

Are Madrean Ecosystems Approaching Tipping Points? Anticipating Interactions of Landscape Disturbance and Climate Change

Donald A. Falk

School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona

Abstract—Contemporary climate change is driving transitions in many Madrean ecosystems, but the time scale of these changes is accelerated greatly by severe landscape disturbances such as wildfires and insect outbreaks. Landscape-scale disturbance events such as wildfires interact with prior disturbance patterns and landscape structure to catalyze abrupt transitions to novel ecosystem configurations. These reorganized landscapes are characterized by new disturbance regimes and potentially dramatic departures in species diversity and distributions, community composition, carbon storage, landscape mesoclimate, and soil and hydrologic processes. Post-transition ecosystems can be highly resilient in their altered state, and resistant to return to pre-disturbance conditions in the current and near-term climate regime, possibly representing alternative metastable states. Severe landscape disturbance interacts with, and may be driven by, climate variation to govern ecosystem dynamics and large-scale ecosystem change. We present a conceptual model organized around six key attributes that may drive ecosystems to rapid change and novel trajectories.

Background

Many studies predict changes in species distributions in response to changing climate. At local scales, community composition reflects changes in the suitability of existing habitat for species persistence. Both modeling and empirical studies suggest that such changes due to climate alone are likely to be expressed at multi-annual to decadal time scales (Allen and Breshears 1998, summarized in Parmesan 2006). Recent meta-analyses of range limit studies (Parmesan and Yohe 2003; Chen and others 2011) found that latitudinal and upper elevational limits in the Northern Hemisphere have moved 6.1-16.9 km northward and 6.1-11.0 m upslope per decade. The mechanisms of climate impacts on ecological communities varies, including shifts in species distributions (Gonzalez and others 2010; Rehfeldt 2006), disease (Pounds and others 2005), and phenology (Crimmins and Bertelson 2009).

In contrast, severe large-scale disturbances can reorganize ecosystems on much shorter time scales of days to months (Overpeck and others 1990). High severity fires can cause extensive mortality, alter soils and hillslope geomorphology, and trigger cascading ecosystem changes, especially in vegetation types for which severe fires are atypical (fig. 1). Landscape fires can cause rapid reorganization of ecosystem mass and energy (McKenzie and others 2011), with the consequence that post-fire recovery can extend over years or even decades.

Post-fire ecological transitions have been observed in multiple sites in Southwestern North America. Iniguez (2009) observed evidence of a 19th century type conversion near Rincon Peak in the Rincon Mountains (fig. 2) from ponderosa pine to an evergreen oak community, which appears to have occurred following a high-severity fire in 1867. Savage and Mast (2005) reviewed post-fire recovery trajectories at 10 ponderosa pine sites in the Southwest that experienced crown fires from 1948-1977. Some sites returned to pine dominance, albeit at higher density than previously, while other areas converted to oak shrubfields, chaparral, or non-forested grasslands. Areas burned in the 1,858-ha 1977 Radio Fire on Mt. Elden outside of Flagstaff, Arizona (Passavoy and Fulé 2006), which burned largely in ponderosa pine, remain dominated by shrubs 45 years post-fire. Similar transitions have been observed in the Santa Catalina Mountains following the 2002-2003 Bullock and Aspen fires.

We posit that it is the *combination* of climate change and severe disturbance that is most likely to trigger abrupt ecosystem transitions into novel configurations, rather than either factor acting separately. These new configurations may be resilient in their new state, and resistant to return to pre-disturbance conditions due to synergistic influences of disturbance and climate (Kitzberger and others 2011). In addition to ecological effects, these transitions also include potentially persistent alterations to geomorphic, soil, hydrological, and biogeochemical systems (Scheffer and others 2001). Such abrupt transitions are predicted to become more common under conditions of altered future climate and amplified disturbance regimes (Flannigan and others 2000; Westerling and others 2006; Zinck and others 2011).

Abrupt ecological change is generally defined as a threshold response in key biotic and abiotic ecosystem components (Anderson and others 2008). Such changes may be expressed in shifts in dominant vegetation physiognomy (for example, from forest to shrub communities), species composition, or community structure. Rapid post-disturbance transitions are especially likely if established individuals of dominant

In: Gottfried, Gerald J.; Ffolliott, Peter F.; Gebow, Brooke S.; Eskew, Lane G.; Collins, Loa C., comps. 2013. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2012 May 1-5; Tucson, AZ. Proceedings. RMRS-P-67. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.



Figure 1—2011 Horseshoe 2 Fire, Chiricahua Mountains.



Figure 2—Remnant southwestern white pine (*Pinus strobiformis*) with multiple fire scars in a netleaf oak (*Q. rugosa*) shrub field originating after stand-replacing fire in 1867, Rincon Peak, Arizona (photo: J.M. Iniguez).

species do not survive a disturbance event. Altered soil, hydrologic, and biogeochemical conditions can reinforce shifts in vegetation types and disturbance regimes, such as a transition from a low-severity forest surface fire regime to a high-severity chaparral shrubland regime (Mayer 2011). Climate provides the envelope within which these

dynamics occur; disturbance provides the trigger for abrupt system reorganization.

