RESTORATION ECOLOGY, RESILIENCE, AND THE AXES OF CHANGE[1]

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ABSTRACT

The Earth system is undergoing rapid, profound anthropogenic change. The primary axes of change include not only the climate system, but also the spread of invasive species, altered biogeochemical and hydrological cycles, modified disturbance regimes, and land degradation and conversion. These factors are influencing the distribution of species and the structure and function of ecosystems worldwide, interacting with climatic stressors that may preclude the persistence of many current species distributions and communities. Ecological disturbances such as wildfires and insect outbreaks can interact with climate variability to precipitate abrupt change on landscape scales. Such changes may limit the feasibility of historically based ecological restoration in many (although by no means all) instances. An alternative emerging approach is based on reinforcing the ecological processes that comprise resilience: resistance, recovery, and reorganization. While resistance and recovery processes fall within a conventional restoration framework, managing populations and ecosystems for reorganization represents a departure from a reference-based restoration approach. When applied to ecosystem management, resilience-based management supplements traditional ecological restoration where stressors of change make the reestablishment of historical communities difficult or maladaptive. We illustrate these ideas with examples drawn primarily from the interior of western North America.

Key words: Disturbance, ecological impacts of climate change, ecological resilience, reference condition, reorganization, resistance, restoration ecology.

The iconic images of our time are of changes in the Earth system that are rapid, global, and out of phase with natural dynamics. Of these, projected changes to Earth's climate system are the most widespread, systemic, and persistent. Collectively, these changes will affect the composition and function of every ecosystem on Earth, terrestrial and marine, in coming centuries. Indeed, mounting evidence indicates that these systemic changes have already begun (Scheffers et al., 2016).

While the impacts of climate change have recently become a dominant concern, many other human impacts on natural ecosystems continue to contribute to pervasive ecological change. Many of these are characteristically local in scale, such as mechanical destruction of streams, wetlands, and other fragile habitats that stand in the way of human ambition. The continued rise of human population, in particular the continued concentration of people in large conurbations, has not only local impacts within a defined metropolitan area, but also extends the ecological and hydrological footprint of large cities into the surrounding landscape, such as multilane ground transportation corridors that represent an absolute barrier to wildlife movement. Similarly, the introduction, growth, and spread of invasive species often begins at a local scale with a point introduction locus, but then spreads to landscape or even regional scales, illustrated by the pervasive spread of the non-native grass *Bromus tectorum* L. throughout interior western North America (D'Antonio et al., 2016). These longstanding causes of degradation and destruction continue to have widespread and persistent adverse ecological impacts, as well as degrade the sources of human well-being (Titeux et al., 2016).

Taken collectively, these multiple anthropogenic impacts on the Earth system interact across scales of space and time (Fig. 1). Each generalized class of impacts represents a domain within which humans influence the composition, structure, and functioning of ecosystems, with effects ranging from moderate and localized to profound and global. In addition, each class of impact interacts with others, creating powerful synergies that accelerate and multiply ecosystem impacts. For example, many invasive species are favored under conditions of altered disturbance regimes and altered biogeochemical inputs, increased urbanization, and changes to

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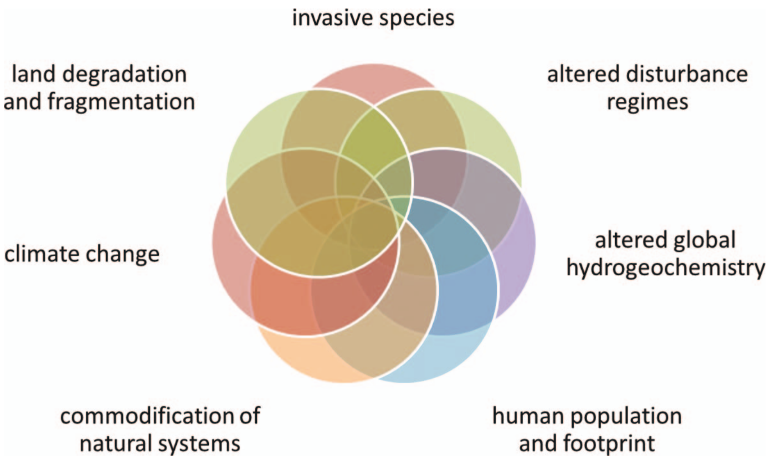

Figure 1. Multiple anthropogenic impacts—axes of change—on the Earth system interact across scales of space and time, including invasive species, altered disturbance regimes, altered hydrogeochemistry, human population and footprint, commodification of natural systems, land degradation and fragmentation, and climate change. Interactions among axes complicate efforts to mitigate impacts and restore ecological function.

temperature and precipitation regimes (Brooks et al., 2004; Baer, 2016). Thus, the problem of invasive species cannot be solved in any permanent way without also addressing its interactions with altered disturbance regimes, biogeochemistry, human land use, and climate change. Similar interactions apply to the other primary groupings of anthropogenic impacts. Collectively, these axes of change and their interactions are creating unprecedented challenges for the world conservation community and seriously threaten the sustainability of global ecosystems.

