Disturbance Regimes and the Historical Range of Variation in Terrestrial Ecosystems

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Glossary

Disturbance regime Cumulative effects of disturbance events over space and time.

Ecosystem management Conservation of major ecological services and restoration of natural resources while meeting society's needs for current and future generations.

Ecosystem process Any exchange of matter or energy within an ecosystem.

Focal landscape Area being evaluated in an HRV analysis. Historical range of variation (HRV) Expression of the full range of landscape characteristics that occurred in the past.

Disturbance Regimes

Picture a tranquil landscape with undulating topography, idyllic streams, scenic glades, and verdant vegetation. Left to its own devices, this landscape would gradually become dominated by late successional communities that would slowly shift in response to climate changes over long time periods. This scene often forms the foundation and reference for most land management across the globe. However, this peaceful panorama rarely happens in nature because gradual successional change rarely drives landscape dynamics. Abrupt change is usually the rule, with vegetation development suddenly truncated by a set of ecological processes more dynamic than succession: disturbance. A wide variety of insect, disease, animal, fire, weather, and even human disturbances can interact with current and antecedent vegetation and climate to perturb the landscape and create a shifting mosaic of diverse seral vegetation communities and stand structures that in turn affect those very disturbances that created them. This complex interaction of vegetation, climate, and disturbance results in unique landscape behaviors that foster a wide range of landscape characteristics, which ensures high levels of biodiversity. The impacts of disturbances on landscape pattern, structure, and function drive most ecosystem processes, and it is disturbances that ultimately set the bounds of management for most landscapes of the world. In this chapter, disturbance regimes are discussed in terms of how they affect landscape dynamics and how historical disturbance regimes can form the range and variation of possible landscape conditions that can be used as a reference for managing today's landscapes.

Background

"Disturbance regime" is a general term that describes the temporal and spatial characteristics of a disturbance agent and the impact of that agent on the landscape. More specifically, a disturbance regime is the cumulative effects of multiple disturbance events over space and time. Any description of a **Mosaic** Spatial patch distribution of vegetation communities.

Scale Temporal or spatial extent before some quantity of interest changes.

Simulation buffer Area surrounding the context

landscape that allows for the spread of spatial processes into the context landscape.

Simulation landscape Area being simulated to produce an HRV time series that usually includes both the context landscape and the simulation buffer.

Succession Process of plant assemblages replacing another; vegetation development.

disturbance regime must encompass an area that is large enough that the full range of disturbance sizes are manifest and with time measurement that is long enough that the full range of disturbance characteristics are captured. It is important to recognize that disturbance regimes are fundamentally different from individual disturbance events; for ecological restoration to succeed, for example, disturbance regimes should be emulated, not individual disturbance events, to fully capture the range and variation of disturbance effects. Biodiversity is intricately linked to disturbance regimes in that disturbances create shifting mosaics of diverse plant communities and habitats across a landscape (Watt, 1947), and the spatial and temporal fluctuations of these communities ensure the conservation of biodiversity (Naveh, 1994). Biodiversity is highest when disturbance is neither too rare nor too frequent on the landscape (Grime, 1973).

In this chapter, disturbance regimes can be generally described by 11 characteristics (Table 1) (Simard, 1996; Agee, 1993, 1998; Skinner and Chang, 1996). The disturbance "agent" is the entity that causes the disturbance, such as wind, fire, and beetles. Sometimes disturbance agents have a "source" that triggers the agent. Lightning can be a source for wildland fire, and heavy snow loads may be the source for avalanches. The disturbance agent occurs at a particular frequency that is often described over a period of time, depending on scale and objective. Point-level measures, such as disturbance return interval and occurrence probability, describe the number of disturbance events experienced over time at one point on the landscape (Skinner and Chang, 1996; Baker and Ehle, 2001). Spatial measures of disturbance rotation and disturbance cycle estimate the number of years it takes to disturb an area the size of the landscape (Johnson and Gutsell, 1994; van Wagner, 1978; Reed et al., 1998). The frequency distribution of disturbance sizes on a landscape or region, for example, will depend primarily on the size and number of the largest events and landscape complexity (Yarie, 1981; Strauss et al., 1989).

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Characteristic	Description	Example					
Agent	Factor causing the disturbance	Mountain pine beetle is the agent that kills trees					
Source, cause	Origin of the agent	Lighting is a source for wildland fire					
Frequency	How often the disturbance occurs or its return time	Years since last fire or beetle outbreak (scale dependent)					
Intensity	A description of the magnitude of the disturbance agent	Mountain pine beetle population levels; wildland fire heat output					
Severity	The level of impact of the disturbance on the environment	Percent mountain pine beetle tree mortality; fuel consump in wildland fires					
Size	Spatial extent of the disturbance	Mountain pine beetles can kill trees in small patches or ac entire landscapes					
Pattern	Patch size distribution of disturbance effects; spatial heterogeneity of disturbance effects	Fire can burn large regions, but weather and fuels can influence fire intensity and therefore the patchwork of tree mortality					
Seasonality	Time of year of that disturbance occurs	Species phenology can influence wildland fires effects; spring burns can be more damaging to growing plants than fall burns on dormant plants					
Duration	Length of time of that disturbances occur	Mountain pine beetle outbreaks usually last for 3–8 years; fires can burn for a day or for an entire summer					
Interactions	Disturbance interact with each other, climate, vegetation, and other landscape characteristics	Mountain pine beetles can create fuel complexes that facilitate or exclude wildland fire					
Variability	The spatial and temporal variability of the above factors	Highly variable weather and mountain pine beetle mortality can cause highly variable burn conditionsm resulting in patchy burns of small to large sizes					

