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Climate Change and Novel Disturbance Regimes in National Park Landscapes

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Introduction

National parks preserve unique elements of the American landscape and are highly valued components of our national heritage. These protected areas provide reference conditions along the continuum of land use from pristine to rural to urban, and their ecological value grows as surrounding landscapes become increasingly developed, fragmented, or degraded (Hansen et al. 2014). Large national parks such as Yellowstone anchor many of our last intact landscapes, and their scientific value for understanding the structure and function of natural ecosystems is unparalleled because management interventions are minimal. As drivers of global change alter ecosystems worldwide, national parks offer irreplaceable opportunities for scientists and resource managers to understand ecological responses to environmental change. Of particular importance is the need to understand consequences of changing climate and disturbance regimes (Turner 2010).

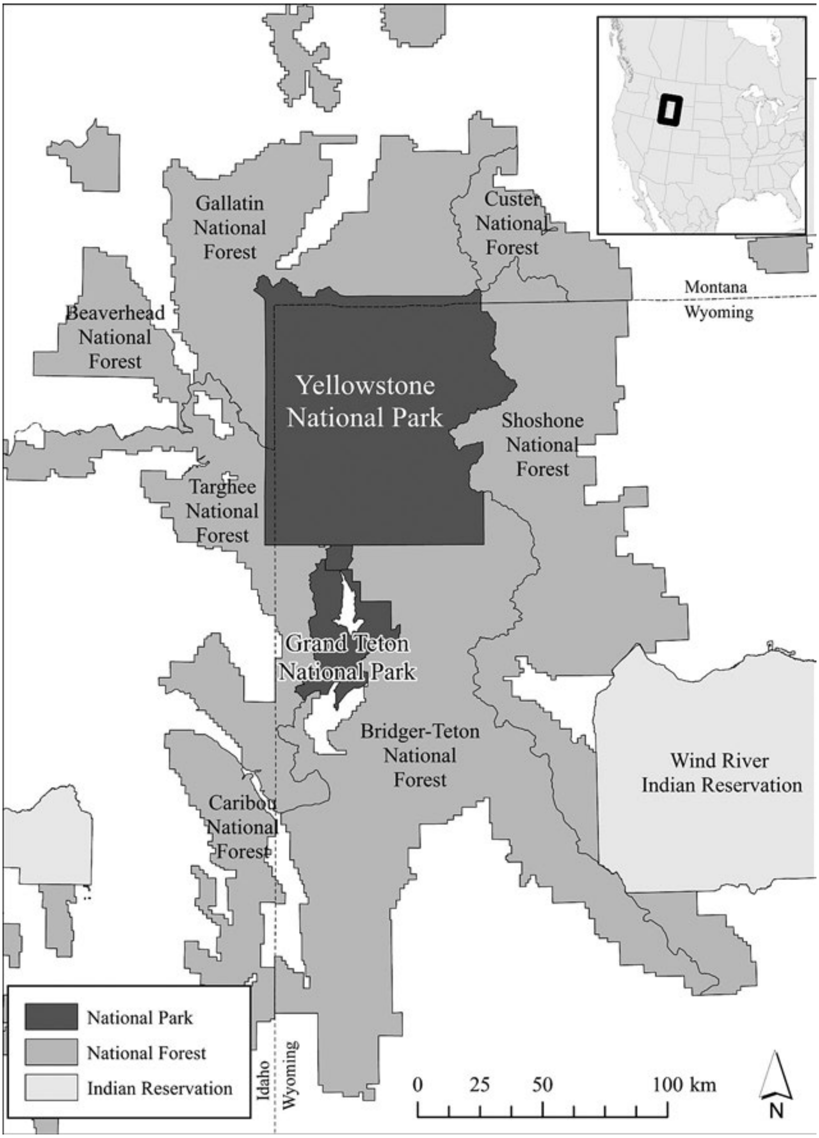
Disturbance is a key process in ecological systems, affecting terrestrial, aquatic, and marine ecosystems over a wide range of scales. Disturbances alter ecosystem states and trajectories, and they can shape ecosystem dynamics long into the future. Scientific understanding of natural disturbances and appropriate management of disturbance-prone landscapes evolved considerably during the 20th century. Ecologists had long upheld balance-of-nature concepts and believed that ecosystems could be maintained in desired but static states over the long term. Natural disturbances were not considered integral or desirable in many ecosystems. Reflecting the science of the time and that widely held equilibrium worldview, the 1963 Leopold Report, *Wildlife Management in the National Parks*, stated: "A national park should present a vignette of primitive America" (Leopold et al. 1963). Understanding of how natural disturbances structure ecosystems increased in subsequent decades (Pickett and White 1985), and ecologists recognized that few ecosystems were ever at equilibrium (Turner et al. 1993; Wu and Loucks 1995). Conventional wisdom about steady-state conditions also was challenged by occurrences of large, severe natural disturbances that captured public attention (Turner, Dale, and Everham 1997). The 1992 Risser report, *Science and the National Parks,* recognized these advances in scientific understanding when it stated: "Ecological science now recognizes that change is central to the structure and functioning of all ecosystems, and it is now evident that the managers of the parks must understand the changes—both natural and anthropogenic—that occur. To conserve ecosystems unchanged is simply impossible" (National Research Council 1992). By the end of the 20th century, disturbance was recognized as ecologically important, and maintaining dynamic ecosystems within their historical range of variability was widely embraced as a management goal (Keane et al. 2009). However, baselines are once again shifting in science and management as global changes accelerate. The magnitude and rate of climate warming make it more difficult to project the future based on past knowledge, and effects on national parks and other protected areas are highly uncertain. What does this imply for national parks? How much will they change? Will future dynamics exceed historical ranges of variation? The 2012 report of the National Park System Advisory Board Science Committee, *Revisiting Leopold: Resource Stewardship in the National Parks,* now states: "National Park Service . . . should . . . steward resources for continuous change that is not yet fully understood" (Colwell et al. 2012).

