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ECOSYSTEMS

Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems

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ABSTRACT

The 1988 Yellowstone fires were among the first in what has proven to be an upsurge in large severe fires in the western USA during the past 20 years. At the time of the fires, little was known about the impacts of such a large severe disturbance because scientists had had few previous opportunities to study such an event. Ecologists predicted short- and long-term effects of the 1988 fires on vegetation, biogeochemistry, primary productivity, wildlife, and aquatic ecosystems based on scientific understanding of the time. Twenty-plus years of subsequent study allow these early predictions to be evaluated. Most of the original predictions were at least partially supported, but some predictions were refuted, others nuanced, and a few postfire phenomena were entirely unexpected. Post-1988 Yellowstone studies catalyzed advances in ecology focused on the importance of spatial and temporal heterogeneity, contingent influences, and multiple interacting drivers. Post-1988 research in Yellowstone also has changed public perceptions of fire as an ecological process and attitudes towards fire management. Looking ahead to projected climate change and more frequent large fires, the well-documented ecological responses to the 1988 Yellowstone fires provide a foundation for detecting and evaluating potential changes in fire regimes of temperate mountainous regions.

Key words: aquatic ecosystems; *Cervus elaphus*; climate; disturbance; elk; fire; landscape; lodgepole pine; paleoecology; *Pinus contorta*; stream invertebrates; succession; coarse wood.

INTRODUCTION

Disturbance is a key component of ecological systems, affecting terrestrial, aquatic, and marine ecosystems over a wide range of scales. Disturbances alter the state and trajectory of an ecosystem and can shape ecosystem dynamics long into the future. Disturbances that are large, severe, and infrequent also capture public attention and often challenge ecological understanding (Turner and Dale 1998). Because disturbance regimes are changing worldwide, it is increasingly important for ecologists to evaluate current understanding of disturbance and synthesize what has been learned from long-term studies of extreme events. Toward this goal, we review studies of the 1988 Yellowstone fires; after

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some 20 years, it is an opportune time to examine what has been learned about large infrequent disturbances and broad-scale ecological processes.

The 1988 Yellowstone fires were among the first in what has proven to be an upsurge in large severe fires in the western US during the past quarter-century (Westerling and others 2006; Morgan and others 2008; Littell and others 2009). Daily images of flame and destruction in Yellowstone caught the public's attention (Smith 1996), and scientists recognized the unfolding opportunity to understand the causes and consequences of a large, infrequent disturbance within one of the most pristine wildland ecosystems of temperate North America. The size and severity of the fires left scientists and managers uncertain about how the ecosystem would respond. A special issue of *BioScience* (39:10) in 1989 focused on this uncertainty, synthesizing scientific understanding of the time and offering predictions about short- and long-term ecological effects of the 1988 fires on vegetation, wildlife, aquatic ecosystems, biogeochemistry, and primary productivity. Those predictions now provide an excellent framework for assessing how understanding has evolved with 20 years of subsequent study, and we address two questions in this review: (1) To what extent were the predictions supported, refuted, or substantially modified by subsequent research? (2) What new understanding about large infrequent fires has emerged since 1988? This review is not exhaustive; rather, it highlights key findings that emerged from postfire studies and synthesizes current knowledge.

Yellowstone researchers summarized studies conducted during the first 10–12 years after the 1988 fires in a book edited by Wallace (2004), providing a valuable reference for the early years after the fires. However, more has been learned and new foci have emerged since those studies were conducted. Notably, most research presented in the 2004 book dealt with population and community responses to the fires, with only limited information on production and biogeochemistry. Interactions of fire with other drivers were not considered, and climate change was mentioned only briefly in the 2004 book. Finally, public perceptions of fire and fire management have continued to evolve in the past decade.

YELLOWSTONE AND THE FIRES OF 1988

The 80,000 km^2 Greater Yellowstone Ecosystem (GYE) is centered on Yellowstone National Park (YNP) and straddles portions of Wyoming, Montana, and Idaho. The GYE is unique in some interesting respects—notably the extensive geothermal features for which the region is famous—but in many ways the GYE is representative of temperate mountain ecosystems throughout western North America. Therefore, what we learn in Yellowstone can be applied judiciously to many other regions where far less research has been conducted.

The diverse topography and geology of the Yellowstone landscape provide a heterogeneous template for ecological characteristics and processes. YNP encompasses approximately 9,000 km^2, most of which lies on a high (elevation ca. 2100–2700 m) volcanic plateau having 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 semi-arid climate. Approximately 80% of YNP is dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) forest, although subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) are 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 generally by cold, snowy winters and dry, mild summers.

Portions of the GYE have a history of intensive resource exploitation—logging, grazing, market hunting, mining—just as in other parts of the Rocky Mountains, as well as an expanding wild-land-urban-interface on many of the private lands. However, the GYE differs from much of the rest of the Rocky Mountain region in that the pre-Columbian flora and fauna remain intact in the GYE, in part because the GYE contains one of the largest tracts of wild, undeveloped land in the continental U.S. (Gude and others 2006). This largely pristine condition makes Yellowstone uniquely suitable for research into natural patterns and processes at multiple spatial and temporal scales.