Theoretical Foundation

The theoretical basis for understanding type conversion behavior derives from alternative stable state theory. This family of models describes the potential of ecological communities to exist in more than one state over relatively long ecological time. Strictly speaking, these ecological configurations are more properly *metastable* states, i.e., displaying quasi-equilibrational behavior over limited domains of time and under a range of external conditions (e.g., long successional sequences in a given climate). Henceforth, we will refer to *alternative metastable state* (AMS) theory, which provides a framework for ecosystem behavior under both historical and current conditions (Elmqvist and others 2003).

By definition, metastable states maintain a given configuration (e.g., a plant community type) within limited degrees of environmental variation. For example, Madrean ponderosa pine stands or encinal woodlands retain their primary characteristics (species composition, physiognomy, biomass distribution) despite interannual variation in rainfall and temperature, or episodic low-severity fires or insect outbreaks, due to the persistence of established individuals and ongoing reproduction. The community can be displaced or reorganized over long (millennial) time by climate variation, which modifies the envelope of suitability, such as has occurred in the Madrean bioregion throughout the late Pleistocene and Holocene (Holmgren and others 2006; Jackson 2006; Van Devender and others 1984). Transient events—unusually severe fires, droughts, or insect outbreaks—have the potential to trigger rapid community reorganization outside of the envelope of metastability, especially if there is widespread mortality and/or alteration of the biophysical template (Folke and others 2004). Thus transient events, in combination with altered climate, may make rapid ecosystem transitions more likely.

Transitions between metastable states are distinguished from ongoing successional change by the rapidity with which state changes occur. This occurs because the boundaries between metastable states are characterized by positive-feedback interactions that create unstable equilibria. Following a major perturbation, the system reorganizes along one of several possible pathways. One potential outcome is a return to the pre-disruption state, but depending on a variety of factors (see below), the system can instead develop along an alternative trajectory. Positive feedback relationships then tend to reinforce a given trajectory once it has been initiated, because species present in the post-disturbance community provide a source of propagates for ongoing recruitment as well as competitors to other species. These same feedbacks create the emergent property of *resilience* in a given condition once it is established. Unstable equilibria are often asymmetric: a change in one direction is not necessarily equally as likely as a reciprocal change in the other, due to mechanisms that tend to reinforce a given configuration. For example, once dry pine forest has been converted to interior chaparral, the resulting new higher-intensity fire regime may tend to favor resprouting chaparral shrub species, and select against a return to slower-growing arboreal life forms with heat-sensitive canopies; similar dynamics are observed in semi-arid ecosystems invaded by cheatgrass (*Bromus tectorum*), which facilitates fire regimes that exclude previously dominant species.

Post-disturbance pathways are sensitive to initial conditions, which are a primary factor in the assembly rules that govern how communities reorganize (Palmer and others 1997; Temperton and others 2004). For example, the presence of survivors and early post-disturbance colonizers can determine establishment order and thus the capture

of space and resources. This early dominance can be reinforced by growth, reproduction, and competition, resulting in a new metastable state. It is also important to recognize that in some cases, what appear to be alternative metastable states may simply represent slower successional dynamics operating on longer time schedules than ordinarily recognized.

A Framework for Anticipating Threshold Change

We propose a model based on six primary factors that appear to determine post-fire ecosystem trajectories under current and near-term climate in Madrean ecosystems. In this model, the post-disturbance trajectory of an ecosystem is influenced by (1) the type and severity of disturbance, (2) persistence or mortality of dominant species in the pre-disturbance community, (3) alteration of the biophysical template (soils, hydrology, topography), (4) landscape structure that governs multiple spatial ecological processes such as dispersal, (5) the local and regional species pools of available post-disturbance colonizers, and (6) respective life history attributes, especially dispersal, recruitment, and competition, and local and regional climate that determines, among other factors, the availability of suitable conditions for recruitment. Interactions among these mechanisms interact to create the emergent properties often associated with macrosystem behavior, including resistance and resilience. These variables can be used to simulate threshold responses in modeling environments (Keane and others 2011).

Type and Severity of Disturbance—A wide range of ecological and Earth system processes are classified as “disturbance,” including wildfire, insect outbreaks, diseases, floods, hurricanes, tsunamis, landslides, earthquakes, severe droughts and pluvials, freezing events, and numerous others. Some of these (insect outbreaks, disease, and fire) are clearly of biotic origin and can, thus, be considered ecological interactions, which operate at least in part in a density-dependent fashion (i.e., effects are a function of density and size of members of a community). Other disturbances (e.g., floods, hurricanes, tsunamis, landslides, earthquakes, severe droughts and pluvials, and freezing events) are expressions of Earth system processes in which ecological effects tend to be density-independent. Surface and mixed-severity fires in the Madrean ecoregion are keystone ecosystem processes that regulate biomass, nutrient cycling, and community structure in a wide range of community types (Swetnam and others 2001).

The introduction of new species into a community can also introduce novel types of disturbance; for example, the rapid spread of non-native African grasses such as buffelgrass (*Pennisetum ciliare*) into upland communities in the Sonoran Desert has introduced a novel fire regime to which most resident species are poorly adapted (McDonald 2009, Stevens and Falk 2009). As discussed below, these shifts in the fire regime can move an ecosystem into a new self-reinforcing metastable state which is highly resistant to return to the pre-invasion condition.

