Aldo Leopold (1949) described a role for wilderness as "land laboratory" almost fifty years ago. If we are going to use HRV to guide management, protecting those intact parts of the landscape that can provide the key to the past is absolutely imperative. This reason alone is sufficient to demand that reserves be a significant component of any strategy that employs HRV as a guide for management.

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