A total of 248 fires were ignited by lightning and by humans in 1988 in the GYE. Together these fires burned approximately 570,000 ha (Figure 1), with 95% of that total accounted for by only seven very large fires (Schullery 1989). Fire weather was extreme: it was the driest summer on record in YNP (Renkin and Despain 1992), as dry cold fronts brought high wind and lightning but no rain. A huge fire-fighting effort (25,000 fire-fighters and an expenditure of $120 million) was effective in protecting most human life and property, but the

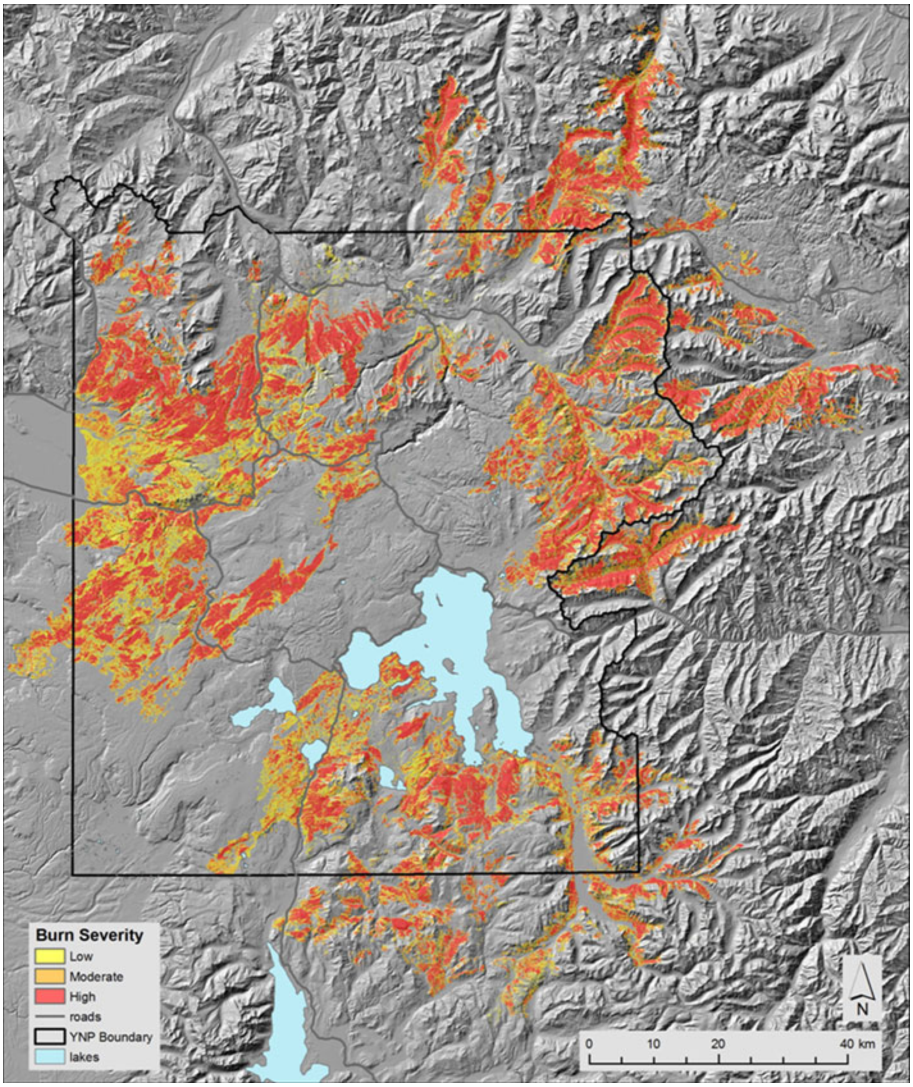

Figure 1. Extent and heterogeneity of the 1988 fires in Yellowstone National Park. Burn severity was calculated using the differenced normalized burn ratio (dNBR) (Key and Benson 2006) from pre-and post-fire Landsat TM images. To reflect observed burn severity characteristics, severity class boundaries were slightly modified from Key and Benson (2006) into the following classes based on dNBR values: unburned (<100); low severity (100–305), moderate severity (306–550); and high severity (>551).

fires could not be stopped until snow came in mid-September (Schullery 1989).

The 1988 Yellowstone fires were widely perceived as unnaturally large and severe and a consequence of 20th-century fire suppression and abnormal fuel build-up. Research in low-elevation western pine forests had documented changes—-from historically frequent, low-severity surface fires to unusually severe crown fires during the modern period (for example, Cooper 1960; Arno 1980)—and this model was applied uncritically by many to the Yellowstone system. Extensive study of fire history in Yellowstone's high-elevation forests was not completed until the summer of 1988, as the fires were burning. This research, based on tree rings, revealed a fire regime very different from that of lower-elevation forests and dominated by infrequent but stand-replacing crown fires. Fires had been infrequent in YNP during the previous 300 years, but large severe fires had occurred in the early 1700s and again in the mid-1800s, long before fire suppression efforts (Romme and Despain 1989). The study further suggested that fuel build-up due to 20th-century fire suppression had not greatly altered Yellowstone's natural fire regime because fires were controlled more by climate and weather than by fuels. Subsequent research (summarized later in this paper) has supported and refined this view of high-elevation fire regimes.