Of the axes of change predicted, changes in Earth's climate system are having the most systemic, global, and potentially persistent impacts. Annual variation in global surface temperature exceeded the envelope of the past 1000 years during the 1990s, and *no* projections of future temperature indicate a return to this naturally bounded envelope for centuries into the future (Fig. 2) (IPCC, 2007). Instead, the current debate within the world climate community revolves around how much global temperatures will increase in the coming century; the most optimistic realistic scenarios (B1-2; RCP 2.6) employed by the Intergovernmental Panel on Climate Change (IPCC, 2014) project a global surface temperature increase of 1.5°C–2°C by 2100; the most pessimistic scenarios (A1,2; RCP 8.5) based on extrapolation of current business-as-usual greenhouse gas (GHG) emissions project temperature increases in the range of 4°C–5°C during this timeframe, with some areas, particularly high latitudes, experiencing significantly greater warming in the range of 7°C–10°C. As atmospheric GHG concentrations have not been as high as current levels in more than 800,000 years, and global temperatures have not been within those ranges for at least the past 3–5 million years, it is clear that planet Earth is already committed to a future in which climate will resemble only partially or not at all the climate of the last millennium, and very likely much longer (Lüthi et al., 2008; Masson-Delmotte et al., 2013).

The impact of such radical changes to Earth's climate system will be economic and social as well as ecological. The Global Risks Report 2016 produced by the World Economic Forum (WEF, 2016) evaluates the failure of climate change mitigation and adaptation to be equivalent to the potential impact of weapons of mass destruction, with the difference that climate change is considered more likely to occur. Ecosystem collapse is also among the most severe impacts on a global economic-social system, highlighting the interactions between pervasive and profound climate change and other sources of degradation.

These developments define the essential scientific and management challenge of our time: How will species and ecosystems adapt to these rapid and profound changes in Earth systems? How will these changes affect ecosystem services that are essential to human society? And in response, can we define and adopt more flexible paradigms of ecosystem conservation and restoration, in order to sustain the environment upon which all life on Earth depends?

Regional Perspective on a Changing World

To understand impacts of the axes of change, as well as to define new approaches to ecosystem

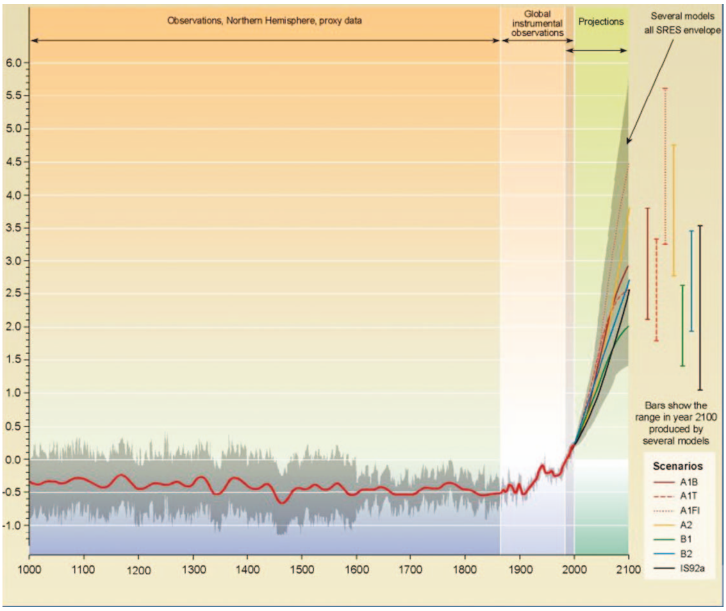

Figure 2. Variations of the Earth's mean surface temperature 1000–2100 CE. Y-axis is departure from 1990 baseline value in °C. The instrumental record becomes reliable in the late 1800s; prior estimates are derived from robust and highly replicated paleoecological reconstruction of global temperature; red line is mean global anomaly; gray shading represents 95% confidence interval. Projections to 2100 (green bar) are based on ensemble means of general circulation models (GCMs) under a range of emission scenarios. Figure from IPCC (2007).

management that respond to these emerging future conditions, regional perspectives are a useful scale of analysis, reflecting geographic variation in ecosystem structure and function, including the characteristic biota, climatology, geomorphology, soils, and human history and land use (Meffe et al., 2002). In addition, many climate projections for the coming century are geographically heterogeneous, suggesting the importance of tuning ecosystem management responses to the characteristic impacts and biota of a given region (Anderegg & Diffenbaugh, 2015).

Southwestern North America provides an illustrative case example. The area has been a semi-arid bioregion for millennia, long before the advent of anthropogenic climate change (Van Devender et al., 1987; Woodhouse et al., 2010). The region lies at latitudes where climate is influenced by the descending limb of the Hadley circulation, as well as relatively strong annual insolation, leading to warm and arid conditions in a band across the globe (Seager et al., 2007). Reconstruction of past climates in the region from the Late Holocene until today traces the evolution of biotic communities using records derived from packrat middens, tree rings, layered sediments, pollen, and other sources (Betancourt et al., 1990; Thompson & Anderson, 2000). Collectively, these lines of evidence indicate northward and up-elevation shifts in biotic communities, with desert and arid grasslands displacing open woodland and forest biomes at lower elevations over the progression of the Holocene, a process that continues today (Brusca et al., 2013). While vegetation is never entirely in equilibrium with climate (Webb, 1986), the persistence of multiple vegetation types and thousands of species across the 4000 m elevation range found in the region suggests a history of dynamic adaptation to spatially and temporally variable environments (Gottfried et al., 2013; Jackson & Blois, 2014).

Despite this record of adaptability, current projections of future climate indicate significant challenges to perpetuation of existing biological communities in southwestern North America (Garfin et al., 2013). Williams et al. (2010, 2013) calculated a forest drought stress index (FDSI) based on regression of tree growth to climate variation using the tree ring record for the past century. In this region the FDSI is primarily a function of warm season temperature and vapor pressure deficit (VPD, atmospheric water demand), and winter precipitation, capturing 82% of tree ring variability over the period 1896–2007. FDSI is highly correlated with other processes, including wildfire area burned, bark beetle outbreaks, tree mortality, and normalized difference vegetation index (NDVI) variability, indicating strong synergistic effects of top-down climate control and ecological responses.