	Table	1	The 11 terms	used to d	lescribe di	isturbance	regimes	in this cl	apter from	Agee	(1993).	. Simard	(1996)	, and Skinner	and Chang	a (1996	j)
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Disturbance "intensity" is the level of the disturbance agent as it occurs on the landscape. Insect and disease intensities are often described by population levels. Wildland fire intensity is described by its heat output. Windthrow intensity can be described by wind speed. "Severity" is different from intensity in that it reflects the impact of that disturbance and its characteristics on the biophysical environment. The primary and direct effects of most disturbance agents are biotic damage and mortality, but some physical disturbances such as fire can act on abiotic factors such as soil fertility, necromass consumption, and atmospheric emissions. Most disturbance regimes are described by their cumulative severities because it is the most important factor that directly impacts land management.

Disturbance

Description

The "sizes" (area) and "patterns" (spatial variability) of disturbance events also shape disturbance regimes and influence biodiversity. Distributions of disturbance sizes reflect critical features of a disturbance regime, and many think that disturbance size distributions support the theory that they are self-organized processes (Malamud, 1998; Ricotta et al., 1999). Moreover, patterns of disturbance severity and intensity often dictate landscape heterogeneity, which influences a wide variety of landscape characteristics such as wildlife habitat, hydrology, biodiversity, and other disturbances (Turner, 1987; Knight, 1987; Gustafson and Gardner, 1996). "Pattern" refers to the size, shape, and spatial location of the perturbed patches. Seasonality is the time of year of the disturbance event because plant and animal phenology can produce differential spatial effects, and disturbance patterns are often linked with the "duration" of the disturbance agent on the landscape, with durations ranging from seconds (wind) and minutes (avalanches) to days (fire) and years (insects).

The last two terms are the most important and tend to cross over all other disturbance descriptive terminology. It is the "variability" of disturbance characteristics such as severity, frequency, and size, coupled with the *interaction* of these characteristics with other disturbance characteristics such as previous patterns, duration, and seasonality, and climate that make disturbance regimes some of the most complex processes governing landscape dynamics and controlling biodiversity. It is this great complexity that confounds the description and classification of disturbance regimes into the simple abstractions often used in land management (Ryan and Noste, 1985). The highly variable spatial and temporal feedbacks and interactions of landscape patterns with disturbance regimes so difficult to understand. It is far more illustrative to present the concept of disturbance regimes with an example from one of the world's most ubiquitous disturbances – wildland fire (Bowman *et al.*, 2009).

Disturbance Regime Example: Wildland Fire

Wildland fire regimes generally result from the cumulative interaction of fire, vegetation, climate, humans, and topography over time (Crutzen and Goldammer, 1993), though there are many other factors that influence disturbance regimes (e.g., other disturbances, weather, and fuels) (Figure 1). These interactions are spatially and temporally correlated. Future fires are influenced in space by the pattern of previously burned stands, fire-prone topographic features (e.g., midslopes, riparian bottoms), and areas with high fuel accumulations (e.g., older stands). They are influenced in time by the timing and severity of past climate (e.g., drought, wind), the rate of vegetation development (e.g., succession), and the frequency of other disturbance events (e.g., previous fires, insect outbreaks). A change in any of these factors will ultimately result in a change in the fire regime, and because all factors are constantly changing, fire regimes are inherently dynamic. For



Figure 1 Four of the most important factors affecting fire regimes and their interactions.

example, climate change can affect fire regimes by altering fire ignition patterns (i.e., lightning), vegetation characteristics, and fuels (Flannigan and Van Wagner, 1991; Balling *et al.*, 1992; Swetnam, 1993). And exotic invasions such as white pine blister rust (*Cronarium ribicola*), cheatgrass (*Bromus tectorum*), and spotted knapweed (*Centaurea maculosa*), have changed fire regimes in many semiarid ecosystems of the US (Whisenant, 1990; Knapp, 1997).

Fire regimes are created by the interaction of bottom-up and top-down controls (Heyerdahl et al., 2001). Bottom-up controls such as vegetation, fuels, topography, and patch distributions dictate fire spread, intensity, and severity at fine scales, and it is the bottom-up controls that can often be manipulated by land management. Coarse-scale, top-down controls are mostly climate and weather, which often dictate fire frequency, duration, and synchrony (Swetnam, 1990). Climate and weather trend signals are often embedded in a complex set of atmospheric teleconnections (simultaneous variations in climate observed over distant areas) interacting with land surface weather patterns. Drought-induced wildfires have been associated with global circulation anomalies such as the El Niño-Southern Oscillation (Swetnam and Betancourt, 1998; Heyerdahl et al., 2002) and more recently the Pacific Decadal Oscillation (Hessl et al., 2004). Coarse-scale, top-down climate interacts with fine scale landscape characteristics to influence the timing, size, frequency, and severity of fire events. As a result, a fire regime is actually a spatial disturbance gradient that does not follow discrete mapping units, so it should not be viewed as an attribute or characteristic of an ecosystem or cover type. Attempts to predict fire regimes solely from fuels (Olson, 1981), vegetation (Frost, 1998), or topography (Keane et al., 2004b) have only partially succeeded because they did not recognize the spatial pervasiveness of fire on the landscape and the multiscale interactions of all factors that control fire dynamics (Morgan et al., 2001)