EVALUATING THE ORIGINAL PREDICTIONS

Disturbance was well established as a focal topic of ecological research by the late 1980s. Concepts such as patch dynamics (Pickett and White 1985), the shifting mosaic steady state (Bormann and Likens 1979; Paine and Levin 1981), landscape equilibrium (Romme 1982), landscape heterogeneity (Turner 1989), and nutrient loss and retention (Vitousek and others 1979) were receiving considerable attention, and restoration of natural disturbance regimes (for example, fire or flooding) was widely discussed (for example, Parsons and others 1986). However, most literature focused on disturbances that were relatively small in extent (for example, gaps) or of low severity (for example, fires in low-elevation pine forests). The 1988 Yellowstone fires were well beyond where theory and empirical data could provide much guidance. It was in this context that the major predictions were set forth in 1989 for the consequences of the 1988 fires (Table 1).

Vegetation

The size and severity of the 1988 fires led Knight and Wallace (1989) to predict multiple postfire successional pathways (Prediction 1) in response to variability in environmental gradients, fire severity, patch size, and prefire cone serotiny. Because the postfire landscape appeared devoid of living vegetation (Figure 2), ecologists implicitly expected that most plant species would re-colonize by dispersal from distant unburned forest. Thus, landscape variability in plant communities was expected to be greatly increased after the fires. This prediction was only partially supported (Table 1). The spatial variability of postfire vegetation was greater than anticipated, but the primary differences were in vegetation structure (especially postfire tree density) rather than plant species richness and composition. Most herbaceous and shrub species in prefire conifer forests re-appeared within the first 1–3 years after fire by sprouting from surviving belowground structures (Anderson and Romme 1991; Turner and others 1997a, 1999). The sprouts grew rapidly and began flowering within the first 1–4 years, and species' cover continued to increase via seedling establishment and continued vegetative sprouting.

The most dramatic postfire variability in vegetation was in stand structure (Figure 3), as postfire lodgepole pine seedling densities varied from 10^1 to 10^6 ha^{-1} (Turner and others 1997a, 2004). Patterns in pine seedling density were driven in part by variation in fire severity but even more so by variation in the local prefire proportion of lodgepole pine trees bearing serotinous cones (which varied from 0 to >80%; Tinker and others 1994; Schoennagel and others 2003). Postfire pine seedlings were most dense where prefire serotiny was high and where the canopy was killed but not consumed by the fire (Turner and others 1997a, 2003). Postfire tree seedling densities were lower in Douglas-fir, spruce-fir, and whitebark pine forests, but most of these stands also were re-stocked soon after the fire via natural seed fall or (for whitebark pine) bird-facilitated dispersal (Tomback and others 2001; Doyle 2004). In most burned conifer stands, total understory biotic cover was close to prefire cover by 1996, and tree seedling density (especially in stands dominated by lodgepole pine) equaled or often greatly exceeded prefire density (Turner and others 2003). Thus, most burned conifer forests quickly recovered prefire species composition and tree density, not through classic ''succession'' or ''relay floristics'' but via direct re-growth or ''initial floristic composition'' *sensu* Egler (1954). Overall, biotic legacies of the prefire forests (Foster and others 1998) were conspicuous in the burned forests and contributed to rapid recovery and compositional stability in the plant community.

Given prior studies of succession and the documented ability of ruderal species to colonize disturbed sites very rapidly, Christensen and others (1989) predicted that burned forests would contain fewer interior species but an increased abundance of edge species and nonnative invaders (Prediction 2). This prediction was not supported (Table 1). Although native annuals and biennials typical of edge environments increased following fire, they rarely dominated a burned stand. Especially notable was the general lack of invasion by nonnative species (Romme and Turner 2004). The nonnative *Cirsium arvense* created some locally dense patches (a few m^2) in some burned conifer forests, often in places where it had been present already before the fire, for example, along trails (Turner and others 1997a). However, its cover had declined in many stands by 2006, apparently because of competition from native species (Wright and Tinker, unpublished data). Thus, the native flora continued to dominate most of the burned area, with only a small shift from long-lived perennial (interior) species to short-lived annuals and biennials.