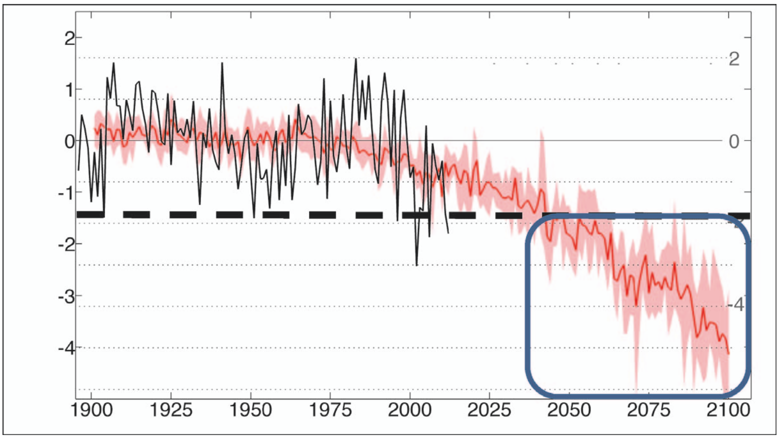

Figure 3. Estimates of the forest drought stress index (FDSI; red line) for southwestern North America during the instrumental record (black line, 1900–present) and future (through 2100; red shading indicates inner 50% of CMIP3 values used to project FDSI). Dashed heavy horizontal line indicates FDSI values below –1.4 corresponding to the deepest droughts of the past millennium. Dashed light horizontal lines indicate anomaly (in standard deviations, right y-axis) from the 1896–2007 mean. Adapted from Williams et al. (2013).

Calibration of FDSI against instrumental climate records for the 20th century allows reconstruction of the index over the past 1000 years, using the regional tree ring record. During this time, the majority of variability in the FDSI is constrained within the interval (–1…1). Significant negative departures reflecting periods of deep drought and excessive water demand, when FDSI experienced negative departures in excess of –1.4, occurred at least six times over the past 1000 years; the most recent of these were a deep and persistent drought in the 1580s, and the contemporary drought that began around 2000. When FDSI is forward modeled using an ensemble of general circulation models (GCMs), it is projected to reach values of –1.4 by the mid-21st century and remain persistently below that value for the remainder of the century, and almost certainly longer (Fig. 3). This occurs primarily because FDSI is influenced strongly by VPD and its exponential increase with temperature. Projected 21st century temperature and VPD increases would drive FDSI into a domain unfavorable for the persistence and growth of the currently dominant tree species in the southwestern United States (Allen et al., 2015).

Contemporary evidence suggests that these processes are already in motion. Range shifts have been recorded for many species, and observed dynamics suggest geographic movement of species bioclimatic envelope as a primary mechanism. Individual species responses can be amplified by interspecific interactions with competitors and pollinators and across trophic levels (Carnicer et al., 2011; Pateman et al., 2012; Urban et al., 2012). In addition to range shifts, many areas of California and interior western North America have experienced unprecedented levels of tree mortality in recent decades (Fig. 4) (Anderegg et al., 2013; Williams et al., 2015). Recent tree deaths in the southwestern Sierra Nevada have exceeded 100 million individuals as of the end of 2016 (USDA-USFS, 2016); similar widespread mortality has been observed in the Southwest, Rocky Mountains, and elsewhere in the continental interior (Allen et al., 2010, 2015). Van Mantgem et al. (2009) found that 87% of forest monitoring plots in undisturbed old forests across the western United States had increasing mortality rates, with the mortality rate doubling every 18 years.

THE ROLE OF DISTURBANCE IN ACCELERATING ECOSYSTEM CHANGE

While the effects of changing climate are expressed over decades to centuries, other ecosystem processes can have profound impacts on much shorter timescales. Paramount among these are large-scale disturbance events, particularly wildfire and insect outbreaks, which can reorganize ecosystems rapidly, leaving dramatically altered ecosystem legacies (Turner, 2010). Large, high-severity wildfires can trigger abrupt, dramatic change, accelerating the pace of landscape transformation from decades to weeks or even days (Falk, 2013; Fig. 5). This occurs because wildfires rapidly transform huge amounts of stored energy in the form of biomass into free kinetic energy, consuming foliage, vaporizing soil organic matter, modifying residual soil structure and chemistry, accelerating sheet erosion and soil loss, and eliminating the refugia and legacies from which post-