Mortality and Persistence—Severe disturbances such as wildfires leave relatively few surviving established individuals, opening up niche and physical space for community-level turnover. Indeed, mortality is one of the two primary ways in which severity is indexed; for example, the U.S. Rapid Assessment of Vegetation Condition after Wildfire (RAVG) program (<http://www.fs.fed.us/postfirevegcondition/index.shtml>) uses multi-spectral reflectance criteria to assess post-fire burn severity, by classifying basal area loss by vegetation type (fig. 3). The extent of mortality among the pre-fire community is a key determinant of post-fire trajectories, because established individuals provide communities with physical structure, seed sources, nurse

plant microenvironments, sources of leaf litter, habitat resources for wildlife, *in situ* geochemical pools such as carbon, nitrogen, and other key nutrients, shade, microclimate regulation, and many other functions. The legacy of persisting individuals also represents the initial conditions for community reassembly, and thus, their presence or absence has a major impact on development of the post-disturbance community.

Soil, Hydrologic, and Geomorphic Effects—Low-severity fires appear to have few adverse effects on soils and geomorphology and can contribute to topsoil development through mineralization of nitrogen into plant-available forms, reduction of litter accumulation that makes mineral soil more accessible to seedling roots, and accelerated decomposition of coarse woody debris. In contrast, severe fires can alter soils and hydrology rapidly and substantially through a variety of mechanisms including soil hydrophobicity, volatilization of nitrogen and other key nutrients, loss of soil organic carbon, and loss of litter and duff layers that assist with slope stabilization (Ice and others 2004; Neary and others 2008; fig. 4).

These direct first-order fire effects (i.e., immediate effects that occur as a direct consequence of combustion) are compounded by a wide range of second-order fire effects including reduced water percolation, increased overland water flow, sheet erosion, sediment fluxes into stream channels, debris flows, bank destabilization, accelerated topsoil loss, and hillslope failures (DeBano and others 1998). For example, extensive post-fire debris flows have been documented in the Huachuca and Chiricahua Mountains (Youberg and others, this volume) in the monsoon season following severe fires in 2011. Recovery times for stream channels and riparian communities after severe debris flows can be on the order of decades to centuries.

Where these effects are slight to moderate in severity and extent, many communities will recover after fire to a state similar to the pre-fire condition. However, when soil and hydrogeomorphic impacts are severe and widespread, an immediate return to the pre-fire condition may be precluded because the biophysical template is no longer suitable. Extensive soil loss also eliminates the soil seed bank, which is a key component of post-disturbance biotic recovery. Hart and others (2005) found that severe fires can also alter the soil microbial communities (both fungal and bacterial) through extensive belowground mortality. These changes can be linked to shifts in plant community composition and changes in key ecosystem processes such as C sequestration, nutrient fluxes, soil physical structure, and plant-microbe mutualisms.

Landscape Structure and Dispersal Processes—The spatial properties of post-fire environments are important determinants of post-fire trajectories. Large fires characteristically leave a legacy of complex landscape mosaics of burn severity across vegetation types. Roughly 4 to 35% of the area within the perimeters of large recent fires in the western United States is classified as high burn severity using delta Normalized Burn Ratio (dNBR), and Normalized Difference Vegetation Index (NDVI) indices (www.mtbs.gov). Moderate severity typically accounts for 20 to 45%, and low severity or unburned areas 33 to 61% (Kotliar and others 2003; Lentile and others 2007). Less is known about the severity patch structure of historical fire regimes, although tree-ring studies in high fire frequency systems such as ponderosa and Jeffrey pine (*P. jeffreyi*) forests indicate that the extent of high-severity effects was generally limited (Swetnam and others 2001; Falk and others 2011). At higher elevations, however, patches were generally larger contiguous areas of high severity in wet mixed-conifer and spruce-fir forests (Margolis and others 2007).

In addition to the proportion of the landscape in each severity class, the size of contiguous patches is an important landscape variable