An unexpected response by a native disturbance-adapted plant species was the widespread but patchy establishment of seedling aspen in 1989 throughout the burned conifer forests and far from mature aspen stands (Kay 1993; Romme and others 1997). Aspen is widely distributed in North America and a common early successional species, but conventional wisdom for the Northern Rockies was that aspen reproduced clonally and not by seed. Genetic studies confirmed that the plants observed throughout the burned conifer forests were indeed seedlings (Tuskan and others 1996; Stevens and

Table 1. Initial Predictions About Effects of the 1988 Yellowstone Fires, Published in *BioScience* (1989), and Evaluations Based on Subsequent Research

Original prediction published in 1989	Original prediction supported?
Vegetation	
(1) Multiple successional pathways related to environmental gradients, fire severity, patch size, and prefire cone serotiny	PARTIALLY—variability was greater than originally anticipated, but reflected differences in vegetation structure more than differences in composition.
(2) Decreased abundance of interior species and increased abundance of edge species and non-native invaders	NO—most long-lived perennial (interior) species re-appeared within 1–3 years; native annuals and biennials increased but did not dominate stands; some non-natives increased locally, but native flora continued to dominate most burned areas
(3) Aspen and willow escape from ungulate browsing	NO—most burned stands re-sprouted strongly, but heavy browsing prevented aspen from growing to tree size; some willows have elongated, but mechanism probably involves wolves and/or climate rather than fire effects
Biogeochemistry and Productivity	
(4) Substantial loss of N through combustion plus increased N mineralization and leaching	PARTIALLY—N was lost in fire and mineralization increased, but microbial immobilization and uptake by recovering plants minimized N loss through leaching
(5) Reduced primary productivity because of N limitation	NO—growth of lodgepole pine seedlings (3–5 years old) was not limited by N, and aboveground net primary productivity was comparable to that of mature forests within a decade postfire in some stands
Terrestrial wildlife	
(6) Initial reduction (1–2 years) in elk survival, calf weights, and elk density because of drought-related reduction in 1988 herbaceous productivity plus forage losses in burned grasslands	PARTIALLY—elk population decreased 38-43% during the first winter after the fire, elk calf mortality doubled and average weights decreased in spring 1989, but principal mechanism was severe winter conditions and hunter harvest outside Park boundaries, not direct effects of fire
(7) Increased elk survival and population growth in years 2–5 because of increased forage quantity and quality in burned areas	YES—elk numbers returned to prefire levels by 1995; forage increases were documented in burned grasslands and forests, and elk were found to select burned areas preferentially after the first 1–3 years
(8) Longer-term (up to 30 years) increase in elk density because of increased forage availability and palatability on elk summer ranges	UNKNOWN—long-term fire effects were overshadowed by effects of wolf reintroduction in 1995
Aquatic ecosystems	
(9) Greatest impacts in smaller streams; where greater proportions of the watershed were burned	YES—largest ecological changes were documented in 1st to 4th order streams
(10) Increased stream discharge, sediment loads, and nutrient input in spring of first year postfire, followed by rapid drop in second year and gradual return to prefire levels	PARTIALLY—all of these variables increased for a time after the fire, but the timing generally was different from prediction
(11) Dramatic increase in stream primary production in summer of first year postfire, followed by gradual decrease through years 2–10	PARTIALLY—primary production increased, but the peak was earlier and more transient than expected, and involved somewhat different mechanisms than predicted

Table 1. continued

Original prediction published in 1989	Original prediction supported?
(12) Early and sustained increase in stream insect biomass and changes in community composition	YES—insect biomass increased and community composition shifted towards greater dominance by disturbance adapted species
(13) Dramatically elevated quantities of in-stream coarse wood in first postfire year, then progressively lower amounts of coarse wood for the next 20+ years	PARTIALLY—the initial pattern was seen, but the timing was different from prediction: in-stream coarse wood increased in year 1 but peak input from snag fall occurred 10-20 yrs postfire and was most evident in small streams
(14) Minimal impacts on fish communities	YES—little change in fish communities or fish growth rates after the fires

Figure 2. A severely burned forest stand in Yellowstone National Park, illustrating total mortality of the canopy and absence of vegetative cover immediately after the fire. (Photo credit: by W.H. Romme, 2010.)

others 1999). Most of the aspen seedlings have since been browsed by ungulates (Forester and others 2007), and even when the plants are not browsed, they usually grow very slowly (Romme and others 2005), perhaps in response to suboptimal environmental conditions and/or competition with postfire lodgepole pines. Nevertheless, these new aspen genets were still relatively abundant as of 2010, and some (especially at higher elevations) had grown taller than browsing height (Figure 4). The long-term fate of this cohort is unknown but may be a harbinger of shifts in species' ranges in response to disturbance and climate change (Landhäusser and others 2010).