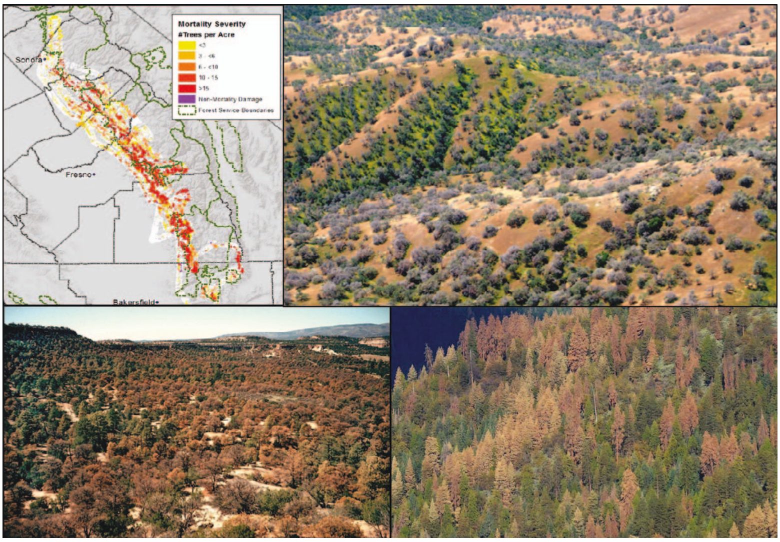

Figure 4. Widespread tree mortality is among the contemporary expressions of persistent warm drought and related insect outbreaks predicted by the forest drought stress index (FDSI). Top left: Remotely sensed estimates of landscape tree mortality in the southern Sierra Nevada; red pixels indicate areas with > 10 recently dead trees/acre (USDA-USFS, 2016). Top right and lower right: Recent mortality in oak woodlands and mixed conifer forest, Sierra Nevada (top right: ibid.; lower right: photo courtesy of Nathan Stephenson, USGS). Lower left: Extensive mortality of piñon (*Pinus edulis* Engelm.) in the Jemez Mountains, New Mexico, following extended warm drought in the early 2000s. Photo courtesy of Craig Allen, USGS.

fire recovery can proceed (Haire & McGarigal, 2010; Johnstone et al., 2016).

Throughout many regions of North America, evidence suggests that wildfires are becoming larger, and that the contiguous landscape areas of high severity are increasing in size, often now in excess of thousands of hectares, and that these changes are being driven by changing climate (Dale et al., 2001; Moritz et al., 2012). For example, prior to 2000 the largest wildfires in Arizona were in the range of 8000–20,000 ha (20,000–50,000 acres) (Fig. 6). However, beginning with the onset of persistent warm

Figure 5. Near-total overstory tree mortality and severely damaged soils on steep slopes of Cochiti Canyon watershed, Jemez Mountains, New Mexico, resulting from the 2011 Las Conchas Fire. Photograph by author.

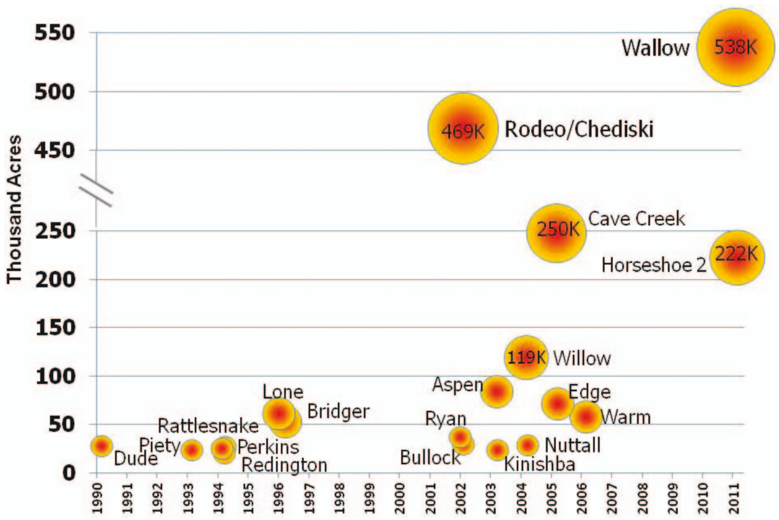

Figure 6. Largest wildfires in Arizona, by year, 1990–2012. Numbers inside symbols are wildfire area in thousands of acres. Data from Southwest Coordinating Center, National Interagency Fire Center. Graphic courtesy of Ann Youberg, Arizona Geological Survey.

drought in the late 1990s and into the 2000s, the size of the largest wildfires increased by an order of magnitude, with multiple wildfires now between 80,000 and 200,000 ha (200,000 and 500,000 acres). Large, abrupt changes in maximum fire size are driven by climate episodes and cannot be attributed to other factors, such as fuel accumulation, which operate on longer timescales. Five U.S. states (Arizona in 2002 and 2011; Colorado in 2002; Utah in 2007; California in 2003; and New Mexico in 2011 and 2012) recorded their largest fires on record during this decade (NIFC, 2016). At a regional scale, area burned during fires > 200 ha in forests and woodlands in the Southwest area has increased over 300% since the 1970s (Melillo et al., 2014).

Recent trends in area burned, and forward projections of wildfire area burned, suggest an increasing impact of wildfire at regional and continental scales in coming decades. These and other projections indicate that wildfire and insect outbreaks will act as multipliers, or perhaps exponents, for the more gradual "ratchet" of climate variability and trend (Jackson et al., 2009). As a result, the proportion of many landscapes undergoing accelerated change is increasing substantially.

Toward an Ecology of Resilience

Most populations, communities, and ecosystems have some inherent degree of resilience to environmental perturbation, including adaptation to climatic variation over time. Species population dynamics, community composition and structure, and ecosystem function are all strongly determined by variation in resource inputs and conditions. Without some capacity to adapt to time-varying environments, including longer-term variation over evolutionary time, most species would go extinct rapidly. What we define and observe as resilience is an emergent property of complex adaptive systems, in this case including species evolutionary processes and ecosystem function (Elmqvist et al., 2003; Filotas et al., 2014), creating a reservoir of "ecological memory," the tendency for past states of an ecological community to influence contemporary or future ecological responses (Bengtsson et al., 2003).