Climate and disturbance regimes are both changing rapidly, and it is increasingly important for ecologists and park managers to understand the past and anticipate what lies ahead. The frequency, severity, and extent of natural disturbances are changing substantially as climate warms; effects on many ecosystems may be profound (Westerling et al. 2006; Seidl, Schelhaas, and Lexer 2011; Parks, Parisien, and Miller 2012; Weed, Ayres, and Hicke 2013; Moritz et al. 2014). In the Northern Rocky Mountains, a region with several national parks, fire and insect outbreaks are key drivers of landscape pattern and ecosystem function. Climate-driven changes in these disturbances will affect most western national parks; indeed, changes may already be underway. Long-term studies in Greater Yellowstone have documented tremendous ecological resilience to these natural disturbances over centuries to millennia, but projected climate change may lead to novel disturbance regimes and unforeseen ecological responses. Understanding the how, when, where, and why of these dynamics is urgent for park management and conservation.

Drawing primarily from our research in Greater Yellowstone and the Northern Rocky Mountains, we highlight the critical role of national parks as living laboratories for scientific research during these times of rapid change, as well as the importance of science for park management. We provide an overview of Greater Yellowstone and its dominant natural disturbances, summarize general lessons that emerged from long-term basic scientific studies, and then consider how future change in climate and disturbance dynamics may affect the landscape. We conclude by advocating for an even stronger commitment to the value of parks for science.

Natural Disturbances in Greater Yellowstone

The 80,000 km^2 Greater Yellowstone Ecosystem is centered on Yellowstone National Park and straddles portions of Wyoming, Montana, and Idaho (fig. 5.1). It includes Grand Teton National Park, seven national forests, the National Elk Refuge, and parts of the Wind River Indian Reservation. Greater Yellowstone is unique in some respects—notably the extensive geothermal features and abundant wildlife for which the region is famous—but it is also representative of temperate mountain ecosystems throughout western North America. Therefore, lessons from Yellowstone are relevant for other regions that are less well studied. Yellowstone National Park encompasses ~9,000 km^2, most of which lies on a high-elevation (~2,100–2,700 m) volcanic plateau with relatively gentle topography. Surrounding the plateau are higher, rugged mountains of various crystalline, sedimentary, and volcanic substrates, as well as broad river valleys and basins characterized by a semiarid climate. Approximately 80% of Yellowstone National Park is dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) forest, although subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) can be locally abundant at high elevations. At lower elevations, Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) forests grade into sagebrush (*Artemisia* spp.) steppe and grasslands. The climate is characterized by cold, snowy winters and dry, mild summers. Some ungulate populations were controlled in the past, and wolves were extirpated and subsequently reintroduced. Nonetheless, in contrast to much of the Rocky Mountain region, the pre-Columbian flora and fauna of Greater Yellowstone remain largely intact, in part because it is one of the largest tracts of wild, undeveloped land in the continental United States (Gude et al. 2006). This largely



5.1. Map of Greater Yellowstone

pristine condition makes Yellowstone invaluable for research into natural patterns and processes at multiple spatial and temporal scales.

Fire

The role of fire has been recognized in Yellowstone for a long time. The early explorers of the Yellowstone region even mentioned it—in his diary of the 1870 Washburn Expedition, Nathaniel Pitt Langford (who later became the first superintendent of Yellowstone National Park) wrote: "Tuesday, September 20—We broke camp at half past 9 o'clock, traveling along the rocky edge of the [Firehole] river bank by the rapids, passing thence through a beautiful pine wood and over a long stretch of fallen timber, blackened by fire, for about four miles" (reprinted by Miller 2009). Based on their route that day, the expedition likely traversed a large fire that occurred circa 1862, the date of origin for lodgepole pine forests along the east side of the Firehole River. In addition, numerous entries in the Washburn Expedition diary report exceedingly slow and difficult travel through areas with abundant downfall—much of which was likely legacy wood from past fires. For example, Langford described pine forests they navigated along the eastern shores of Yellowstone Lake a couple of weeks earlier:

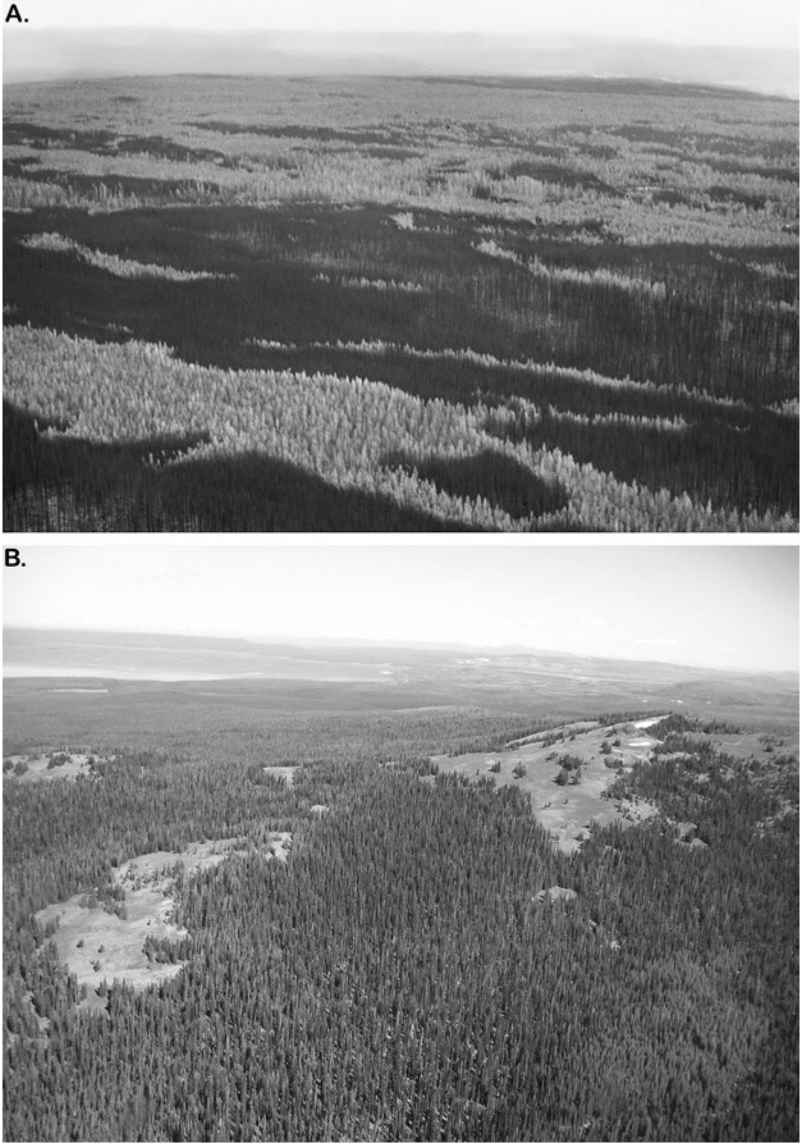
> Tuesday, September 8—Our journey for the entire day has been most trying. . . . The difficulty of . . . making choice of routes, extricating the horses when wedged between the trees, and readjusting the packs so that they would not project beyond the sides of the horses, required constant patience and untiring toil.
>
> Wednesday, September 9— . . . through fallen timber almost impassable in the estimation of pilgrims. . . . Frequently, we were obliged to rearrange the packs and narrow them, so as to admit of their passage between the standing trees. (reprinted by Miller 2009)

Based again on their route, the expedition was probably slogging through dense lodgepole pine regeneration and fallen, fire-killed trees where the forest had burned circa 1840. (The even-aged pines were about 160 years old in 1999, and Langford's description well matches our recent attempts to traverse impenetrably dense 25-year-old postfire lodgepole pine forests.)

Fire-history studies based on extensive tree-ring analyses found that large stand-replacing fires had burned in Yellowstone during the 18th and 19th centuries (Romme 1982; Romme and Knight 1982; Romme and

Despain 1989). This work also revealed a dynamic landscape mosaic of stand ages in response to infrequent, high-severity fire. Romme's research had been designed to address fundamental questions in ecology about disturbances and equilibrium, and such studies could only be addressed in large wildland landscapes like Yellowstone. His results were of great interest to forest landscape ecologists because his studies quantified spatial-temporal dynamics over a large landscape and documented a non-steady-state system. However, this basic scientific understanding also proved essential for park managers when the hot, dry summer of 1988 produced large wildfires throughout Greater Yellowstone. The science was crucial for placing those fires in context and recognizing that they were consistent with the historical disturbance regime.

The 1988 Yellowstone fires were among the first in what has proven to be an upsurge in large severe fires in the western United States during the past 20 years. The fires burned under extreme drought and high winds, and ultimately they affected ~600,000 ha in Greater Yellowstone. Compared with previous 20th-century fires, their size and severity were a surprise to scientists and managers, and ecological effects of the fires were highly uncertain. Little was known at that time about the impacts of such a large severe disturbance because scientists had had few previous opportunities to study such an event. Soon after the fires, ecologists generated testable predictions regarding short- and long-term effects on vegetation, wildlife, aquatic ecosystems, biogeochemistry, and primary productivity based on scientific understanding of the time (see the November 1989 special issue of *BioScience*). Many studies were initiated to evaluate these ideas, and results of this body of research were synthesized at postfire milestones of 10 years (Turner, Romme, and Tinker 2003; Wallace 2004) and 20 years (Schoennagel, Smithwick, and Turner 2008; Turner 2010; Romme et al. 2011). The new understanding gained from those studies has proven extremely valuable and relevant to fire policy throughout the western United States (Weeks 2012; Stephens et al. 2013). The 1988 fires created novel opportunities to study postfire succession and ecosystem processes in a wilderness setting. In particular, they offered a natural landscape-level experiment in which ecological effects of spatial patterns could be tested (fig. 5.2a). Results established benchmarks for early postfire dynamics in western conifer forests, and Turner's and Romme's studies provided compelling examples of the ecological role of landscape pattern (e.g., Turner et al. 1997). After more than 25 years, ongoing studies of the young postfire forests continue to add new knowledge and insights. Young forests are increasing in extent throughout the western United States in response to



5.2. Disturbance-created heterogeneity in Greater Yellowstone. *A*, the 1988 fires created a mosaic of patches that vary in size, shape, and severity across the landscape. Photo by M. G. Turner, October 1988. *B*, bark beetle outbreaks create a fine-grained mosaic of tree mortality, as shown here for spruce beetle outbreaks in Engelmann spruce. Photo by M. G. Turner, June 2006.

greater fire activity, and understanding their dynamics is essential for good stewardship of these rapidly changing landscapes.