Herbivore-mediated consequences of the 1988 fires for vegetation were also hypothesized 20 years ago. In response to increased abundance of a preferred resource, foraging theory suggested that consumers might shift from a scarce resource to the abundant one. Browsing by elk (*Cervus elaphus*) and other native ungulates had suppressed regeneration of aspen and willow (*Salix* spp.) on Yellowstone's winter ungulate range for several decades (NRC 2002). However, because forage quantity and quality are often enhanced by fire, Singer and others (1989) hypothesized that fire-induced vegetation changes could alter herbivory such that aspen and willow would escape from the chronic heavy browsing by elk and other native ungulates (Prediction 3). The hypothesized mechanism involved prolific sprouting of both plant species in burned stands, which would satiate browsers, and increased herbaceous production, which would provide alternative food sources. This prediction was not supported (Table 1). Burned aspen and

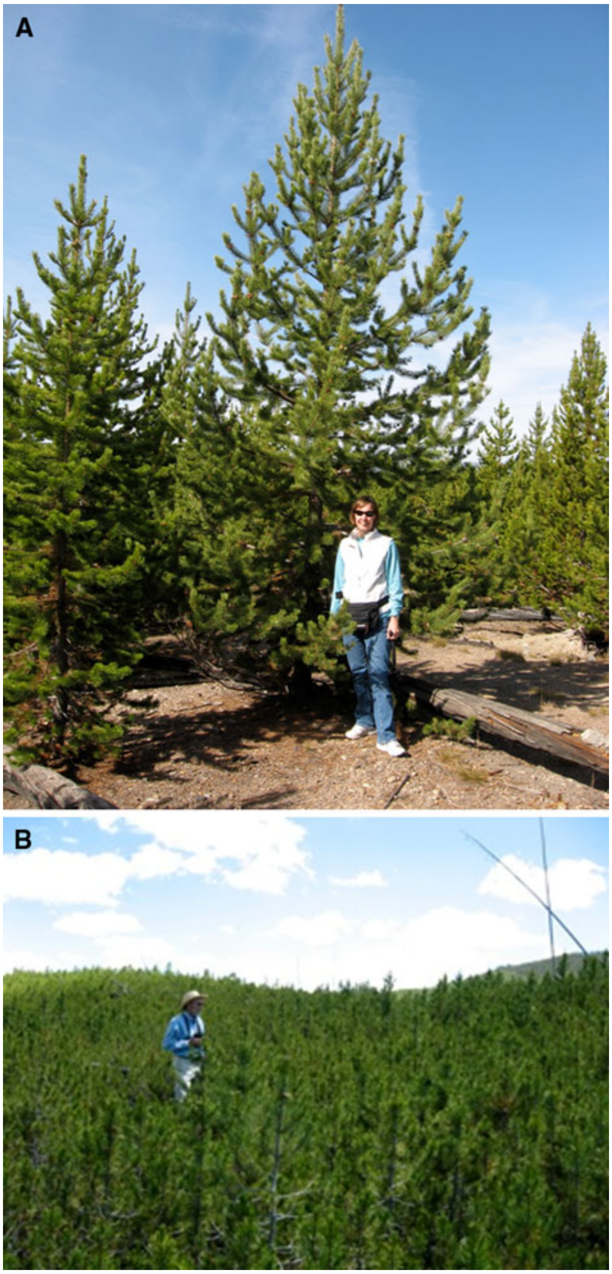

Figure 3. Contrasting lodgepole pine regeneration after the 1988 Yellowstone fires as observed after about 20 years: **A** 3700 stems ha^{-1} and total ANPP (herb + tree) = 4.8 Mg C ha^{-1} y^{-1}; **B** 450,000 stems ha^{-1} and total ANPP = 5.3 Mg C ha^{-1} y^{-1}. Lodgepole pine density and ANPP were measured in 2005. (Photo credits: **A** by W. H. Romme 2008; **B** by M. G. Turner 2010.)

Figure 4. A new genet of quaking aspen (*Populus tremuloides*) that established as a seedling after the 1988 Yellowstone fires at an elevation (2600 m) higher than the local pre-fire distribution of aspen, and that has grown above browsing height and will likely develop into a new aspen clone. (Photo credit: by M.G. Turner, 2008.)

willow did indeed produce abundant sprouts, and herbaceous forage was enhanced, but heavy elk browsing pressure continued unabated after the fire. Thus, very few sprouts grew above browsing height (Romme and others 1995), and regeneration of tree-sized aspen still was not observed outside of exclosures as of 2007 (Kauffman and others 2010). Although some willows and cottonwood on the northern ungulate winter range have elongated since 1988, the mechanism apparently involves not direct effects of the 1988 fires, but lower elk densities (Creel and Christianson 2009; Kauffman and others 2010) or altered elk behavior in response to wolves that were reintroduced in 1995 (Ripple and Beschta 2004; Beyer and others 2007).

Biogeochemistry and Terrestrial Productivity

Ecosystem studies of experimental clearcuts in a variety of forested ecosystems had demonstrated that disturbance was often associated with nutrient loss (for example, Likens and Bormann 1977). Nitrogen loss can be of particular concern because it is often a limiting nutrient in terrestrial ecosystems and excess nitrate can impair surface-water quality (Dodds and Welch 2000). Although consequences of fire for nutrient cycling had been studied (for example, Wright 1976; Raison 1979), there were no prior studies of large, stand-replacing fires (Smithwick and others 2005a). Based on what had been reported previously for forest disturbances, Christensen and others (1989) and Knight and Wallace (1989) predicted substantial nitrogen (N) losses from terrestrial ecosystems (Prediction 4), resulting from combustion and subsequent increases in postfire erosion, N mineralization, and leaching, especially in the most severely burned areas. This prediction was only partly supported (Table 1).