COMPONENTS OF ECOLOGICAL RESILIENCE

"Ecological resilience" can be defined as the ability of an ecological entity to recover its distribution, abundance, or function to a predisturbance state following perturbation or disturbance (Hobbs & Suding, 2009). Ecological resilience has three primary expressions: resistance, recovery, and reorganization (Harrison, 1979; Halpern, 1988; Millar et al., 2007). "Resistance" is the ability of an ecological entity (typically at the level of an individual) to persist despite a disturbance or stressor. For example, fire-adapted trees with thick bark, lifted crowns, and deep roots are able to resist (that is, survive and continue growing despite) surface fires of a normal range of intensity (Falk, 2006). Many species have evolutionary adaptations to drought, conferring the ability to survive, grow, and reproduce under conditions of lower soil water potential that

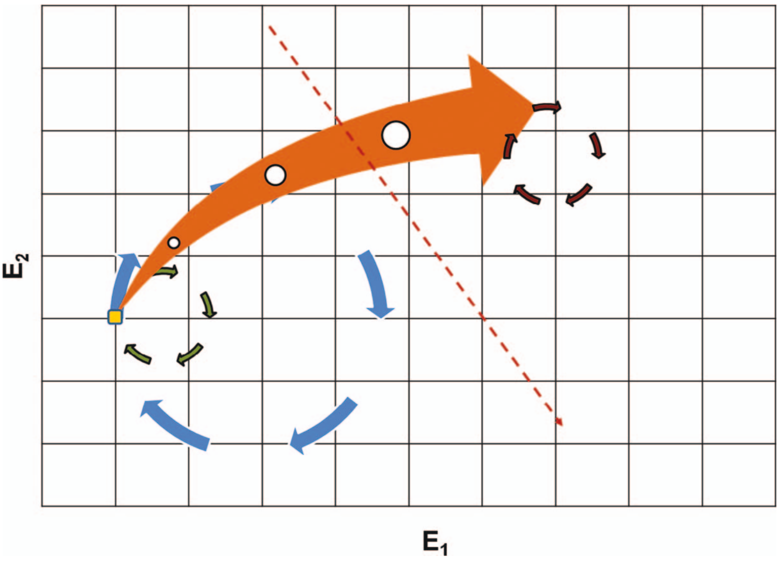

Figure 7. Conceptual model of ecosystem resistance, recovery, and reorganization. E_1 and E_2 represent environmental axes, e.g., a community gradient from a tree-dominated community to shrub and grass dominance, and the proportion of early-successional species. The yellow box represents axis coordinates at the time of disturbance; length of vectors represents time. Green arrows indicate minor perturbation from initial conditions, or resistance. Blue arrows indicate a slower and more divergent recovery pathway, eventually returning toward initial conditions. Extreme disturbance crosses a threshold (dashed line), resulting in reorganization in a new resilience domain (red arrows).

would be lethal to non-drought adapted species. The net effect of resistance is to facilitate persistence of individuals through periods of stress.

Recovery can be a property of either individuals or populations and indicates the capacity to recover structure or function following impact of a disturbance that exceeds a resistance threshold. In other words, once resistance has been overcome, an organism or population must have mechanisms of recovery if it is to persist. At the level of individual, recovery may include rebuilding some anatomical or physiological process, e.g., regrowing foliage to rebuild a canopy damaged by fire or insects, or reestablishing the functional continuity of phloem and xylem following mechanical injury or cavitation (Krause & Raffa, 1996). At a population level, recovery entails either vegetative or sexual reproduction to replace individuals killed during a disturbance event. The net effect of recovery processes is to maintain or reestablish either individual-level function or population size.

These processes can be visualized in two dimensions along environmental, resource, or population axes (Fig. 7). An organism with high resistance to a given stressor would not be perturbed from the starting condition (yellow box). When a low-severity stressor is applied (e.g., low-intensity wildfire or soil disturbance), displacement from the initial condition is minor, and the system returns to pre-disturbance configuration rapidly, reflected in the short response loop (green arrows). This recovery type might be characteristic of a fire-adapted woodland-grassland ecotone, in which woody species are replaced temporarily by fast-regenerating grasses. As disturbance intensity increases, displacement of the system by disturbance is larger in magnitude and requires a longer time to return to its starting condition (blue arrows). For example, in southwestern North America, conifer forests with significant post-fire mortality are often replaced by successional shrubs or post-fire specialists such as *Populus tremuloides* Michx. (Aspen) or *Ceanothus fendleri* A. Gray for several decades, although eventually the successional trajectory will converge toward pre-disturbance conditions, assuming favorable climate.

Under conditions of more extreme disturbance, or in unstable environments, the system can be perturbed beyond a threshold (dashed line in Fig. 7). In this case, return to the pre-disturbance (forested) domain is precluded, and the system becomes resilient in a new alternative state, such as a grass- or shrub-dominated community (red arrows). Such "tipping point" responses typically involve combinations of climate stress and disturbance severe enough to exceed both resistance and recovery thresholds (Burkett et al., 2005; Allen, 2007; Brock

Figure 8. Invasion of *Pennisetum ciliare* (L.) Link (buffelgrass) into a stand of saguaro cactus (*Carnegiea gigantea* (Engelm.) Britton & Rose) in an upper Sonoran Desert community increases fine fuel loads and continuity, elevating the likelihood of an uncharacteristic spreading high-severity fire. Photograph from Stevens and Falk (2009), courtesy of University of Arizona Desert Laboratory.

& Carpenter, 2010; Dai et al., 2012; Perretti & Munch, 2012). The system is then resilient in its new state and can be highly resistant to return to its pre-disruption configuration (Kitzberger et al., 2012; Scheffer et al., 2012; Schwilk & Keeley, 2012). Common examples of persistent alternative states include post-fire conversion from forest to shrub communities (Savage et al., 2000), conversion of desert ecosystems to arid grassland following invasion by non-native grasses (Fig. 8; Stevens & Falk, 2009), and conversion of Great Basin shrubland to communities dominated by non-native annual grasses such as *Bromus tectorum* (Brooks & Chambers, 2011).