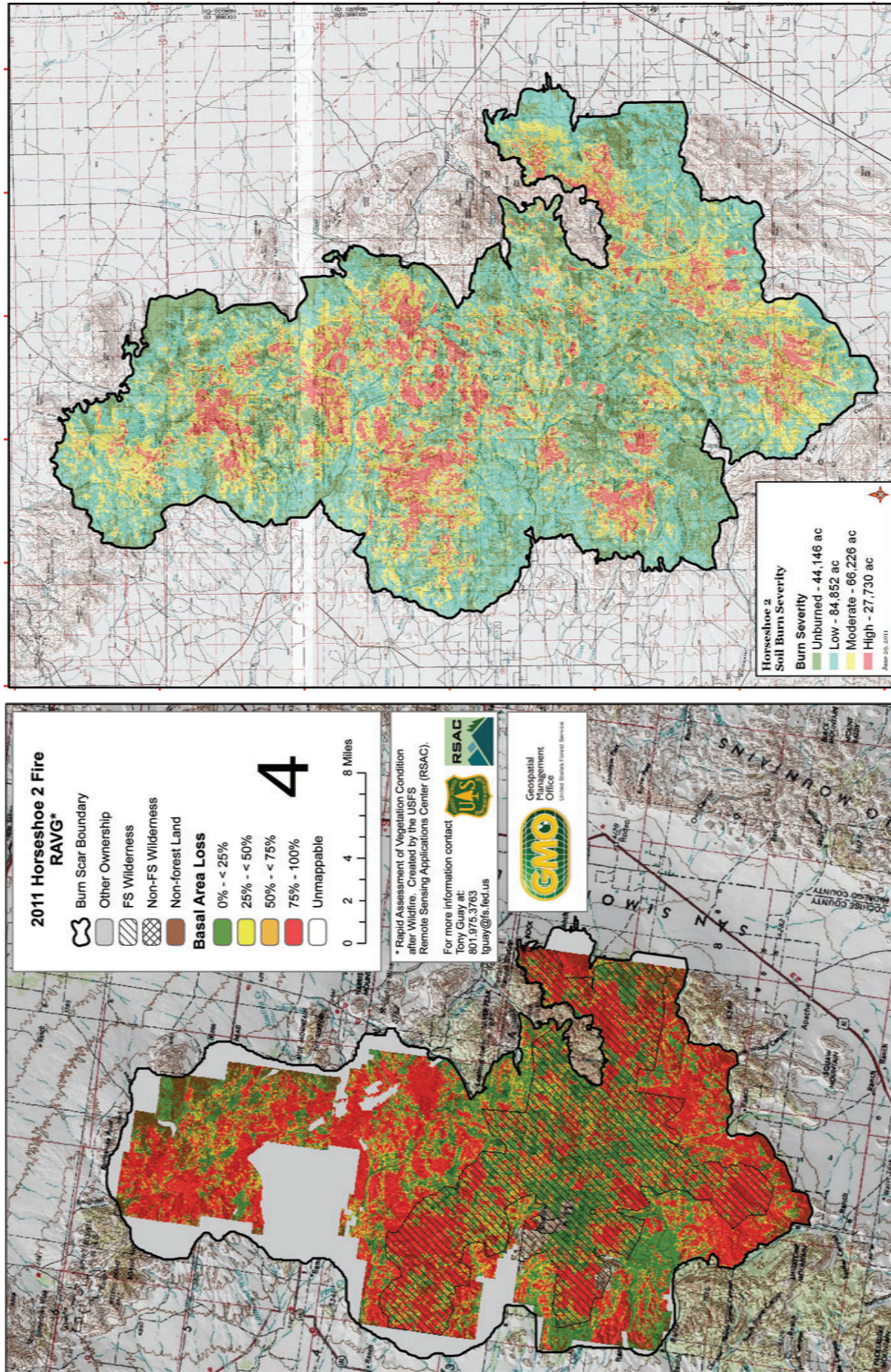


Figure 3—Burn severity images from 2011 Horseshoe 2 fire, Chiricahua Mountains, Arizona. Left: Vegetation burn severity, Rapid Assessment of Vegetation Condition after Wildfire (RAVG), USFS Remote Sensing Applications Center (RSAC, (<http://www.fs.fed.us/postfirevegcondition/index.shtml>)). Right: soil burn severity (MTBS, www.mtbs.gov).

(Haire and McGarigal 2010). In contrast to historical fire regimes, contemporary fires often create large patches of high-severity fire effects in the order of 1,000-10,000 ha in size in what were formerly low-severity/high-frequency systems such as ponderosa pine and dry mixed conifer forests where such patches are believed to have been historically of 10-100 ha (fig. 5). The resulting altered landscape structure such as anomalously large high-severity patches following extreme disturbance events may restrict seed dispersal of previously dominant species while favoring other species with rapid long-range dispersal. For example, Bonnet and others (2005) found that most post-fire seed dispersal following a high-severity fire in a South Dakota ponderosa pine forest was restricted to approximately 150 m from seed sources on the edge of residual forest. By this measure, the centers of high severity patches larger than 10 ha with a minimum lateral dimension of ≥ 300 m would require multiple generations for propagules to reach the interior by natural dispersal processes. Species with longer-range dispersal or with persisting vegetative potential (e.g., sprouting species) would have a significant advantage in capturing post-fire occupancy (Haire and McGarigal 2010).

Local and Regional Species Pools—The pool of species available to recolonize a site following disturbance is a key determinant of post-fire ecological trajectories (Menninger and Palmer 2006). Even when suitable biophysical conditions exist for establishment, species must be present and be able to reproduce to become part of the developing community. Clearly, species that can persist through disturbance have a significant advantage over others that must disperse to the site. Persistence is, in turn, a function of evolved life history attributes that reflect a range of evolutionary responses to disturbance (Bond and van Wilgen 1996). For example, the thick bark and lifted crowns characteristic of ponderosa and Jeffrey pines are widely understood as adaptations to surviving low-intensity fires burning in surface fuels, in which survivorship of mature individuals is maximized (Keeley and Zedler 1998). Other species including Chihuahua pine (*P. leiophylla*) and many Madrean oaks (*Quercus* spp.) can resprout after being top-killed, providing a persistence mechanism that may facilitate rapid post-fire occupancy (fig. 6). Aspen (*Populus tremuloides*) clones similarly employ a vegetative life history strategy for post-fire response, although both oaks and aspen also reproduce sexually. These reproductive strategies allow these native species to capture post-fire



Figure 4—High soil and vegetation burn severity on steep slopes of Cochiti Canyon, 2011 Las Conchas fire, Jemez Mountains, New Mexico.



Figure 5—Large high-severity burn patch, 2011 Horseshoe 2 fire, Chiricahua Mountains, Arizona.