Total N stocks were initially reduced by fire, but immediate N losses were less than expected because the fires did not burn deeply into the soil where a large pool of N resides (Turner and others 1999; Smithwick and others 2009; but see Bormann and others 2008 who reported more substantial soil N losses after a high-severity fire in Oregon). The prediction of significant early postfire N leaching was not supported. On the contrary, subsequent studies have shown that early postfire lodgepole pine forests conserve N, even on severely burned sites (Turner and others 2007). Although elevated N concentrations were seen in several 1st and 2nd order streams draining burned catchments, notably those in steep terrain underlain by friable volcanic substrates (Brass and others 1996; Minshall and others 1997), N concentrations were negligible even during snowmelt in other small streams draining burned catchments of gentle topography and stable substrates (Minshall and others 1997; Romme and Turner 2004). Soil microbes and the rapidly recovering herbaceous plants were important N sinks soon after fire (Metzger and others 2006), and young lodgepole pine trees became a significant N sink as they grew (Turner and others 2009). A postfire chronosequence study indicated that N losses to fire are recovered relatively quickly, within 40–70 years (Smithwick and others 2009), although the sources of this replenishment (for example, N fixation rates) are not well understood.

Because N commonly limits productivity in lodgepole pine forests (Fahey 1983), a corollary to the prediction of high N loss with fire was that N would limit primary productivity in the postfire forests (Prediction 5) at least temporarily (Knight and Wallace 1989). This prediction also was not supported (Table 1). A fertilization experiment demonstrated that growth of lodgepole pine seedlings 3–5 years postfire was not limited by inorganic N (Romme and others 2009), and aboveground net primary productivity (ANPP) in dense stands of lodgepole pine saplings was comparable to that of mature stands only a decade after the fire (Reed and others 1999; Turner and others 2004). Net ecosystem production (NEP) is expected to remain negative for several decades as fire-killed biomass continues to decompose (Kashian and others 2006). However, even at 15–17 years after the fires, ANPP did not appear to be limited by N availability (Turner and others 2009). Thus, rather than losing nutrients as expected, Yellowstone's burned forests effectively conserved N via accelerated microbial activity in the largely undamaged soils plus rapid recovery and uptake by the plant community (Turner 2010). Partly as a result of efficient nutrient conservation, primary production reached surprisingly high rates within only a decade after the fires. However, the variation among stands is enormous, and although the stands are still in the aggradation phase (Bormann and Likens 1979), they will likely reach peak productivity at different times (Figure 5). This period of maximum variation in structure and function across the landscape raises new questions about spatial and temporal variation in limiting factors. Continued study of the different trajectories of biomass accumulation (Figure 5) may reveal some of the mechanisms underpinning the development of young postfire forests.

Terrestrial Wildlife

Initial predictions focused primarily on Yellowstone's large ungulate species. Direct fire-caused mortality of large animals in 1988 was surprisingly low (Singer and others 1989), but indirect effects of the fires on vegetation were expected to influence wildlife populations over short and long time frames. Singer and others (1989) predicted that elk survival, calf weights, and elk density would be reduced in the first year after the fires because of drought-related reductions in 1988 herbaceous productivity plus the loss of winter forage in

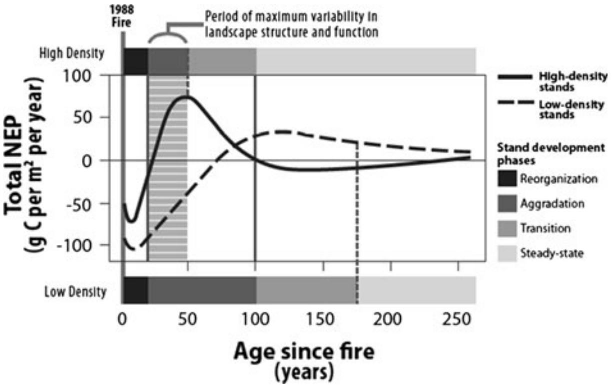

Figure 5. Alternative trajectories of net ecosystem production (NEP) and biomass accumulation in post-1988-fire stands that initiated with high versus low lodgepole pine density (adapted from Kashian and others 2006). These stands will proceed through several phases of ecosystem development (*sensu* Bormann and Likens 1979) over coming decades. Stand structure and function are expected to eventually converge among all stands developing after the 1988 Yellowstone fires (Kashian and others 2005a, b). However, we anticipate that this suite of same-age stands is now entering the period of greatest spatial and temporal variation in ecosystem structure and function, and thus provides special research opportunities.

burned grasslands (Prediction 6). This prediction was supported, although the mechanism involved severe winter weather and hunter harvest outside the Park as well as direct effects of drought and fire (Table 1). The winter immediately following the fires was particularly harsh for the northern Yellowstone elk herd and resulted in a 38–43% decline (Figure 6), 14–16% of which was due to hunter harvest (Singer and others 1989). Behavioral responses by elk supported predictions of poor forage conditions due to drought, fire, and heavy snows. Elk moved to winter ranges 4–6 weeks earlier than usual, and many elk moved out of the Park to unburned winter ranges (Lemke and others 1998). Elk use of burned areas in early winter declined 45%, and diets consisted of more poor-quality trees and less energy-rich grasses than in previous years (Singer and others 1989; DelGuidice and Singer 1996; Vales and Peek 1996). Calf weights were down by 17% the following summer, and calf mortality doubled in comparison to previous years (Singer and others 1989).