The role of ignition in the formation of fire regimes is relatively misunderstood. Although fires can start from several sources such as spontaneous combustion, volcanic eruptions, and sunlight magnification, two sources start most wildland fires – lightning and humans. Ignition patterns are quite different between lightning and humans, with lightning strikes being mostly randomly distributed across landscapes over long temporal scales (Fuquay, 1980; Van Wagtendonk, 1991). Historical and contemporary peoples, however, have tended to light more fires along major transportation routes and settlements. These ignition patterns can create different fire regimes, depending on the geographical location. Lightning strikes in moist, productive ecosystems rarely start a fire because the fuel is too wet most years and the lightning occurs in the seasons when fuel is the wettest (Barrows *et al.*, 1977; Fuquay, 1980). Humans, however, can start fires when the fuel is driest and can control the number and types of ignition.

Fire regimes are most often described in terms of severity and frequency (Agee, 1998; Heinselman, 1981) (Table 1) because these two factors are usually the most important to land management and also because these two characteristics are probably the most important factors in creating fire regimes. In general, species with fire-adapted survival traits such as thick bark, high crowns, and sprouting tend to dominate landscapes with frequent fires, whereas other fire-adapted traits such as serotiny, soil seed banks, and far-ranging dispersal become important as fires become less frequent (Grime, 1979; Connell and Slayter, 1977). Although the size, pattern, and shifting mosaic of fire severity can be quite complex, severity types are often grouped into three general categories: (1) nonlethal surface fires, (2) mixed-severity fires, and (3) standreplacement fires. Nonlethal surface fires are usually frequent and burn surface fuels at low intensities, causing low mortality (<10%). Stand-replacement burns are usually rarer and reduce or kill the majority of the dominant vegetation, often trees and shrubs (90%) (Brown, 1995) as both lethal surface fires and active crown fires (Agee, 1993). Mixedseverity burns contain elements of both nonlethal surface and stand-replacement fires mixed in time and space (Arno et al., 2000; Perry et al., 2011). Passive crown fires, patchy standreplacement fires, and low-intensity underburns are common in mixed-severity burns (DeBano et al., 1998). Typically, mixed-severity fires are used to describe an area of patchy burn patterns created during one fire event. However, mixed-severity fire regimes can also be used to describe mixed-severity fires over time (e.g., nonlethal surface fire followed by stand-replacement fire) (Shinneman and Baker, 1997). There are other fire regime types, including ground fires (i.e., fire burning extensive organic layers), but they are not as prevalent as these three types (Agee, 1993).

Fire frequency and severity can be finely to broadly quantified using a number of field methods (Swetnam *et al.*, 1999; Humphries and Bourgeron, 2001; Heyerdahl *et al.*, 2001). Fire scar dates can be measured from trees, snags, stumps, and downed logs, but scarred trees are rarely distributed across large regions and diverse ecosystems at the densities needed to adequately describe fire regimes and corresponding landscape characteristics (Heyerdahl, 1997). Landscapes with long fire return intervals dominated by stand-replacement fire, for example, contain few fire-scarred trees. Charcoal samples from lake and ocean sediments and soil profiles provide important sources of historical fire data, but the temporal resolution of the data is often inadequate for quantifying the annual variation in fire regimes (Whitlock and Millspaugh, 1996). Burn-boundary maps or fire atlases are another source for quantifying fire regimes, but these maps usually span a short temporal scale and rarely describe fire severity (Rollins *et al.*, 2001).

Perhaps the best way to illustrate the impact of a fire regime on the landscape is to describe a specific example from the high mountains of western North America (see Box 1). Whitebark pine (Pinus albicaulis) forests are declining across most of their range because of the combined effects of the modification of three disturbance factors (Arno, 1986). Furthermore, predicted changes in climate brought about by global warming could further exacerbate the decline by increasing the frequency and duration of beetle epidemics, blister rust infections, and severe wildfires (Logan and Powell, 2001; Running, 2006). The loss of whitebark pine could have serious consequences for the biodiversity of upper subalpine ecosystems because it is considered a keystone species (Tomback et al., 2001). This "stone" pine produces large, wingless seeds that are an important food source for more than 110 animal species (Hutchins, 1994). In the Yellowstone ecosystem, the endangered grizzly bear (Ursus arctos horribilis) depends on whitebark pine seeds as a major food source, which it raids from red squirrel (Tamiasciurus hudsonicus) middens.

One major goal of ecosystem management, especially in the case of whitebark pine restoration, is to emulate historical disturbance regimes on contemporary landscapes to promote those processes that were considered necessary for healthy ecosystems. However, as is evident from the previous discussions, the complexity, interactions, and variability of disturbance regimes makes implementing historical disturbance regimes difficult if not impractical. An easier and more straightforward method of assessing ecosystem condition and evaluating ecosystem health was needed. The variability of historical disturbance regimes on landscape dynamics provided a foundation for a novel method of assessing ecosystem condition.