Tipping point behavior is frequently characterized by hysteresis, in which the recovering system returns to its pre-disruptions state via a pathway different from the original degradation (May, 1977; Suding & Gross, 2006). The result can be multiple post-disturbance trajectories and alternative meta-stable states arising from interacting influences of extensive adult mortality, soil and hydrologic alteration, large disturbance patch sizes and resulting dispersal limitations, and a post-disturbance microclimate unfavorable for re-establishment of the pre-disturbance–dominant species (Suding et al., 2004; Haire & McGarigal, 2010; Falk, 2013). Following mortality events, species persistence has been overcome and recovery is dependent on recruitment, but climate may preclude establishment, especially during periods of drought or under future climate trajectories (Seager et al., 2007; Colwell & Rangel, 2009; Jackson & Hobbs, 2009).

As an example: in 2011 a very large mixed-severity fire (Las Conchas) burned over 63.250 ha (156,293 acres) in pine and mixed-conifer forests in northern New Mexico. The fire created uncharacteristically large patches of complete overstory tree mortality and severe soil damage (Fig. 5). In the months and years following the fire, the previously co-dominant species in mixed-conifer forest—*Pinus ponderosa* P. Lawson & C. Lawson (ponderosa pine), *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco (Rocky Mountain Douglas-fir), and *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. (white fir)—have been largely unable to reestablish in these high-severity patches due to the lack of seed sources within patches, long distances exceeding seed dispersal distance from unburned edges, extreme soil erosion and steep slopes, and a period of summer drought that was lethal to tree seedlings (Falk, 2013; Coop et al., 2016). Instead of recolonization by dominant mixed-conifer tree species, many landscapes in this region have type-converted at least temporarily to shrub-dominated systems dominated by drought- and fire-tolerant species such as *Quercus gambelii* Nutt. (Fig. 9). Other research in the Jemez Mountains indicates that these oak-dominated patches may remain stable in their new configuration, thus representing patches of type-converted landscape (Guiterman et al., 2015).

Figure 9. Persistent post-disturbance type conversion from conifer forest to *Quercus gambellii* Liebm. shrubland following the 2002 Dalton Fire in the Sangre de Cristo Mountains, New Mexico. Photograph courtesy of Craig Allen, USGS.

MAPPING RESILIENCE THEORY TO ECOSYSTEM RESTORATION AND MANAGEMENT

These ecological dynamics and responses to disturbance create the need for a resilience-based paradigm as a necessary evolution of restoration ecology in a rapidly changing world (Falk & Millar, 2016). The inexorable pressure of changing climate, punctuated by interactions of episodic severe landscape disturbance and regional pools of both native and non-native drought- and fire-tolerant species, means that many ecosystems, once disturbed, are unlikely to return spontaneously to their predisturbance condition (Spittlehouse & Stewart, 2003; Drever et al., 2006). While ecological restoration efforts can reverse some of these changes, others may be inevitable and even adaptive (Harris et al., 2006; Jackson & Hobbs, 2009; Millar, 2014). Differentiating between these outcomes represents the crux of the problem of how to apply the ecology of resilience under future conditions of disturbance and climate in a way that maintains diverse and sustainable communities (Sagarin & Pauchard, 2010; Reynolds et al., 2013; Messier et al., 2015).

A resilience-oriented approach to restoration involves, in appropriate circumstances, relaxation of the principle that restoration has as its ideal endpoint a configuration as similar as possible to the predisruption reference condition; indeed, this is a bedrock principle of ecological restoration (Higgs et al., 2014). Reference conditions are necessarily dynamic, and in any reasonable form of restoration ecology these are understood to represent a dynamic range of variability, not static conditions (Falk, 1990; Choi, 2007). Moreover, ecosystems have substantial material and informational legacies that tend to buffer change and facilitate recovery (Johnstone et al., 2016). Nonetheless, combinations of disturbance, climate change, landscape-scale invasion by a non-native species, anthropogenic dispersal barriers, altered biogeochemical cycles, and other factors may make restoration s. str. difficult, if not impossible, to achieve, and in some cases potentially even maladaptive (Hobbs et al., 2014). Discriminating adaptive change from degradation thus becomes a crucial distinction, difficult to make even under the best of circumstances, let alone for ecosystems confronting novel climate or ecological context.

The core of a resilience strategy is to build on the innate abilities of species and natural systems to respond to and recover from disturbance or changing environments (Walker et al., 2004; Cross et al., 2012; Chazdon, 2017). A fundamental premise of restoration ecology is to support systems that are self-sustaining to the greatest extent possible without continuous human resource input or environmental modification. Therefore, an understanding of the means by which populations, species, and communities respond to disturbance should underlie a resilience-based strategy (Falk, 2006). These adaptations include population and genetic adaptations to variable environments (Stockwell et al., 2016),

Figure 10. Mechanically thinned (right) and unthinned (left) dry mixed conifer forest, Lassen Volcanic National Park, California. Photo courtesy of Calvin Farris, NPS.

dispersal and migration strategies, and contraction to refugia during periods of unfavorable climate, potentially re-radiating in a subsequent climatic period (Wang et al., 2010). Thus, a resilience ecology approach would have three primary phases, reflecting these underlying ecological mechanisms (Millar & Stephenson, 2015).

PROMOTE RESISTANCE AND PERSISTENCE

The tools of restoration ecology can be applied to assist existing individuals and population to resist stress and thus persist. For example, many species of plants have evolutionary adaptations to wildland fire. The basal apical meristem in perennial bunchgrasses is widely understood as an adaptation to both herbivory and fire (Anderson, 2006). Similarly, many species of trees, particularly conifers, have anatomical and morphological adaptations to fire, including thick bark, lifted crowns, and relatively heat-tolerant foliage (Agee, 2000). Many species of shrubs and trees native to fire-prone ecosystems, particularly Mediterranean chaparral and semi-arid shrubland communities, have evolved resprouting capacity that permits rapid recolonization in a post-fire environment, a life history property shared with many Madrean oaks (*Quercus* L. spp.) and *Pinus chihuahuana* Engelm. (Chihuahua pine).