Singer and others (1989) also predicted increased elk survival and population growth 2–5 years postfire because of increased forage quantity and quality in burned areas (Prediction 7). This prediction was supported (Table 1). The elk population size returned to prefire levels by 1995 (Figure 6), consistent with predicted forage growth and a series of average and mild winters. Forbs in the grassland and sagebrush communities on the ungulate winter range recovered within the first year after the fire. Full recovery of graminoids was immediate in wet meadows, took 2–3 years on grasslands, and somewhat longer in sagebrush-grasslands (Norland and others 1996; Singer and Harter 1996; Tracy and McNaughton 1996; Singer and others 2004; Tracy 2004). On winter range, herbaceous productivity did not increase greatly, but a short-lived and spatially variable pulse in forage quality was evident during the first few postfire years (Norland and others 1996, Tracy and McNaughton 1996). On summer range, Singer and others (2004) found that grass biomass in wet meadows increased 20% in both the first and second years after the fires whereas forb biomass generally was not higher except for some fire-stimulated species like fireweed (*Epilobium angustifolium*). In burned lodgepole pine forests on elk summer range, perennial herbs, grasses and grass-like plants increased rapidly within the first 4 years (Singer and others 2004; Turner and others 1997a, 1999).

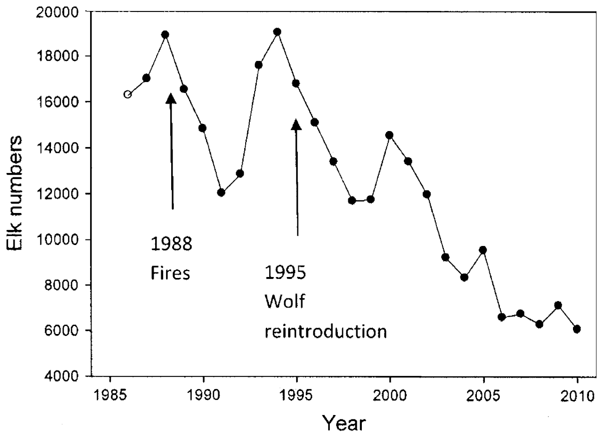

Figure 6. Number of elk estimated in the Northern Range elk herd in Yellowstone National Park from 1985 to 2010. *Sources*: Vucetich and others (2005): 1985–2004; Center for Resources, Yellowstone National Park, unpublished data: 2005–2010.

Patterns of elk habitat use after the 1988 fires were consistent with forage recovery patterns. Elk avoided or used burned forest randomly during the first 3 years postfire (Norland and others 1996; Singer and Harter 1996). However, elk selected burned forests during summer 12–14 years postfire (Boyce and others 2003; Mao and others 2005). Similarly, elk avoided burned grasslands the first postfire winter but selected burned grasslands 40–50% more often than unburned grasslands 2–3 years after the fires (Pearson and others 1995; Singer and others 2004).

Singer and others (1989) predicted that elk density and carrying capacity would increase over the longer term (up to 30 years) because of increased forage availability and palatability on elk summer ranges (Prediction 8). This prediction is difficult to evaluate empirically because wolf reintroduction in 1995 profoundly influenced elk population dynamics and obscured trends related only to effects of the 1988 fires, as discussed later in this paper.

Aquatic Ecosystems

The classic Hubbard Brook experiment had demonstrated empirically how changes in upland ecosystems can profoundly alter streams, and the river continuum concept provided a theoretical basis for predicting varying terrestrial influences on different portions of a stream (Vannote and others 1980). Therefore, it was expected that the 1988 fires would have significant but spatially and temporally variable consequences for aquatic ecosystems. Minshall and others (1989) predicted that fire-related impacts would be greatest in smaller streams, where greater proportions of the watershed were burned (Prediction 9). This prediction was supported (Table 1). The 1988 fires burned only small proportions of the watersheds of large 5th order streams like the Firehole and Lamar Rivers, and fire-related impacts in these streams were minor, but greater than 50% of the watersheds of several smaller streams were burned. Subsequent study focused on 1st to 4th order streams, where the magnitude of change was generally related to proportion of the catchment burned (Minshall and others 1997, 2001). Fire severity, gradient, extent of channel confinement, proximity to bedrock, and relative amount of groundwater input also influenced fire impacts and postfire recovery patterns; for example, high-gradient streams underwent greater physical disturbance and displayed earlier and greater changes in channel cross-section morphology than low-gradient streams (Robinson and others 1996; Minshall and others 1997; 1998). Specific initial predictions by Minshall and others (1989) and subsequent findings are summarized in Figure 7 and illustrated in Figure 8; we highlight just a few.