Bark Beetle Outbreaks

Outbreaks of native species of bark beetle (Dendroctonae) have also been part of Greater Yellowstone for a long time. Native bark beetles of the genus *Dendroctonus* undergo episodic population outbreaks that result in widespread mortality of host trees through pheromone-mediated mass attacks (Wallin and Raffa 2004; Raffa et al. 2008). From about 2003 to 2012, Greater Yellowstone experienced widespread outbreaks of bark beetles, including the mountain pine beetle (*Dendroctonus ponderosae*) in lodgepole and whitebark pine, spruce beetle (*Dendroctonus rufipennis*) in Engelmann spruce, and Douglas-fir beetle (*Dendroctonus pseudotsugae*) in Douglas-fir. The recent outbreak was mostly in the eastern and northern parts of Greater Yellowstone and involved multiple tree and beetle species (Simard et al. 2012), whereas an earlier outbreak in the 1970s and 1980s affected the western and southern portions of Greater Yellowstone and involved mostly lodgepole pine and the mountain pine beetle (Furniss and Renkin 2003; Lynch et al. 2006). Across the western United States, recent outbreaks appear to be more extensive, more homogeneous, and more severe in their effects on stand and landscape structure compared with previous outbreaks (Raffa et al. 2008; Meddens, Hicke, and A. Ferguson 2012). It was widely believed that tree mortality resulting from beetle outbreaks would increase the likelihood of severe fires, and likewise that trees injured by fire would be more susceptible to beetle attack. Empirical evidence for this conventional wisdom was lacking, and testing it required extensive intact forests in which both disturbances occurred in the absence of intensive forest management.

Greater Yellowstone again provided an opportunity for basic landscape-level research on these potential disturbance interactions (fig. 5.2b). Empirical studies documented changes in stand structure and ecosystem process rates and revealed substantial capacity of the forests to withstand beetle outbreaks (Simard et al. 2011; Griffin, Turner, and Simard 2011; Donato, Harvey, et al. 2013). Modeling studies suggested that the likelihood of severe fire might not be worsened by beetle outbreaks (Simard et al. 2011), and subsequent empirical (Harvey et al. 2013, 2014) and modeling studies (Donato, Simard, et al. 2013) in Greater Yellowstone supported this notion. Research in national park and wilderness areas also provided a baseline for evaluating effects of postdisturbance management (e.g., Griffin, Simard, and Turner 2013; Donato, Simard, et al. 2013). Like the fire studies, these studies in Greater Yellowstone are providing valuable insights about disturbance in western forests (Harvey, Donato, and Turner 2014) and informing regional land management (Wells 2012; Carswell 2014).

Lessons from Yellowstone about Natural Disturbances

Given the wealth of disturbance studies in Greater Yellowstone, what general lessons have been learned that apply to other places, to other national parks, and to the expansive forests of the western United States? Here, we summarize six general scientific lessons that have emerged from our long-term studies in Yellowstone.

1. *Large, infrequent, severe fires are "business as usual" in subalpine forest landscapes.* Although the 1988 fires were large and severe, we have learned that such fires are not unusual in Greater Yellowstone. There is *no evidence* that the size or severity of the 1988 fires resulted from human activities, such as fire suppression. Large, stand-replacing fires have occurred during warm, dry periods in the historical past (Romme and Despain 1989) and during past millennia (Meyer and Pierce 2003; Millspaugh, Whitlock, and Bartlein 2004; Whitlock et al. 2008; Higuera, Whitlock, and Gage 2011), and the biota are well adapted to these events. Fire return interval varies with elevation, averaging about 170 years at sites less than 2,300 m above sea level and about 290 years at sites more than 2,300 m (Schoennagel, Turner, and Romme 2003). Many subalpine and boreal forests have similar infrequent, high-severity fire regimes (Turner and Romme 1994). Thus, it is not so surprising after all that the region's forests have regenerated rapidly following recent large fires.

2. *Natural disturbances are important sources of landscape heterogeneity.* In contrast to claims made by some observers of the 1988 fires and recent beetle outbreaks, even large, high-severity disturbances are spatially heterogeneous. The 1988 fires created a complex (and, to many observers, even beautiful) mosaic of burned and unburned patches across the landscape (Turner et al. 1994), and patterns created by natural fires differed markedly from patterns of forest harvesting in Greater Yellowstone (Tinker, Romme, and Despain 2003). New vistas were revealed, wildflowers bloomed prolifically, and openings in the forest offered new resource patches to be used for wildlife. The bark beetle outbreaks created a very fine-grained mosaic, because tree mortality is not complete within stands. For example, outbreak severity (percentage of basal area killed by beetles) ranged from 36% to 82% in lodgepole pine stands sampled in 1981 and 2007, during each of

the two most recent outbreaks in Greater Yellowstone (Simard et al. 2012), and from 38% to 83% in Douglas-fir stands attacked between 1980 and 2010 (Donato, Harvey, et al. 2013). Disturbance-created heterogeneity (see fig. 5.2) is functionally important, establishing patterns of stand and landscape structure that sustain ecosystem processes for decades to centuries.