Restoration treatments aimed at promoting resistance and persistence can be most effective by engaging these evolved strategies. For example, the elevated levels of mortality observed in many western North American montane conifer populations due to combinations of high temperature and vapor pressure deficit (VPD) exacerbated in densely packed stands where too many trees (compared to historical stand structure) are competing for limited soil moisture (Anderegg et al., 2013). Historically, these stands were more open in structure, with a relatively small number of large trees comprising the majority of basal area. A restoration treatment to promote persistence to this stressor would be to reduce competitor stem density and basal area, allocating a greater proportion of the limited available soil moisture resource for large overstory trees, as well as regenerating seedlings (Kolb et al., 2007; D'Amato et al., 2013). Similarly, fire is a keystone process to maintaining open stand conditions in many forest types; reintroduction of the natural fire regime and the resulting resumption of seedling and sapling mortality to historical rates would help maintain open, lower-density stand conditions conducive to resistance and persistence of established individuals (Fig. 10) (North et al., 2012).

PROMOTE RECOVERY POTENTIAL

Once the resistance of established individuals has been overcome and mortality occurs, the next phase of resilience is post-disturbance recovery, for which the processes of ecological succession and community assembly provide a model (Horn, 1974; Temperton et al., 2004; Bascompte & Stouffer, 2009). Fundamentally, recovery involves reproduction and establishment of new individuals of plants and animals, replacing those lost to mortality. Suites of early-seral species are adapted to capitalize on the resources and environments typical of early-successional environments, including tolerance for high levels of insolation, variable soil moisture and nutrient levels, variable nesting and feeding resources, rapid dispersal of propagules, rapid early growth rates, and other properties characteristic of disturbance-adapted species. As succession proceeds, other species may replace the early-successional component and eventually bend the arc of succession toward the pre-disturbance community. Species such as aspen and *Pinus contorta* Douglas ex Loudon subsp. *latifolia* (Engelm.) Critchf. (interior lodgepole pine) are highly disturbance adapted and can persist on the landscape only if there is either a mosaic of disturbance patches, or episodic large-scale mortality promoting their competitive advantage derived from evolved life history attributes (Brown, 1975). Recovery processes are also dependent on favorable environmental conditions, resources, and symbionts including soil biota and mycorrhizal fungi (Cairney & Bastias, 2007).

A resilience-based recovery strategy builds on these post-disturbance adaptive responses (Larson et al., 2013). The strategy must begin with a clear analysis of the processes that led to the mortality episode. For example, a recovery strategy from long-term drought may differ from one designed to mitigate the effects of a severe wildfire or other more localized disturbance. Generally speaking, an effective resilience recovery strategy will mimic the natural process of succession and community assembly, utilizing the evolved ability of certain species to thrive in recently disturbed environments, and over time progressively adding in later successional species, either intentionally (that is, by restorative action), or by allowing other species and the regional pool to colonize the site by natural dispersal processes (Mackey et al., 2012). Recovery actions include outplanting of seeds or establishing juvenile individuals, or release of captive-bred animals as is commonly done for mammals, fish, birds, and other taxa (Pérez et al., 2012). Reintroducing essential symbionts (such as mycorrhizal associates, pollinators, or biotic dispersal agents) are part of the way that a resilience strategy mimics natural successional processes. Soil amendments or modification of aquatic chemistry are also a component of this phase to restore the biophysical template on which other species will depend. Recovery actions are typically concentrated at the population level, in contrast to persistence and resistance, which are primarily properties of individuals. Assisted natural regeneration can be a component of a recovery-based strategy when natural dispersal or recruitment is limiting (Chazdon & Uriarte, 2016).

REALIGNMENT OR REORGANIZATION

Over time, nearly all species show evidence of the capacity to adapt to novel environments (Jackson et al., 2009). This is evident in the fossil record, which documents the ability of species to track climatic change over ecological and evolutionary timescales (Davis, 1990). Species migrate at rates generally consistent with the length of their reproductive cycle, dispersal abilities, and other factors. At millennial to multi-millennial timescales, plant communities disassemble and reassemble as species respond individualistically, sensu Gleason (1926) to climate during periods of rapid change. For example, during the Pleistocene–Holocene transition the range of *Pinus monophylla* Torr. & Frém. (singleleaf piñon) has expanded northward along the western North American Great Basin for the past 12,000 years, reaching some currently occupied sites in northwestern Nevada in only the last three to four centuries (Grayson, 2011). Paleoecological evidence demonstrates conclusively that the reorganization of communities, and range shifts of individual species, are fundamental properties of adaptation to changing environments (Jackson, 2006; Stewart, 2009; Booth et al., 2012).

Resilience ecology departs from the traditional domain of restoration in this third phase, which potentially involves intentional reorganization of ecological communities. While it can be argued that reorganization is a natural adaptive response, restoration ecology has by convention relied on reference conditions (either historical or contemporaneous) to guide restorative activity, although more dynamic models of reference conditions are developing (Balaguer et al., 2014; Higgs et al., 2014). The reference framework remains valid in many circumstances, perhaps most, because of the powerful inertia of ecological legacies as well as the imperfectly understood ability of species and populations to persist and recover from disturbance and changing environments (Johnstone et al., 2016). Relaxing the centrality of the reference condition is a significant departure from traditional restoration principles and cannot be undertaken lightly or without careful consideration.