Historical Range and Variation

The Background

To effectively implement ecosystem management, land managers found it necessary to obtain a reference or benchmark to represent the conditions that described fully functional ecosystems (Cissel et al., 1994; Laughlin et al., 2004). Contemporary conditions could be evaluated against this reference to determine status, trend, and magnitude of change and also to design treatments that provide society with its sustainable and valuable resources while also returning declining ecosystems to a more natural or sustainable condition (Hessburg et al., 1999b; Swetnam et al., 1999). Ecologists and land managers were beginning to recognize that landscapes were not static but constantly changing, so it was critical that these reference conditions represented the dynamic character of ecosystems and landscapes as they vary over time and across space (Watt, 1947; Swanson et al., 1994). Describing and quantifying ecological health has always been difficult because ecosystems are highly complex, with immense biotic and

Box 1 Whitebark pine ecology, management, and HRV

Whitebark pine is a long-lived, seral tree of moderate shade tolerance that can live well beyond 400 years (one tree is more than 1300 years), and on many sites it is eventually replaced, in the absence of fire, by the shade-tolerant subalpine fir (*Abies lasiocarpa*), with minor amounts of spruce (*Picea engelmannil*) and mountain hemlock (*Tsuga mertensiana*) in the mesic parts of its range (Arno and Hoff, 1990; Keane, 2001). Clark's nutcracker (*Nucifraga columbiana*) plays a critical role in the dispersal of whitebark pine's heavy, wingless seed (Tomback, 1998; Lorenz *et al.*, 2008) (**Photo 1**). The bird harvests seed from purple cones during late summer and early fall and carries as many as 100 of them in a sublingual pouch to sites as far as 10–20 km away, where it buries as many as 15 seeds in caches 2–3 cm below the soil surface. Seeds that remain unclaimed eventually germinate and grow into whitebark pine trees (Tomback, 2005). Nutcrackers often cache in open areas with a high degree of ground pattern in high-mountain settings that are often created by wildland fire (Morgan and Bunting, 1989).



Photo 1 Clark's nutcracker harvesting seeds from a whitebark pine (Photo by D. Tomback).

Three types of fires describe the diverse fire regime that occurs in whitebark pine forests (Morgan and Bunting, 1989; Murray et al., 1998). Some high elevation whitebark pine stands experience nonlethal surface fires because sparse fuel loadings and widely spaced trees foster lowintensity fires (Keane et al., 1994). The more common, mixed-severity fire regime is characterized by fires of mixed severities in space and time, creating complex mosaics of tree survival and mortality on the landscape (Murray, 2008; Arno and Weaver, 1990). Burned patches are important caching habitat for Clark's nutcracker because it prefers to cache in nearby burned patches, probably because of the heavy seeds (Norment, 1991). Many whitebark pine forests in Montana, northern Idaho, and the Cascades originated from large stand-replacement fires that occurred at long time intervals (greater than 250 years) where nutcrackers cache whitebark pine great distances (Keane et al., 1994; Murray, 2008). The great variability in historical fire severity, frequency, pattern, and size has ensured the continued dominance of whitebark pine on upper subalpine landscapes in western North America.

disturbance variability and diverse processes interacting across multiple space and time scales from genes to species to landscapes, and from seconds to days and centuries. One central concern with implementing ecosystem management was identifying appropriate reference conditions that could be used to describe ecosystem health, prioritize those areas in decline for possible treatment, and design feasible treatments for restoring their health (Aplet *et al.*, 2000).

The relatively new concept of historical range and variability (HRV) was introduced in the 1990s to bring understanding of past spatial and temporal variability into ecosystem management (Cissel et al., 1994). HRV provided land-use planning and ecosystem management a critical spatial and temporal foundation to plan and implement possible treatments to improve ecosystem health and integrity (Landres et al., 1999). Why not let recent history be a yardstick to compare ecological status and change by assuming that recent historical variation represents the broad envelope of conditions that supports landscape resilience and its self-organizing capacity (Hessburg et al., 1999b)? Managers initially used "target" conditions developed from historical evidence to craft treatment prescriptions and prioritize areas (Harrod et al., 1999). However, these target conditions tended to be subjective and somewhat arbitrary because they represented only one possible situation from a wide range of conditions that could be created from historical disturbance and vegetation dynamics (Keane et al., 2002). This single objective, targetbased approach was then supplanted by a more-comprehensive theory of HRV that incorporated the full variation and range of conditions that occurred across multiple scales of time and space into a metric of ecosystem health.

The idea of using historical conditions as reference for land management is not new (Egan and Howell, 2001). Since the 1990s planners have been using target stand and landscape conditions that resemble historical analogs to guide landscape management, and research has provided various examples (Christensen et al., 1996; Fulé et al., 1997; Harrod et al., 1999). However, the inclusion of temporal variability of ecosystem elements into land management has only recently been employed. Landres et al. (1999) presented some of the theoretical underpinnings behind HRV and extensive reviews, and other background material on HRV and associated terminology can also be found (Egan and Howell, 2001; Swanson et al., 1994; Kaufmann et al., 1994; Morgan et al., 1994; Foster et al., 1996; Millar, 1997; Aplet and Keeton, 1999; Hessburg et al., 1999a; Perera et al., 2004; Veblen, 2003). This section was taken from material in Keane et al. (2009). The major advancement of HRV over the historical target approach is that the full range of historical ecological characteristics is used as the critical criterion in the evaluation and management of ecosystems (Swanson et al., 1994). It is this variability that ensures continued health, self-organization, and resilience of biodiversity, ecosystems, and landscapes across spatiotemporal scales (Holling, 1992). Understanding the causes and consequences of this variability is key to managing landscapes that sustain ecosystems and the services they offer to society.