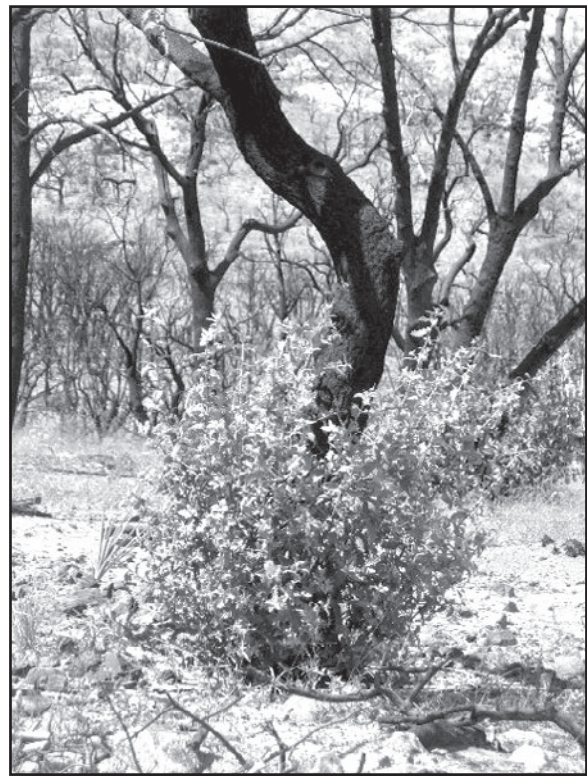


Figure 6—Rapid resprouting of oaks following 2011 Monument Fire, Huachuca Mountains, Arizona.

environments quickly and to persist once established. For example, Gambel oak (*Q. gambellii*) was observed resprouting within weeks of both the 2000 Cerro Grande Fire and the 2011 Las Conchas Fire in the Jemez Mountains, New Mexico. These evolutionary adaptations to post-fire colonization suggests that type conversions (e.g., from pine-dominated forest to oak-dominated scrub), however long they may persist, are part of the historical post-fire behavior of Madrean ecosystems. However, other factors (such as climate and landscape

change) may render these conversions permanent, or at least more persistent than in pre-settlement environments.

By contrast, in upper Sonoran Desert communities in the Madrean bioregion, the primary agents of abrupt and radical change in the native fire regime are invasive non-native grasses. These changes are among the clearest expressions of tipping point behavior in Madrean ecosystems. Natural Sonoran Desert vegetation provides very low fine fuel mass and connectivity due to the dominance of intermingling woody vegetation for much of the year and wide spacing of established plants. Under these conditions, ignitions rarely generate a spreading fire due to the lack of sufficient spatially-continuous fine fuels to sustain a chain reaction. As a result, fires in the Sonoran Desert are rare and low intensity (heat per unit area-time). Consequently, most species of the community lack adaptations to survive fire.

Introduced African grasses, particularly buffelgrass, have changed the fuel environment in Sonoran communities by infilling interspaces with increased, spatially continuous fine fuels (fig. 7). In addition, the foliage of buffelgrass is persistent for many months after curing, increasing the flammability of the fuel bed for the driest months of the year. Buffelgrass is fire tolerant, a formidable belowground competitor (Olsson and others 2011; Stevens and Falk 2009), and can rapidly assume dominance in the herbaceous community. The net result is that areas that have been invaded by buffelgrass become converted to a novel community type with high herbaceous fuel loads of up to 600-1,200 g/m², two orders of magnitude more than un-invaded desert (McDonald 2009) and frequent high-intensity fires that are lethal to many native desert species. Columnar cacti such as saguaro (*Carnegiea gigantea*) are particularly susceptible due to their thin epidermis that is easily damaged by levels of heat typically generated in a wildfire. Once the “grass-fire cycle” is established, the community is resilient in its new configuration and resistant to return to the pre-invasion state (Brooks 2008).

Climate Change—The “bioclimatic envelope” is a central determinant of species distributions and climate variables are key dimensions in a species’ niche space. Niches are non-spatial combinations of multiple variables that define the conditions under which a species can maintain a non-negative population growth rate (λ). The niche is the product of species evolution, including phenotypic plasticity; where $\lambda \geq 1$, a population is self-sustaining (Colwell and Rangel



Figure 7—Prescribed experimental burn in buffelgrass stand, Altar Valley, Arizona (photo: C. J. McDonald).

2009). When the hyperdimensional niche volume is mapped onto geographic space, the result is the total potential spatial distribution of a species in the absence of competition or other limiting factors. Regional climate along with soils, topography, and hydrology also provides the context for the distribution of biotic communities.

Although climate-species and climate-community relationships are mechanistic, they are not deterministic; many more community configurations are possible within a given climate envelope at a given location and few species occupy their entire potential geographic range. In niche theory, the *realized niche* is the portion of the total *fundamental niche* hypervolume that a species occupies. Realized niche space is narrower than the fundamental niche for any given axis due to competition, dispersal limitations, and other factors. The geographic expression of the realized niche is the potential habitat of a species. Similar relationships hold for the distribution of biotic communities as assemblages of multiple interacting species. These non-deterministic relationships are the foundation for the potential for alternative metastable states.