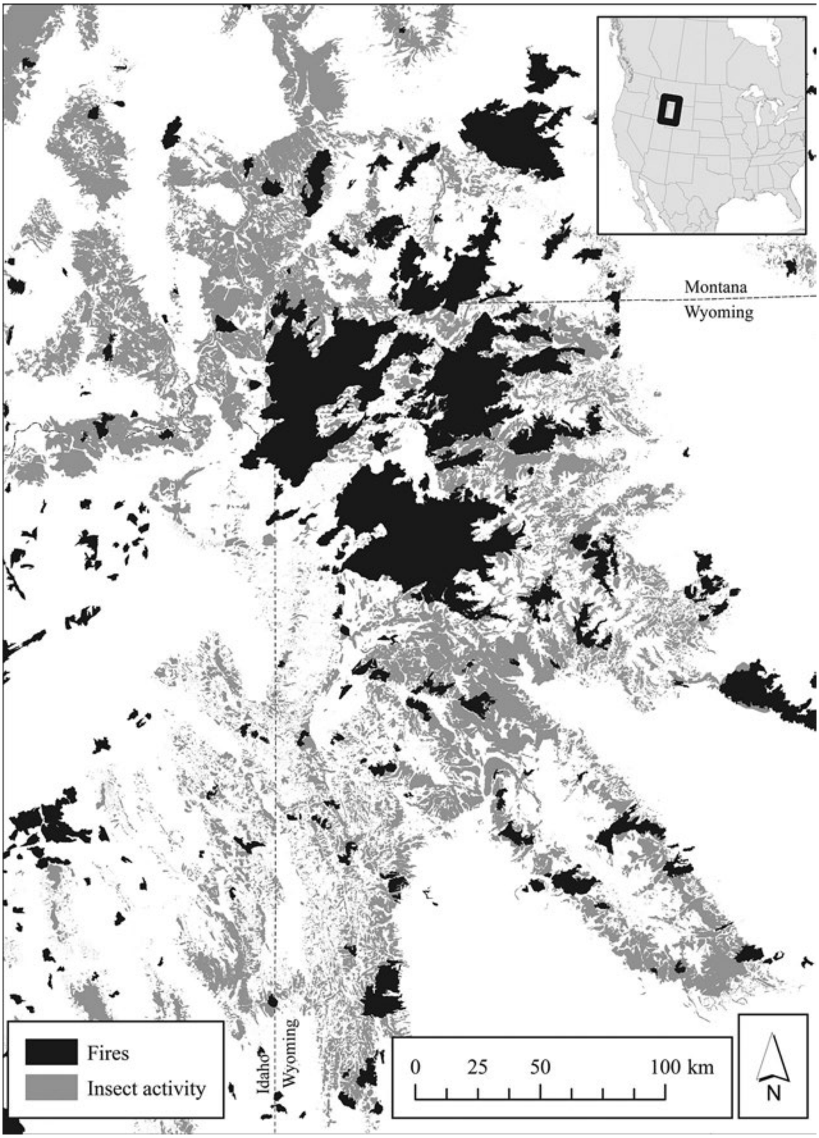
3. *Beetle outbreaks kill trees but do not destroy forests.* Bark beetles attack large trees, and conspicuous red crowns of beetle-killed trees can make it appear as if the entire forest is dying. However, this is not the case. Even in very severe outbreaks (e.g., when more than 90% of tree basal area is killed by beetles), postoutbreak forests usually contain many more live than dead trees. Trees underneath the canopy are often too small to be killed by beetles, and these trees experience accelerated growth rates postoutbreak. In addition, mature nonhost trees often escape an outbreak unscathed (Simard et al. 2011; Donato, Harvey, et al. 2013). Rapid growth of surviving trees, coupled with slow decay of beetle-killed trees, results in recovery of preoutbreak biomass carbon storage within a few decades postoutbreak (Donato, Simard, et al. 2013). Wildflowers and grasses also respond rapidly when mature trees die, taking advantage of newly available resources (e.g., nutrients, water, space) and effectively conserving nutrients in disturbed stands (Griffin, Turner, and Simard 2011). These outbreak-induced changes may also benefit forest wildlife. High-quality forage provided by nutrient-rich herbaceous plants, coupled with increased habitat structure complexity from snags and falling beetle-killed trees, attracts elk, deer, moose, and birds across many guilds (Saab et al. 2014). In short, the death and decadence following beetle outbreaks is counteracted by rapid stimulation of life and growth.

4. *Climate is an important driver of fire and bark beetle outbreaks.* Studies continue to demonstrate that climate—particularly warm, dry conditions—is the key driver of large, stand-replacing fires as well as bark beetle outbreaks (Westerling et al. 2006; Raffa et al. 2008; Bentz et al. 2010; Krause and Whitlock 2013). In western conifer forests, it is the extremely warm, dry, and windy summers that are responsible for most of the area burned (Westerling et al. 2006). Historically, most summers were too moist and cool to support large fires, even though fuels were abundant, and fires were not enormous in moderately dry years (Turner and Romme 1994). Warm, dry conditions also foster bark beetle outbreaks because drought-stressed trees are more vulnerable to beetle attack (Raffa et al. 2008). Of course, climate also interacts with other variables, such as topography, past disturbance history, and antecedent forest structure, to determine the size and severity of a given disturbance event. However, climate is often the strongest

influence among candidate variables, especially in mid- to high-elevation western conifers (Westerling et al. 2006; Harvey et al. 2014). Because of its importance, changes in climate are likely to alter fire and bark beetle outbreak dynamics in western landscapes.

5. Beetle outbreaks do not cause or worsen fire impacts, and fires do not cause or worsen beetle outbreaks. Bark beetle outbreaks and fires both occur under warm, dry conditions that stress trees, weakening their defenses against insects, and increase flammability, raising the likelihood of fire occurrence. Warm temperatures during winter also increase overwinter survival of bark beetles and can sustain an outbreak from one year to the next. However, both disturbances are responding to a similar driver, rather than directly affecting one another. Beetle outbreaks do alter the fuel structure of forests at the stand scale (Simard et al. 2011; Donato, Harvey, et al. 2013) and may affect the way fire behaves (Jenkins et al. 2012). However, contrary to expectations, when wildfires burn through beetle-affected stands, most measures of fire severity (effects on the ecosystem) are unrelated to outbreak severity and are largely similar to those in unaffected stands (Harvey et al. 2013, 2014; Harvey, Donato, and Turner 2014). Instead, fire severity in beetle-affected landscapes is driven by two of the main factors affecting any wildfire: weather and topography. Further, postfire tree regeneration is generally robust in previously beetle-affected landscapes as long as seed sources remain (i.e., surviving trees or viable cones)—as in any wildfire. Postfire regeneration was robust in beetle-killed lodgepole pine forests because serotinous cones were still present (Harvey et al. 2014), but poor in beetle-killed Douglas-fir forests because seed sources were absent (Harvey et al. 2013). Regarding the converse interaction in which fires are expected to cause beetle outbreaks in surrounding forests, recent research in Greater Yellowstone demonstrates that fire-injured trees provide local refugia for beetle populations but generally do not generate extensive outbreaks in healthy trees because reproductive success is low (Powell, Townsend, and Raffa 2012).