The Concept

The theory behind HRV is that the broad historical envelope of possible ecosystem conditions such as burned area, vegetation cover type area, and patch size distribution can provide a representative time series of reference conditions to guide land management (Aplet and Keeton, 1999) (see Figure 2 as an example). This theory assumes the following: (1) Ecosystems are dynamic, not static, and their responses to changing processes are represented by past variability (Veblen, 2003); (2)



Figure 2 An example of a simulated time series for southwestern Montana, USA, mountainous landscape showing the five most dominant succession communities for simplicity. Also shown are the simulated average and the composition of the current landscape with only one succession class present (Keane *et al.*, 2008).

ecosystems are complex and have a range of conditions within which they are self-sustaining, and beyond this range they transition to disequilibrium (Egan and Howell, 2001; Wu *et al.*, 2006); (3) historical conditions can serve as a proxy for ecosystem health (Swetnam *et al.*, 1999); (4) the time and space domains that define the HRV are sufficient to quantify observed variation (Turner *et al.*, 1993); and (5) the ecological characteristics being assessed for the ecosystem or landscapes match the management objective (Keane *et al.*, 2002). In this chapter, we will focus the discussion on historical variations of landscape, not stand dynamics, and specifically landscape composition (i.e., aerial extant of vegetation communities) and structure (i.e., patch distributions).

Any quantification of HRV requires an explicit specification of the spatial and temporal context. The spatial context is needed to ensure that the variation of the selected landscape attribute is described across the most appropriate area relative to the spatial dynamics of ecosystem or landscape processes. The variability of the area occupied by a vegetation type over time, for example, generally decreases as the spatial context increases until it reaches an asymptote, which can be used to approximate optimal landscape size (Fortin and Dale, 2005; Karau and Keane, 2007). The optimal size of evaluation area will depend on (1) the ecosystem attribute evaluated, (2) the dynamics of major disturbance regimes, and (3) the relevant management issues (Tang and Gustafson, 1997). Fine woody fuel loadings, for example, would vary across smaller scales than coarse woody debris loads (Tinker and Knight, 2001).

The time scale over which HRV is evaluated must also be specified to properly interpret the underlying biophysical processes that influenced historical ecosystem dynamics, especially climate (Millar and Woolfenden, 1999). The HRV of landscape composition evaluated from 1300 to 1600 AD might be entirely different if evaluated from 1600 to 1900 AD because of the vast differences in climates and land use between those periods (Mock and Bartlein, 1995). Temporal scale and resolution is usually dictated by the temporal depth of the historical evidence used to define and describe HRV, but they can also be selected to match specific management objectives. These time and space scale constraints are both a benefit and limitation of the HRV concept.

One advantage of the HRV approach is that it can use many elements to describe ecosystems, stands, or landscapes at any scale (Egan and Howell, 2001). The HRV of tree basal area, for example, can be assessed at the stand, landscape, and regional spatial scales; similarly, the HRV for landscape composition and patch structure can be computed for a watershed, National Forest, or an entire region. This multiscaled, multicharacteristic approach allows HRV attributes to be matched to the specific land management objectives at their most appropriate scale. For instance, fuel managers might decide to evaluate the HRV of coarse woody fuels and severe fire behavior at a watershed level (Hessburg et al., 2007) to manage landscapes for continued ecological integrity and high biodiversity. Similarly, each HRV element can be prioritized or weighed based on its importance to the land management objective. This forms the critical linkage to adaptive land management in which iterative HRV analyses can be used to balance trade-offs in landscape integrity of ecosystems with other social issues and economic values. Perhaps the biggest advantage of HRV is that it forced land managers to recognize the dynamic character of landscapes in crafting management plans (Keane et al. 2009).

Its Application

HRV has been used in many land management projects. The departure of current conditions from historical variations have been used to prioritize and select areas for possible restoration treatments (Reynolds and Hessburg, 2005; Hessburg et al., 2007) or to identify areas to conserve biological diversity (Aplet and Keeton, 1999). US fire management agencies have used fire regime condition class (FRCC), which is based on HRV of fire and vegetation dynamics, to rate and prioritize lands for fuel treatments (Hann and Bunnell, 2001; Schmidt et al., 2002; Hann, 2004) (http://www.frcc.gov). The HRV of patch size and contagion was demonstrated to design the size of treatment area and landscape composition to select the appropriate management treatments to mimic patch characteristics (Keane et al., 2002). Keane et al. (1996) used the HRV approach to design coarse-scale restoration of the previously discussed whitebark pine ecosystem in the Pacific Northwest.

Reference conditions for HRV have been described for many ecosystems across the western US and Canada. Veblen and Donnegan (2005) synthesized available knowledge on forest conditions and ecosystem disturbance for national forest lands in Colorado, USA. The ecological and economic implications of forest policies designed to emulate historical fire regimes were investigated by Thompson *et al.* (2006) using a simulation approach. Historical vegetation and disturbance dynamics for southern Utah were summarized in the Hood and Miller (2007) report. Wong *et al.* (2003) compiled an extensive reference of historical disturbance regimes for the entire province of British Columbia, Canada. Several studies have detailed historical variations in upland vegetation for two national forests in Wyoming (Dillon *et al.*, 2005; Meyer *et al.*, 2005). Although these studies are good qualitative references for understanding and interpreting historical conditions, they do not provide the quantitative detail needed to implement the described reference conditions directly into management applications.