A relatively conservative example of adaptive realignment beyond the reference condition would involve outplanting different genotypes of a target species from those found presently in a restoration area. Given current and projected climate trends, a reasonable strategy for maintaining a species within its current range might be to enhance drought resistance or heat tolerance by outplanting more drought-adapted genotypes from nearby populations (Butterfield et al., 2016; Gross et al., 2016). As climate suitability zones shift, such within-species genotypic mixing may become more widely practiced and even essential.

A greater degree of intervention may be called for where disturbance and climate interactions threaten the persistence of an entire ecological community. For example, fire has been excluded from many fire-adapted forests over the past century, resulting in unnaturally high fuel accumulation and dense structure, predisposing these communities to uncharacteristically severe fires, causing high levels of mortality over large contiguous landscape areas. These high-severity fires can compound the effects of drought stress, which in addition to causing mortality can also create conditions unfavorable for seed germination and seedling establishment. An offsetting strategy integrating these two factors could include a combination of thinning (to reduce fuel accumulation and spatial continuity), and in-planting of some drought-tolerant species into the community. These proactive measures would have the net effect of making the community both more fire tolerant and also more drought tolerant, reducing the risk of a complete loss of ecosystem services due to drought mortality and severe fire (Millar & Stephenson, 2015). This approach falls outside of a traditional restoration paradigm, in the sense that forest structure and species composition are being modified proactively outside of the strict historical range of variability. Such pro-adaptive strategies exemplify a resilience-oriented approach and may be required in some cases to protect larger values at risk.

A strategy that departs most strongly from a historically grounded restoration paradigm is assisted migration, the intentional release of organisms outside of their current or documented recent historical range (McLachlan et al., 2007; Stone, 2010). Assisted migration aims to establish new populations outside of a species' range. Assisted migration actively anticipates climate adaptation, although clearly it is not possible to introduce organisms entirely outside of their viable climate envelope under current conditions. Assisted migration has been accomplished most successfully when it is (1) incremental, consisting of short-range introductions adjacent to the current range of species; (2) targeted to ecologically analogous sites where the species would most likely occur following a successful natural dispersal process; and (3) taking full account of essential species interactions such as pollinators, dispersal agents, mycorrhizal symbionts, prey species and other food resources, and other interspecific factors (Pérez et al., 2012). Assisted migration has been both defended and criticized in the restoration literature, and the ethics and guidelines for its responsible practice are not yet fully articulated. However, it appears likely that assisted migration will continue to be practiced as an essential component of maintaining ecological resilience in the face of changing climate and other axes of change.

In all of these cases, an option is to allow species to adapt to changing climate geography by dispersing and colonizing new areas on their own means, as they have done throughout their evolutionary history. Natural dispersal and colonization is a reasonable non-interventionist null model, and in many cases may constitute a sufficient restoration strategy. However, the intersecting axes of change may inhibit the ability of species to adapt geographically; invasive non-native species, major human-built barriers, altered disturbance regimes, large-scale land use patterns such as agricultural conversion, and disruption of continuous hydrologic flows in streams and rivers can all constitute insurmountable barriers to species movement over time. In addition, the geographic velocity of climate ("climate velocity") projected in the coming century exceeds the documented dispersal rates of many groups of organisms (Loarie et al., 2009). The ability of species to track climate autonomously by dispersal and colonization may be particularly challenging for edaphic specialists, or for aquatic species in regions where continuous stream flow is interrupted. A resilience-based strategy based on intentional species translocation may become necessary in some cases to counteract the effects of climate velocity.

CONCLUSIONS

The interacting axes of change in the modern world compel a reevaluation of the premises of traditional restoration theory (Halpin, 1997; Falk & Millar, 2016). While much of the restoration paradigm remains intact, and indeed essential, certain changes will be necessary if restoration is to fulfill its potential to assisting nature to adapt to a rapidly changing world (Benson & Garmestani, 2011; Rist & Moen, 2013). Maintaining ecological resilience has always been a goal of restoration ecology. However, what is required to meet this goal now and in the near future is changing rapidly.

Three questions can be posed of a resilience ecology strategy, to ensure that departures from traditional restoration principles are warranted and effective: (1) Which kinds and degrees of change are destructive of ecological sustainability, and which are adaptive in a rapidly changing world? Not all stasis is adaptive, and not all change is adverse. Resolving these differences will be imperative for the practice of resilience ecology, as practice extends into circumstances that are unfamiliar ground in ecology as well as restoration. (2) How will a resilience ecology approach be realized on the ground? Do we understand the ecological processes of resistance, recovery, and reorganization that guide ecological trajectories well enough to apply them as the basis for restoration practice? How can outcomes be evaluated under such high uncertainty, and what are the indicators of success? Until resilience can be mapped onto the needs and practices of ecosystem managers, resilience ecology will remain a body of theory with untested potential. (3) If we relax strict fidelity to reference conditions, how can we ensure that resilience measures will have the desired effect of enhancing the larger property of resilience? This question may be particularly challenging in cases where managers have to decide whether to fight to maintain a species population in situ, or concentrate on community modification and species relocation into areas with a more promising future. While this may not be difficult for some widespread plant or animal communities, the loss of iconic populations represents a fundamental ethical challenge to a resilience-based paradigm.

In the end, the most important role of ecological restoration may be to expand the resilience space in which ecosystems can adapt to rapidly changing and challenging environments. While profound change may be inevitable in some areas, the starting point for a resilience-based model must remain to protect nature as we find it wherever that is feasible, and to assist adaptation to an uncertain future.

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