6. Forests of Greater Yellowstone have been remarkably resilient to natural disturbances. Collectively, our long-term studies of natural disturbances in Greater Yellowstone have documented tremendous ecological resilience. Paleoecological studies have also demonstrated long-term resilience in disturbance and vegetation dynamics over the past 10,000 years (Whitlock and Bartlein 1993; Whitlock, Shafer, and Marlon 2003; Millspaugh, Whitlock, and Bartlein 2004; Higuera, Whitlock, and Gage 2011). Natural disturbance has not been an ecological catastrophe. Disturbances structure this landscape; between 1984 and 2010, most of Yellowstone has been influenced by disturbance (fig. 5.3). These disturbances produce a dynamic



5.3. Greater Yellowstone is strongly influenced by natural disturbances, as shown by areas affected by fire and insect outbreaks between 1984 and 2010. Map generated by B. J. Harvey from USDA aerial detection survey data (http://www.fs.fed.us/foresthealth/) and Monitoring Trends in Burn Severity (MTBS) data (Eidenshink et al. 2007; www.mtbs.gov).

mosaic in which forest ages and tree densities vary substantially across the landscape and through time. Ecosystem recovery from natural disturbances has not required any management intervention (Romme and Turner 2004). However, accelerating rates of environmental change pose new challenges.

Future Climate Change and Disturbance in Yellowstone

Earth's climate is warming, and this warming can only be explained by accounting for human-caused emissions of greenhouse gases, especially carbon dioxide. Warming will continue throughout the 21st century, even if greenhouse gas emissions are reduced. The rate and magnitude of projected climate change heighten the urgency for scientists to anticipate and managers to prepare for changes in national parks. In Yellowstone, forests have been resilient to past changes in climate and disturbance regimes, as forests have regenerated well following past disturbances. Will resilience be guaranteed if the magnitude of future changes exceeds variability during the past 10,000 years? Projected climate changes could lead to novel disturbance regimes and unforeseen ecological responses. Answers to questions of resilience will depend on the variables used to assess change in the system and the scales at which resilience is measured. An environmental change that leads to a state transition, such as from forest to nonforest, would indicate a lack of *forest* resilience at particular locations. However, the *ecosystem* might be considered resilient if other native species expand in place of trees, and ecosystem functions are maintained (e.g., carbon sequestration, nutrient cycling, and provision of wildlife habitat). Furthermore, habitats (such as forests) could retreat from some places but expand at others while maintaining their extent at a regional scale. Thus, resilience is a multifaceted concept.

As climate warms, park managers will likely consider whether to let changes occur as they will or to intervene to try to redirect or slow rates of change (Marris 2011). *We assert that parks and protected areas are* ***not*** *the place for management to redirect or alter ecosystem responses to climate change*. Such activities can be implemented in many other landscapes and may be desirable in more intensively used areas. However, national parks and protected areas provide critical reference conditions for understanding how ecosystems respond to rapid change, and knowledge gained will ultimately inform what is done in other places. To maintain the capacity for ecosystems to adapt to environmental change, park managers could focus on minimizing other threats that would limit the ability of native species to respond.

For example, managers might intensify efforts to control aggressive nonnative invaders such as cheatgrass (*Bromus tectorum*), which we have observed at low-elevation, dry topographic positions following recent fires in Greater Yellowstone. Affording native species the opportunities to disperse and shift ranges will be critical for ecosystems to adapt to climate change. Providing for connectivity of natural areas over large landscapes is essential, and securing regional connectivity will require cooperation among multiple land managers.

As for future climate and disturbance, what is expected for Yellowstone? Temperatures in the Northern Rocky Mountains have warmed over the past few decades, especially at middle elevations (Westerling et al. 2006; Shuman 2012). This warming is associated with earlier timing of spring snowmelt (Pederson et al. 2011), warmer summer conditions, and a longer growing season and fire season. Climate models predict continued warming, with average spring and summer temperatures increasing 4°C–6°C by the end of the 21st century (Westerling et al. 2011). The pace of current warming is much faster than the warming at the end of the Pleistocene and happening in a world affected by other human impacts, such as habitat fragmentation. Future precipitation remains uncertain, but recent trends in observed climate indicate an overriding effect of temperature that exacerbates drought during the growing (and fire) season. A warmer, drier future for Greater Yellowstone appears most likely for the coming decades. Summers as hot and dry as 1988 are likely to occur with increasing frequency throughout the 21st century, and to become the norm by the latter part of the century (Westerling et al. 2011).

Implications of climate warming for natural disturbance regimes are substantial. The frequency, extent, and severity of fires in the western United States have already increased with warming (Westerling et al. 2006; Weed, Ayres, and Hicke 2013), and landscapes are changing rapidly as mature conifer forests are increasingly reset by severe fire to early successional stages (Johnstone, Chapin, et al. 2010; Johnstone, Hollingsworth, et al. 2010; O'Connor et al. 2014). In the Northern Rocky Mountains, novel fire regimes that are well outside even paleoecological ranges of variability are predicted during the 21st century (Westerling et al. 2011; Liu, Goodrick, and Stanturf 2013). Peterson and Littell (2014) projected a more than 600% increase in median area burned in Greater Yellowstone and the Southern Rocky Mountain region with only a 1°C rise in temperature. Westerling et al. (2011) projected an even greater increase in burning. Summers conducive to widespread burning, like 1988, would become common, and years without any large fires, which were frequent historically, would become rare. Consequences of such changes for forest landscapes may be profound.

Greater Yellowstone continues to offer an unparalleled opportunity to understand how intact ecosystems and landscapes respond to changing climate and disturbance regimes. In such large heterogeneous landscapes, scientists can measure responses of the biota to changing conditions, evaluate mechanisms of resilience that may apply broadly across ecosystems, and potentially identify early indicators of ecosystem change. The need for creative, long-term measurement programs that are sensitive to anticipated changes in climate and disturbance regimes is more important now than ever before. We suggest two priorities.