Quantification of HRV demands temporally deep and spatially explicit historical data. Data sets that represent longterm empirical landscape dynamics are rarely available, inconsistent, and difficult to obtain (Humphries and Bourgeron, 2001; Barrett et al., 2006). Historical reconstructions of landscape characteristics can be made from many sources if they exist for a particular landscape (see Egan and Howell, 2001, for a summary). Historical vegetation conditions can be reconstructed or described from (1) pollen deposits in lake or ocean sediments; (2) plant macrofossil assemblages deposited in middens, sediments, soils, and other sites; (3) dendrochronological stand reconstructions and fire scar histories; (4) land survey records; and (5) repeat photography (Gruell et al., 1982; Arno et al., 1995; Humphries and Bourgeron, 2001; Friedman et al., 2001; Montes et al., 2005; Schulte and Mladenoff, 2005). Unfortunately, these data have either a confined or unknown spatial domain because they were collected on a very small portion of the landscape, or they pertain to a broad, undefined area (middens, lake sediments) and lack spatial specificity with respect to patterns. Moreover, some ecosystems on a landscape have little evidence of past conditions with which to quantify HRV, and any available data are usually limited in temporal extent. In general, those methods that describe HRV at fine time scales, such as tree fire scar dating, are constrained to multicentenary time scales, whereas those methods that cover long time spans (millennia), such as pollen and charcoal analyses, have a resolution that may be too coarse for management of spatial patterns of structure and composition (Swetnam et al., 1999).

For most landscape-level HRV quantification, there are three main sources of spatial data to quantify historical conditions (Keane *et al.*, 2006; Humphries and Bourgeron, 2001). The best sources are spatial chronosequences or digital maps of historical landscape characteristics over many time periods. Unfortunately, temporally deep and spatially explicit time series of historical conditions are missing for many US landscapes because aerial photography and satellite imagery are rare or were nonexistent before 1930 AD and comprehensive maps of forest vegetation are scarce, inconsistent, and limited in coverage prior to 1900. Tinker *et al.* (2003) quantified HRV in landscape structure using digital maps of current and past landscapes in the Greater Yellowstone Area from aerial photos and stand age interpretation.

Another HRV data source is to substitute space for time and collect spatial data across similar landscapes, from one or more times, across a large geographic region (Hessburg *et al.*, 1999a, 1999b). This assumes landscapes of similar biophysical environments with similar disturbance and climatic

regimes can provide a representative cross section of temporal variation of landscape dynamics. In effect, differences in space are equivalent to differences in time, and inferences may be drawn regarding variation in spatial pattern that might occur at a single location over time. However, subtle differences in landform, relief, soils, and climate make each landscape unique, and grouping landscapes may tend to overestimate range and variability of landscape characteristics (Keane *et al.*, 2002). Landscapes may be similar in terms of the processes that govern vegetation such as climate, disturbance, and species succession, but topography, soils, land use, and wind direction also influence vegetation development and fire growth (Knight, 1987).

A third approach for quantifying HRV involves using computer models to simulate historical dynamics to produce a time series of simulated data to compute HRV statistics and metrics. This approach relies on the accurate simulation of succession and disturbance processes in space and time (Keane et al., 2002a). Many spatially explicit ecosystem simulation models are available for quantifying HRV patch dynamics (Gardner et al., 1999; Mladenoff and Baker, 1999; Humphries and Baron, 2001; Keane et al., 2004a), but most are (1) computationally intensive, (2) difficult to parameterize and initialize, and (3) overly complex, thereby making them difficult to use, especially for large regions, long time periods, and inexperienced staffs. However, those landscape models designed specifically for management planning may oversimplify vegetation development and disturbance. Even the most complex landscape models rarely simulate spatial interactions between climate, fire dynamics, and vegetation development at the scales needed to quantify HRV because of the lack of critical research in those areas and the immense amount of computer resources required for such an effort. Even with its shortcomings, simulation modeling is the most common method of creating HRV time series, and many studies have used simulation modeling to quantify HRV time series for landscapes and ecosystems using a wide variety of models. Nonspatial models such as VDDT (Beukema and Kurtz, 1995) were used to estimate landscape composition in a wide variety of areas from the Pacific Northwest to the northern Rocky Mountains (Hann et al., 1997; Barbour et al., 2007; Kurz et al., 1999). The LADS model (Wimberly et al., 2000) was used for the Oregon Coast Range to determine the appropriate level of old growth forests to quantify HRV in landscape structure (Nonaka and Spies, 2005), and to simulate the effect of forest polices (Thompson et al., 2006). McGarigal et al. (2003) quantified historical forest composition and structures of Colorado landscapes. Keane et al. (2002) simulated historical landscape patch dynamics using the LANDSUM model for northern Rocky Mountain USA landscapes. The LANDFIRE prototype project quantified historical time series for landscapes across the US using the LANDSUM model (Keane et al., 2007) (Figure 3).