Bioclimatic envelope (BCE) models are used widely to generate null hypotheses for potential species responses to climate change. In a BCE framework, changing climate conditions require a species to follow one of two possible pathways (Colwell and Rangel 2009). One alternative is that the species retains its current niche requirements. In this case, the species must move geographically to remain within its potential habitat zone of suitable climate. In an era of increasing global and regional temperatures, this is usually interpreted as pressure to move upslope or poleward. Thus, in this potential adaptive response, niche space is retained, and adaptation occurs by movement in geographic space. The second alternative is the converse; the species adapts its niche requirements *in situ* to new conditions but retains its current geographic distribution; in other words, the species evolves. Many species contain alleles, present in the population at low frequency, that may provide the basis for adaptation to novel conditions (e.g., tolerance of higher temperatures or drought). As climate changes, these alleles may increase in their frequency and the species’ niche space is altered to fit current conditions. Most species also retain some phenotypic plasticity, which retains fitness under variable conditions within the current genotypes and may facilitate local adaptive responses.

Climate variability and secular (anthropogenic) trend provide the envelope in which threshold responses may occur (Alley and others 2003; McNeall and others 2011). Species distributions represent current geographic range in most BCE modeling, and thus implicitly, the climate tolerance of established individuals. However, the niche space for recruitment—the “regeneration niche”—is not only smaller than the niche space for established individuals but occupies the cooler, wetter domain of the niche (fig. 8). Established individuals of a species such as ponderosa pine or Douglas-fir (*Pseudotsuga menziesii*) can persist through dry years and even sustained periods of drought and high temperatures, but these same conditions are lethal for recently germinated seedlings. Thus, a projected warmer and drier climate in the Madrean ecoregion may not allow for post-fire regeneration of previously dominant species, especially if there is high disturbance-related mortality.

In addition to regulating species distributions and post-fire regeneration, altered climate also increases the probability of severe fires (Flannigan and others 2000). Fire initiation and spread are facilitated by warmer, drier, windier conditions that reduce fuel moistures and promote the combustion chain reaction (Pyne and others 1996). Fire severity may also increase under these climatic conditions, due to decreased live fuel moistures and the resulting increased flammability of vegetation. Finally, the length of fire season is projected to increase

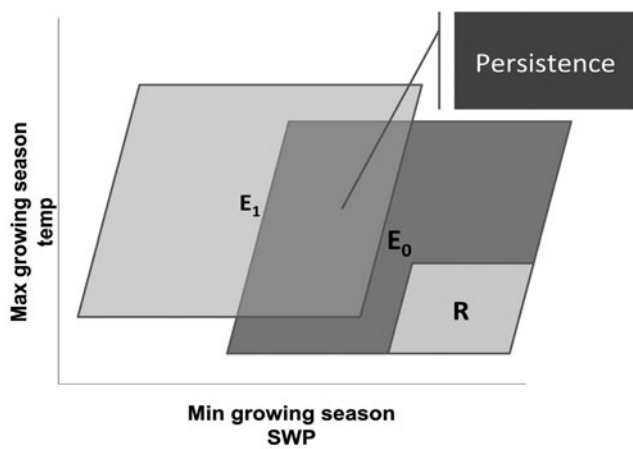


Figure 8—The climate state space in which established individuals can persist (E_0), illustrated here on axes of minimum growing season soil water potential (SWP) and maximum growing season temperature. Most climate projections for the Madrean bioregion indicate generally warmer and drier conditions (E_1). Established individuals can persist in the intersection of these two spaces. However, climate requirements for seedling recruitment (R) are in the cooler, wetter domain of the climate space, which no longer intersects climate regime E_1 .

with changing climate and seasonality, as reflected in the increased number of days with energy release component (ERC) greater than critical values (Brown and others 2004). Thus, altered climate may play an additional destabilizing role in Madrean ecosystems by direct alteration of fire regimes.

As Flannigan and others (2000) observe, “The almost instantaneous response of the fire regime to changes in climate has the potential to overshadow importance of direct effects of global warming on species distribution, migration, substitution and extinction...[F]ire is a catalyst for vegetation change.” The collective effect of disturbance-climate interactions is to rapidly and persistently change landscape patterns and processes including disturbance regimes, vegetation composition, carbon dynamics, and hydrologic balance (Breshears and others 2005; O’Connor and others 2011). The central challenge confronting ecosystem scientists and managers is to understand how fire behavior and legacies of prior disturbance may interact with climate variability to influence post-fire recruitment and ecosystem trajectories, and how these transitions can be managed to maintain sustainable ecosystems.

Broader Impacts

The potential for abrupt ecological and hydrologic change in response to climate and disturbance is of central importance to ecosystem management in a changing world. As climate change progresses, species assemblages and ecosystem disturbance regimes are already changing in ways that challenge the foundations of ecosystem management, especially in arid and semi-arid regions (Allen and Breshears 1998; Aronson and others 1993; Breshears and others 2005; Quijada-Mascareñas and others, in press). Major fires, insect outbreaks, forest dieback, and other phenomena are already creating new and serious stressors to terrestrial ecosystems (Overpeck and others 1990). Moreover, the character, function, and integrity of ecosystems are fundamental to human society in innumerable ways. Thus, if ecosystems begin to change abruptly and profoundly, the

impacts are likely to ripple through human society as well as the biosphere itself.