First, the importance of long-term study in Greater Yellowstone and other national parks cannot be overemphasized. Long-term study of the ecological consequences of the 1988 Yellowstone fires has already produced a tremendous amount of new knowledge (Turner 2010; Romme et al. 2011), and these data now provide the benchmarks against which the consequences of future fires can be compared. The 1988 fires and ecological responses to those fires represent the historical fire regime that characterized this region throughout most of the Holocene. The fires burned mostly in mature and old-growth forests, also typical of previous large fires in Yellowstone. Postfire trajectories after mid-21st-century fires may differ significantly from those measured following the 1988 fires, and it will be important to document these future postfire dynamics, as well as to continue following long-term development of the post-1988 forests. Future fires will likely burn in younger stands, and postfire recovery will occur under substantially warmer and possibly drier conditions. Comparing future fires and fire effects with what we saw after 1988 will allow the magnitude of departure from the historical fire regime to be measured.

Second, there is a critical need to understand mechanisms and identify early warning signs of major qualitative changes in the landscape. For instance, forests could be converted to shrublands or grasslands after fire if fire intervals become so short that trees cannot reach reproductive age before the next fire occurs, or the climate becomes unsuitable for survival of postfire tree seedlings. What conditions lead to loss of forest resilience, and the nature and rates of species responses to changing tree distributions, are not known; indeed, long-term studies in protected areas may provide the basis for new understanding of what constitutes ecosystem resilience. Large national parks and protected areas are ideal places for studying such patterns because they capture a wide range of disturbances, environmental conditions, and genetic diversity, and landscape management interventions are minimal. The value of national parks for such studies is exemplified by a recent study of tree regeneration following recent fires in Yellowstone, Grand Teton, and Glacier National Parks (Harvey, Donato, and Turner 2016). Sampling was conducted in 184 plots that burned as stand-replacing fire, and data shows that subsequent years of drought substantially reduced postfire tree establishment. Detecting such signals of gradual environmental change cannot be readily done in managed ecosystems. In another example, direct effects of climate on postfire tree establishment are being addressed experimentally in Yellowstone (W. D. Hansen et al., unpublished data). Seed-germination experiments that compare current and projected midcentury climate will identify temperature and moisture conditions that allow tree seedlings to establish in recently burned forest soils. Initial results suggest that warmer climatic conditions at lower treeline may be dangerously close to conditions that preclude successful lodgepole pine establishment. Observational and experimental field studies are also providing the basis for modeling the longer-term implications of alternative mechanisms and rates of change across larger landscapes. Detecting change is but a first step; understanding how ecosystems respond, and which ecological patterns and processes are resilient to future perturbations, is critical, and national parks offer irreplaceable opportunities for such study.

As climate and disturbance regimes change, Yellowstone will become increasingly valuable for its critical role in allowing processes and changes to play out with minimal intervention, providing a benchmark for understanding how natural systems will change and adapt. Forests of Greater Yellowstone may be less resilient to future fires than they were to the massive fires of 1988. However, Yellowstone will continue to evolve as environmental conditions change, just as it did at the end of the Pleistocene and throughout the Holocene. It will not be "destroyed" in the future, only changed. Native plants and animals will still be present, even though relative abundances may change and some new species may arrive. Moreover, because so much of the western landscape has been altered by human land use, Greater Yellowstone, with its large area of contiguous and diverse natural habitats, will be crucial for sustaining a wide variety of species that cannot persist elsewhere. Yellowstone is a dynamic, vital, intact ecosystem that holds many secrets yet to be revealed.

Parks for Science, and Science for Parks

Climate warming and changing disturbance regimes are inevitable; changes are coming fast, and many are already underway. Ecological effects of climate change are likely to be much more substantial and far-reaching than we realized even just a decade ago. The past may not predict the future—we may well be heading beyond the range of climatic and ecological conditions that have characterized the last 10,000 years and moving quickly into uncharted territory. Scientists and managers must be alert to potential tipping points and thresholds beyond which major qualitative changes will take place. During these times of rapid change, the importance of national parks as living laboratories for scientific research only increases.

Parks for Science

We strongly advocate for a renewed and strengthened commitment to "parks for science." As we have shown for Greater Yellowstone, national parks represent some of the best places for research designed to understand causes and consequences of environmental change independent of management effects. Because they contain ecosystems shaped primarily by natural processes, national parks can be sensitive sentinels of change. For example, climate-driven changes in range distributions of species may be detectable sooner in national parks than in highly developed landscapes. Many large national parks include high-elevation and high-latitude systems that have already been identified as extremely vulnerable to effects of global climate change. Changes in the biota and in ecosystem processes and services must be understood in the absence of the myriad other factors that confound attribution of cause and effect in human-dominated landscapes. National parks serve as natural laboratories for studying effects of environmental change in areas not confounded by management or direct human impacts. In essence, national parks provide the reference conditions against which the effects of manipulating nature elsewhere can be assessed.

Research on how national parks sustain ecological processes, ecosystem services, and integrity of the larger landscape is also of high priority. National parks are often key to maintaining benefits from nature that are valued well beyond the park boundaries. With ongoing climate change, national parks will be increasingly important for sustaining the regional biota (e.g., migratory animal populations, vegetation communities, and genetic diversity). Parks are often of significance for delivering clean water to downstream aquatic systems and sustaining hydrologic ecosystem services valued by human communities. Parks may serve as refugia for aquatic populations and as source populations for degraded biota found in downstream aquatic ecosystems. The need to understand how changing landscape mosaics will influence future delivery of ecosystem services is now widely recognized (e.g., Turner, Donato, and Romme 2013). National parks provide an array of benefits and values to people—even to people who never visit—including benefits to local economies, land values, ecosystem services, and existence value. Understanding how these benefits of nature may change in the future is important for park management.