There is a common misconception that long-term simulation model HRV outputs are inappropriate because the simulation of fire and landscape dynamics occurred while unrealistically holding climate and fire regimes constant (Keane *et al.*, 2006). This would be true if the objective of the modeling were to replicate historical fire events. However, the primary purpose of HRV modeling efforts is to describe variation in historical landscape dynamics, not to replicate them. Simulation modeling allows the quantification of the entire range of landscape conditions by simulating the static historical fire regime for long time periods (e.g., thousands of years) to ensure all possible fire ignitions and burn patterns are represented in the HRV time series. In contrast, HRV time series from empirical historical records will tend to underestimate variation of landscape conditions because there are a limited number of fire events in the historical record. Model input parameters represent the actual temporal context, whereas the simulation time represents the length of time needed to adequately capture the range and variation of historical conditions. Because the temporal domain of model parameters often represents only four or five centuries, it may seem that only 500 years of simulation are needed. However, the parameters quantified from sampled fire events that occurred during this time represent only one unique sequence of the fire ignitions and growth that created the unique landscape compositions observed today. If these events happened at different times or in different areas, an entirely different set of landscape conditions would have resulted.

Its Limitations

Although easily understood, the concept of HRV can be quite difficult to implement due to scale, data, and analysis limitations (Wong and Iverson, 2004). Inappropriate temporal and spatial scales to evaluate landscapes will introduce bias and increased variability into the computation of HRV statistics because the scales of climate, vegetation, and disturbance interactions are inherently different across landscapes (Morgan et al., 1994). Karau and Keane (2007) found that simulated HRV chronosequences of landscapes smaller than 100 km² had increased variability in landscape composition due to the truncated spatial dynamics of simulated disturbance processes as they ran into the landscape boundary. This is why HRV approaches are inappropriate when applied on small areas such as stands. A Douglas-fir stand that was historically dominated by ponderosa pine, for example, may be appear to be outside HRV, but if it is within a 100-km² landscape composed primarily of ponderosa pine, it will certainly be within HRV. However, when evaluation landscapes are large ($>500 \text{ km}^2$), it is often difficult to detect significant changes caused by ecosystem restoration or fuel treatments implemented on small areas (Keane et al. 2006). There is an optimal landscape extent for HRV simulation, but this optimum depends on subtle differences in topography, climate, and vegetation across large regions, and it also changes with spatial resolution.

There are few statistical techniques to compare HRV time series data to current landscape composition and structure (Figure 2). Many have used departure statistics to describe the dissimilarity of current conditions from historical variations to prioritize and select areas for possible restoration treatments (Reynolds and Hessburg, 2005; Hessburg *et al.*, 2007) or areas to conserve biological diversity (Aplet and Keeton, 1999). These departure methods use the similarity metrics from landscape and community ecology to estimate departure from



Figure 3 The computation of departure from HRV used in the LANDFIRE project (Keane *et al.* 2007). A simulated historical landscape composition time series is created using the LANDSUMv4 model for a landscape reporting unit (focal landscape). This time series is then compared to current conditions using an ecological similarity analysis to compute fire regime condition class (FRCC). FRCC is a three-category ordinal index reflecting the degree of departure from historical conditions, with red indicating areas where the landscapes are the most departed.

HRV, and most have limitations when used in HRV applications (Keane *et al.*, 2011) (Figure 3). For example, the Sorenson's index is sensitive to the number of classes used to describe the landscape (Keane *et al.*, 2008, 2011). Furthermore, some departure indices are insensitive to subtle changes in landscape composition when the same categories appear in all time sequences. Better multivariate statistical techniques with hypothesis testing are needed for more-credible HRV analyses.

Many limitations are associated with the use of the simulation approach to quantify HRV (Keane et al., 2011). It is impossible to build a model that includes all those landscape and ecosystem processes that directly affect those variables selected to represent the HRV time series. Information and data concerning the important processes and their linkages used to construct models is often inadequate. And, as model complexity increases, so does instability, computational requirements, input parameters, and reliability; there is a tradeoff between model complexity and applicability. Simple, empirical modeling approaches are easier to understand and yield the most accurate answers, but they are limited in scope, data intensive, and often incapable of directly simulating complex interactions. Mechanistic modeling approaches include greater detail in simulating ecological processes, making them more robust and comprehensive; these models, however, can be inaccurate, difficult to use, and somewhat unstable. There is also a lack of sufficient expertise and input parameter data to parameterize and execute most models, and it is difficult to test and validate models because there are few spatial historical time series that are temporally deep and in the right context for comparison with model results (Keane and Finney, 2003). As a result, the simulated variation also includes undesirable and unquantifiable sources such as unintended stochasticity, model flaws, inadequate parameterization, and oversimplifications. No single model will satisfy the varied HRV demands of management, so compromises in simulation design must always be made. The best model might not be the most useful because (1) few people know how to run the model, (2) there may be insufficient computer resources (software, hardware requirements) to run the model, and (3) there may be insufficient field data for input parameter approximation to run the model. Most HRV simulation projects are designed around the people responsible for their completion.

One major problem in defining landscapes for HRV quantifications is that the landscape edges create artificial boundaries across which spatial processes such as seed dispersal and wildland fire spread cannot traverse. Areas near the edge of the landscape, for example, have a limited number of surrounding pixels from which a seed can fall or a fire can spread into them (Figure 4). Spatial processes such as fires cannot immigrate into the simulation landscapes, resulting in decreased occurrence near landscape edges. This problem is exacerbated by biophysical processes such as fire, seed dispersal, and insect migrations that are controlled by directional vectors such as wind that differentially act on parts of a landscape. Areas downwind, for example, have a higher probability of burning than those upwind (Keane et al., 2002a). The best way to mitigate the edge effects is to surround the simulation landscape with a buffer (Figure 4). Each

landscape is unique, so buffer width may differ for each setting. HRV simulations should be inspected to determine if the buffer is large enough to minimize edge effects within the context landscape, keeping in mind that simulation time increases exponentially as landscapes get larger.