Acknowledgments

Ann Lynch, Rocky Mountain Research Station, U.S. Forest Service, Tucson Arizona, and Linda Wadleigh, Fire and Aviation Management, Southwestern Region, U.S. Forest Service, Flagstaff, Arizona, provided valuable reviews and suggestions on the original manuscript. The author also acknowledges the contributions of Craig Allen (U.S. Geological Survey, Los Alamos, New Mexico); Christopher Baisan (Laboratory of Tree-Ring Research, University of Arizona, Tucson); David Breshears (School of Natural Resources and the Environment, University of Arizona); Corinne Dolan (School of Natural Resources and the Environment, University of Arizona); William Edwards (Coronado National Forest, Douglas, Arizona); Calvin Farris (National Park Service, Klamath Falls, Oregon); Peter Fulé (School of Forestry, Northern Arizona University, Flagstaff, Arizona); Brooke Gebow (The Nature Conservancy of Arizona); Perry Grissom (Saguaro National Park); Jose Iniguez (Rocky Mountain Research Station, U.S. Forest Service Flagstaff, Arizona); Mark Kaib (U.S. Fish and Wildlife Service, Albuquerque, New Mexico); Rachel Loehman (Fire Sciences Laboratory, Rocky Mountain Research Station, U.S. Forest Service, Missoula, Montana); Ellis Margolis (Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona); Adrian Quijada-Mascareñas (School of Natural Resources and the Environment, University of Arizona); Melissa Savage (Four Corners Institute, Santa Fe, New Mexico); Christopher Stetson (Coronado National Forest, Douglas, Arizona); Elaine Sutherland (Rocky Mountain Research Station, U.S. Forest Service Missoula, Montana); Thomas Swetnam (Laboratory of Tree-Ring Research, University of Arizona, Tucson); Andrea Thode (School of Forestry, Northern Arizona University, Flagstaff, Arizona); and Craig Wilcox (Coronado National Forest, Douglas, Arizona).

References

- Allen C.D.; D.D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid response to climate variation. *Proceedings of the National Academy of Sciences US*. 95(25):14839-14842.
- Alley, R.B.; [and others]. 2003. Abrupt climate change. *Science*. 299: 2005-2010.
- Andersen, T., J. Carstensen, E. Hernandez-Garcia, and C.M. Duarte. 2008. Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution*. 24:49-57.
- Aronson, J., C. Floret, E. LeFloc’h, C. Ovalle, and R. Pontanier. 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A view from the South. *Restoration Ecology*. 1: 8-17.
- Bond, W.J., and B. van Wilgen. 1996. *Plants and fire*. Chapman & Hall: New York.
- Bonnet, V.H., A.W. Schoettle, and W.D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research*. 35:37-47.
- Breshears, D.D., [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences US* 102(42):15144-15148.
- Brooks, M.L. 2008. Plant invasions and fire regimes. In Zouhar, K.J.K. Smith, S. Sutherland, and M.L. Brooks (Eds.), *Wildland fire in ecosystems: fire and nonnative invasive plants*. Gen. Tech. Rep. RMRS-GTR-42, Vol. 6. U.S. Forest Service, Ogden, UT.
- Brown, T.J., B.L. Hall, and A.L. Westerling. 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: An applications perspective. *Climatic Change*. 62:365-388.