Resource interpretation programs implemented by the US National Park Service (NPS) could emphasize the importance of parks for science, taking advantage of the unique opportunities to educate visitors. Ecological literacy and scientific understanding is arguably at a low point in the United States (Mooney and Kirshenbaum 2010), and opportunities for the public to understand the role of science are desperately needed. Rather than having all evidence of scientific study hidden from visitors, research in the parks could be publicized with pride, with an emphasis on how much can be learned from these intact landscapes. Research-related interpretation could accomplish two goals. First, it would create opportunities for the public to be exposed to the process of science, for them to witness the human side, the creativity, trial and error, and innovation that go into research. By humanizing science, we may be able to foster greater understanding and appreciation for science among the general public. Second, showcasing science in the parks could engage the public in discussion of regional conservation and resource issues. Research could be a conversation starter that leads visitors to a deeper understanding of the park and its surroundings.

Greater opportunities for comparative study across national parks in the United States and worldwide could also be explored. The United States is recognized throughout the world for leadership in establishing and protecting national parks, and scientific studies that compare and contrast ecological responses to global change in different protected areas could add even greater value to research in any one park. For example, the European Union recently funded a study of 22 national parks and protected areas spanning a range of biogeographic regions in Europe and beyond. What about partnering with international protected areas to develop an even more comprehensive understanding of our changing planet? The National Park System includes 30 parks recognized as UNESCO Biosphere Reserves and 10 designated as World Heritage Sites (National Research Council 1992). Such networks offer opportunities yet to be explored.

Science for Parks

Of course, science also should continue to address issues related directly to park management, and NPS decision makers should seek and use the best available science. Managers must rely on science for guidance in understanding novel conditions and risks to parks, now and in the future (Colwell et al. 2012). For climate change and disturbance, this will require computer-based modeling to explore potential future scenarios along with observational studies that may detect early indicators of ecological change in particular national parks. Science should inform the stewardship and management of national parks. For example, management-relevant questions might include the following: Should parks be actively managed in response to changing climate, or should a hands-off policy be continued? How should nearby lands be managed so that the integrity and character of our national parks do not degrade as environmental conditions change?

Externally funded research conducted in national parks will help strengthen the foundation of park management and complement management-oriented research. For example, externally funded and peer-reviewed science on fire history in Yellowstone provided critical information needed by park managers in 1988. Externally funded and peer-reviewed research also provided crucial data about drivers and dynamics of Yellowstone's northern range when Congress mandated an independent review of ungulate management (National Research Council 2002). These and many other examples show that research helps rather than hinders park management. However, the management relevance of curiosity-driven science may not be immediately obvious, and national parks can sometimes seem unsupportive of science, considering it to conflict with the NPS mission. It is notable that even the Wilderness Act explicitly recognizes science as an appropriate purpose for and use of wilderness. National parks are often managed as wilderness, and it can be difficult to have research approved. We strongly support the imperative to respect the resource and mission of the NPS, but processes for conducting scientific research in national parks have become increasingly bureaucratic in recent decades—just when the urgency to understand causes and consequences of regional change is growing. Appropriate experimentation and research installations should be encouraged, rather than considered a nuisance. National parks will benefit by actively embracing scientific research, recognizing that today's basic science may well provide the foundation for tomorrow's policy decisions.

Conclusions

Accelerating rates of environmental change will affect our national parks during coming decades. As we have shown for Greater Yellowstone, biotic communities are often well adapted to particular disturbances occurring in a given climate space. As we look to the future, the potential for interacting, novel disturbance regimes and climates to fundamentally change ecosystem structure and function is real. Consequences of such changes are important but difficult to anticipate, and how climate-disturbance interactions will affect regional landscapes and our national parks is only beginning to be explored. National parks play a critical role as living laboratories for scientific research, and science is crucial for park management during these times of rapid change. We wholeheartedly endorse the following statement from the 2012 *Revisiting Leopold* report: "The need for science—to understand how park ecosystems function, monitor impacts of change (even from afar), inform decision makers and their decisions, and enrich public appreciation of park values—has never been greater. In addition, the National Park System is an extraordinary national asset for advancing science and scholarship—from new discoveries of valuable genetic resources to monitoring benchmarks for environmental change" (Colwell et al. 2012).

Our research on disturbance and changing climates in Greater Yellowstone has led to general lessons about natural disturbances and demonstrated the importance of science as climate and disturbance regimes change in the 21st century. Many national parks offer comparable opportunities to understand effects of changing climate and disturbance regimes in natural ecosystems. For example, other large western national parks, including Yosemite, Rocky Mountain, and Glacier, can yield additional insights into effects of fire, insect outbreaks, and climate. Coastal US national parks, such as Virgin Islands, Everglades, Cumberland Island, Cape Lookout, and Acadia, offer opportunities to study hurricanes and climate. In desert parks, such as Canyonlands and Joshua Tree, we can learn the limits of resilience to changing temperature and precipitation regimes in drought-tolerant organisms and ecosystems. National parks remain among the best places for scientists to understand ecological responses to environmental change in the absence of factors that confound attribution of cause and effect. Studying these majestic landscapes is an honor, a privilege, and a responsibility. We hope that our research and that of the many other scientists studying national parks will aid stewardship of these national treasures in the years ahead.

Acknowledgments

We thank Steve Beissinger and David Ackerly for comments on this manuscript. Support for research underpinning this manuscript is gratefully acknowledged from the following sources: the National Science Foundation (BSR-9016281, BSR-9018381, and DEB-9806440), the National Geographic Society, the Andrew W. Mellon Foundation, the Joint Fire Science Program (grant numbers 06-2-1-20, 09-1-06-3, 09-3-01-47, 11-1-1-7, and 12-3-01-3), a National Park Service George Melendez Wright Climate Change Fellowship to BJH, and a National Science Foundation Graduate Research Fellowship to WDH (DGE-1242789).

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