The shape of the focal landscape is also an important factor in the simulation of HRV landscape dynamics. Fire frequencies in long, thin landscapes, for example, tend to be underestimated because simulated fires rarely reach their full size because they reach the landscape boundary first. Even with a large buffer, simulated fires spread quickly across a thin context landscape and burn only a fraction of its full size. Keane et al. (2002a) found fire frequencies were approximately 20-40% less in long landscapes with high edge. Many like to use watersheds to define simulation landscapes, but watersheds are often long and linear with high edge, making them somewhat undesirable for HRV simulation. The best shapes are squares, rectangles or circles that are large enough to contain both the buffer and context landscapes. The directional orientation of the simulation landscape is also important. Long, thin landscapes that are oriented perpendicular to the wind direction will have far less burned area over time than the same landscapes oriented parallel to the wind (Keane et al., 2002a). The orientation is especially important if elongated landscapes are positioned at right angles to the wind direction; they will tend to have significantly less fire and narrow HRV time series.

Perhaps the most important limitation of the HRV application is that it may no longer be a viable concept for managing lands in the future because of expected climate warming and increasing contemporary human activities across the landscape (Millar et al., 2007). Tomorrow's climates might change so rapidly and dramatically that they will no longer be similar to historical climates that created past conditions, and the continued spread of exotic plants, diseases, and other organisms by human transport will permanently alter ecosystems. Climate warming is expected to trigger major changes in disturbance processes, plant and animal species dynamics, and hydrological responses (Botkin et al., 2007; Schneider et al., 2007) that may create new plant communities, change biodiversity assemblages, and alter landscapes where they will be quite different from historical analogs (Notaro et al., 2007). Whitebark pine, for example, is predicted to significantly decline under new forecast climates, so does it make sense to restore the species on landscapes where they are predicted to be reduced? Therefore, it may seem obvious that using historical references may no longer be reasonable in this rapidly changing world. However, a critical evaluation of possible alternatives may indicate that HRV, with all its faults and limitations, might be the most viable approach for the near term because it has the least amount of uncertainty.

One other alternative to HRV is to forecast the future variations of landscapes under changing climates using highly complex spatial, empirical, and mechanistic models, and this option is fraught with compounding uncertainties. The range of predictions for future climate from the major general circulation models may actually be greater than the variability of climate over the past two or three centuries (Stainforth *et al.*, 2005). This uncertainty increases when we factor in society's



Figure 4 Illustration of the edge effect when simulating fire regimes across landscapes and mitigation of this effect through the inclusion of a buffer in the simulation landscapes.

projected responses to climate change through technological advances, behavioral adaptations, and population growth (Schneider *et al.*, 2007). Moreover, the variability of climate extremes, not the gradual change of average climate, will drive

most ecosystem response to the climate-mitigated disturbance and plant dynamics, and these extreme events are the most difficult to predict (Easterling *et al.*, 2000, Smith, 2011). Uncertainty will also increase as the climate predictions are extrapolated to the finer scales and longer time periods that are needed to quantify future range and variation (FRV) for landscapes. And this uncertainty will surely increase as we try to predict how ecosystems will respond to this simulated climate change (Araujo et al., 2005). Mechanistic and empirical ecological models that simulate climate, vegetation, and disturbance dynamics across landscapes are often missing detailed representations and interactions of disturbance, hydrology, land use, and biological processes that will catalyze most climate interactions (Notaro et al., 2007). Moreover, little is known about the interactions of climate with critical plant and animal life-cycle processes, especially reproduction and mortality (Keane et al., 2001; Gworek et al., 2007; Ibanez et al., 2007; Lambrecht et al., 2007), yet these process could be the most important in determining species response to climate change (Price et al., 2001). Given large cumulative uncertainties involved in predicting future climates and subsequent ecosystem responses, it may be that HRV time series may have significantly lower uncertainty than any simulated predictions for the future. Recall that large variations in climates of the past several centuries are already reflected in the parameters used to simulate HRV time series. So before throwing the HRV baby out with the climate change bathwater, it may be more prudent to wait until simulation technology has improved enough to create credible FRV landscape pattern and composition time series for regional climate forecasts based on extensive model validation and testing, and this may take decades. In the meantime, it is doubtful that the use of HRV to guide management efforts will result in inappropriate activities considering the large genetic variation in most species (Rehfeldt et al., 1999; Davis et al., 2005).

In conclusion, the concept of HRV has a valid place in land management, at least for the near future. Landscape models can be used to simulate fire regimes and their interaction with climate and vegetation to create HRV time series that can be used as reference conditions to assess, plan, evaluate, design, and implement ecosystem-restoration treatments. HRV should be used to guide land management and not as a target on which to evaluate success or failure. There are few measures of ecosystem health that match the scale, scope, flexibility, and robustness of HRV analysis.

Appendix

List of Courses

- 1. Landscape Ecology and Management
- 2. Ecosystem Management

See also: Biodiversity and Ecosystem Services. Computer Systems and Models, Use of. Conservation Biology, Discipline of. Ecosystem Services. Fires, Ecological Effects of. Impact of Ecological Restoration on Ecosystem Services. Landscape Legacies. Landscape Modeling. Modeling Biodiversity Dynamics in Countryside and Native Habitats. Restoration of Biodiversity, Overview. Wildlife Management

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