- Chen, I.-C., J.K. Hill, R. Ohlemüller, D.B. Roy, and C.D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science*. 333:1024-1026.
- Colwell, R.K., and T.F. Rangel. 2009. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences US*. 106 (Supplement 2):19651-19658.
- Crimmins, T.M., M.A. Crimmins, and C.D. Bertelson. 2009. Flowering range changes across an elevational gradient in response to warming summer temperatures. *Global Change Biology*. 15:1141-1152.
- DeBano, L.F., D.G. Neary, and P.F. Ffolliott. 1996. Fire's effects on ecosystems. John Wiley & Sons, New York.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488-494.
- Falk, D.A., E.K. Heyerdahl, P.M. Brown, C.A. Farris, P.Z. Fulé, D. McKenzie, T.W. Swetnam, A.H. Taylor, and M.L. Van Horne. 2011. Multiscale controls of historical fire regimes: New insights from fire-scar networks. *Frontiers in Ecology and the Environment*. 9:446-454.
- Flannigan, M., B. Stocks, and B. Wotton. 2000. Climate change and forest fires. *The Science of the Total Environment*. 262:221-229.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C.S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology & Systematics*. 35:557-581.
- Gonzalez, P., R.P. Neilson, J.M. Lenihan, and R.J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography*. 19:755-768.
- Haire, S.L., and K. McGarigal. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology*. 25:1055-1069.
- Hart, S.C., T.H. DeLuca, G.S. Newman, M.D. MacKenzie, and S.I. Boyle. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology & Management*. 220: 166-184.
- Holmgren, C.A., J.L. Betancourt, and K.A. Rylander. 2006. A 36,000-yr vegetation history from the Peloncillo Mountains, southeastern Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 240: 405-422
- Ice, G.G., D.G. Neary, and P.W. Adams. 2004. Effects of wildfire on soils and watershed processes. *Journal of Forestry* 102 (6):16-20.
- Iniguez, J.M., T.W. Swetnam, and C.H. Baisan. 2009. Spatially and temporally variable fire regime on Rincon Peak, Arizona, USA. *Fire Ecology* 5(1):3-21.
- Jackson, S.T. 2006. Vegetation, environment, and time: The origination and termination of ecosystems. *Journal of Vegetation Science* 17:549-557.
- Keane, R.E., R.A. Loehman, and L.M. Holsinger. 2011. The FireBGCv2 landscape fire and succession model: A research simulation platform for exploring fire and vegetation dynamics. Gen. Tech. Rep. RMRS-GTR-255. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Keeley, J.E., and P.H. Zedler. 1998. Evolution of life histories in *Pinus*. In D.M. Richardson (Ed.), *Ecology & biogeography of Pinus*. Cambridge University Press: Cambridge, UK: 219-250
- Kitzberger T., E. Araoz, J.H. Gowda, M. Mermoz, and J.M. Morales. 2011. Decreases in fire spread probability with forest age promote alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems* DOI: 10.1007/s10021-011-9494-y.
- Kotliar, N.B., S.L. Haire, and C.H. Key. 2003. Lessons from the fires of 2000: Post-fire heterogeneity in ponderosa pine forests. In Omi, P. N. and L. A. Joyce (Eds.), *Fire ecology, fuel treatments, and ecological restoration*. Proc. RMRS-P-29. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 277-280.
- Lentile, L.B., P. Morgan, A.T. Hudak, M.J. Bobbitt, S.A. Lewis, A.M.S. Smith, and P.R. Robichaud. 2007. Post-fire burn severity and vegetation response following eight large wildfires across the western United States. *Fire Ecology*. 3(1):91-108.
- Margolis E.Q., T.W. Swetnam, and C.D. Allen. 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research*. 37: 2227-2241.
- Menninger, H.L., and M.A. Palmer 2006. Restoring ecological communities: From theory to practice. In Falk, D.A., M.A. Palmer, and J.B. Zedler (Eds.), *Foundations of restoration ecology*. Island Press, Washington, DC. Pp. 88-112
- Mayer, G.G., and A.H. Khalany. 2011. Grass trumps trees with fire. *Science*. 334:188-189.
- McDonald, C.J. 2009. Management of non-native perennial grasses in southern Arizona: Effects of prescribed fire and grazing. Ph.D. Dissertation. School of Natural Resources, University of Arizona, Tucson.
- McKenzie, D., C. Miller, and D.A. Falk (Eds.). 2011. *The Landscape ecology of fire*. Ecological Studies Series No. 213, Springer, Dordrecht, Netherlands.
- McNeill, D., P.R. Halloran, P. Good, and R.A. Betts. 2011. Analyzing abrupt and nonlinear climate changes and their impacts. *Climate Change*. 2:663-686.
- Neary, D.G., K.C. Ryan, and L.F. DeBano (Eds.). 2008. *Wildland fire in ecosystems: effects of fire on soils and water*. Gen. Tech. Rep. RMRS-GTR-42-vol.4. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 250 p.
- O'Connor, C., T.W. Swetnam, G. Garfin, and D.A. Falk. 2011. Human pyrogeography: A new synergy of fire, climate and people is reshaping ecosystems across the globe. *Geography Compass*. 5/6:329-350.
- Olsson, A.D., J. Betancourt, M.P. McClaran, and S.E. Marsh. 2011. Sonoran Desert ecosystem transformation by a C_4 grass without the grass/fire cycle. *Diversity and Distributions*. 18(1):10-21.
- Overpeck J.T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature*. 343:51-53.
- Palmer, M.A., R.F. Ambrose, and N.L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology*. 5:291-300.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. 37:637-69
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 421:37-42.
- Passovoy, M.D., and P.Z. Fulé. 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. *Forest Ecology and Management*. 223:237-246.
- Pounds, J.A. and others. 2005. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*. 439:161-165.
- Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. *Introduction to wildland fire*. 2nd Edition. John Wiley & Sons, New York.
- Quijada-Mascareñas, A., D.A. Falk, J. Weiss, M. McClaran, J. Koprowski, M. Culver, S. Drake, S. Marsh, W. van Leeuwen, A.M. Lynch, and M. Skroch. [In press]. Potential multi-scale ecological effects of climate change in Sky Island ecosystems. *The Open Ecology Journal*.
- Rehfeldt, G.E., N.L. Crookston, M.V. Warwell and J.S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*. 167:1123-1150.
- Savage M., and J.N. Mast. 2005. How resilient are ponderosa pine ecosystems after crown fires? *Canadian Journal of Forest Research*. 35: 967-977.
- Scheffer, M., [and others]. 2001. Catastrophic shifts in ecosystems. *Nature*. 413:591-596.
- Stevens, J., and D.A. Falk. 2009. Using invasion ecology theory to explain buffelgrass success and restoration potential in the American Southwest. *Ecological Restoration* 27:417-427.
- Swetnam, T.W., C.H. Baisan, and J.M. Kaib. 2001. Forest fire histories in the Sky Islands of La Frontera. In G.L. Webster and C.J. Bahre (Eds.), *Changing plant life of La Frontera: Observations on vegetation in the United States/Mexico Borderlands*. University of New Mexico Press, Albuquerque: 95-119.
- Temperton, V.M., R.J. Hobbs, T. Nuttle, and S. Halle (Eds.). 2004. *Assembly rules and restoration ecology*. Island Press, Washington, DC.
- Van Devender, T.R., J.L. Betancourt, and M. Wimberly. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. *Quaternary Research*. 22(3): 344-360.
- Westerling A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase western U.S. wildfire activity. *Science*. 313 (5789): 940-943.
- Zinck, R. D., M. Pascual, and V. Grimm. 2011. Understanding shifts in wildfire regimes as emergent threshold phenomena. *American Naturalist*. 178(6): E149-E161.

The content of this paper reflects the views of the authors, who are responsible for the facts and accuracy of the information presented herein.