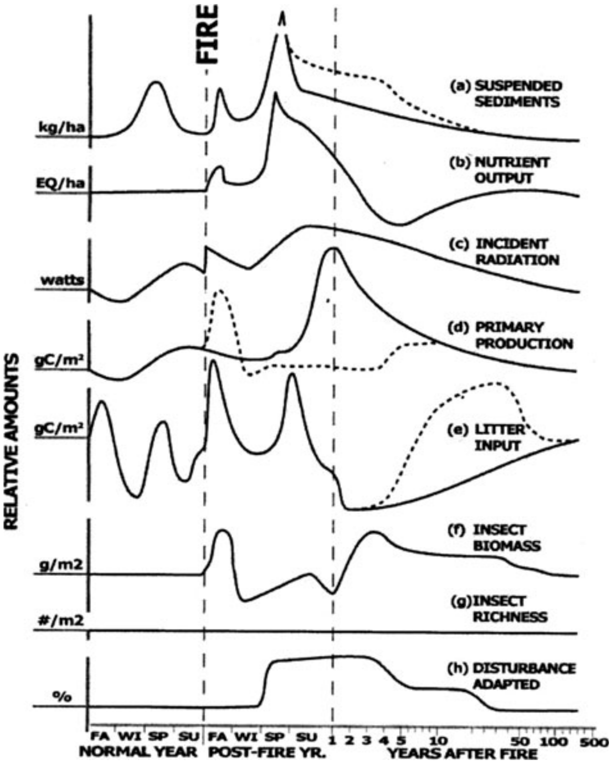

Figure 7. Generalized recovery sequences for selected stream ecosystem variables in extensively burned catchments following the 1988 Yellowstone fires: initial predictions in 1988 (*solid lines*) and documented post-1988 trends (*dashed lines*).

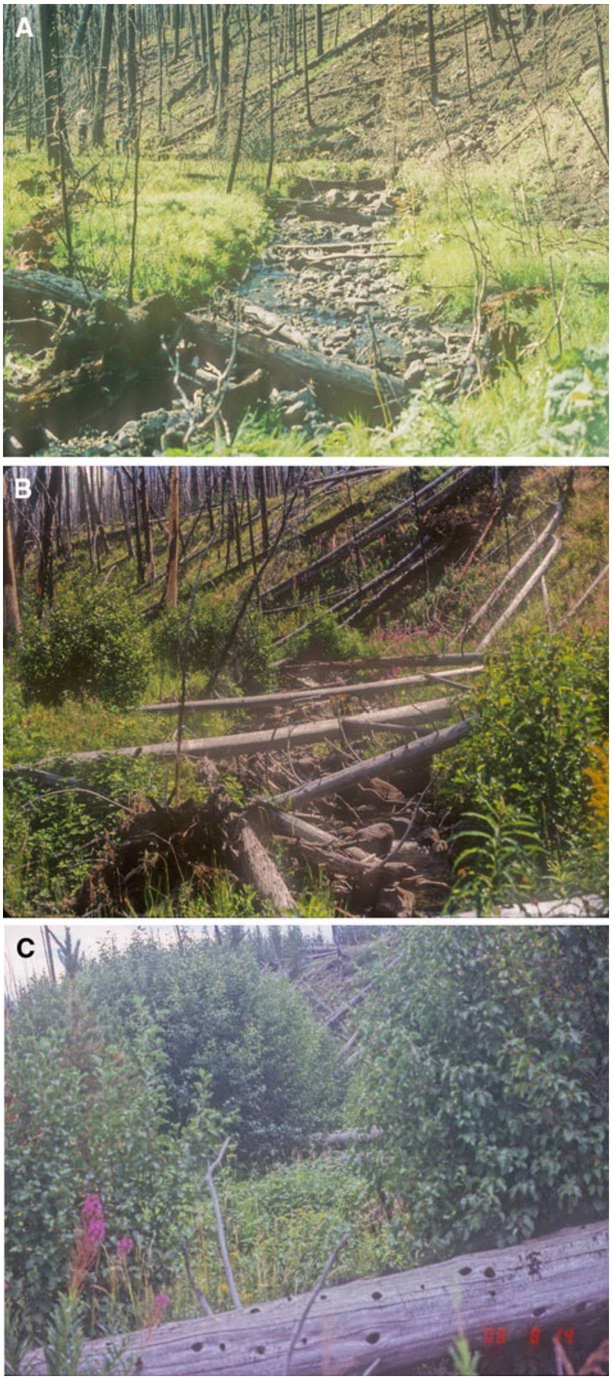

Figure 8. Stream channel and riparian conditions along a 2nd order stream in northeastern Yellowstone National Park **A** 1 year, **B** 10 years, and **C** 20 years after the 1988 fires. (Photo credits: by G. W. Minshall).

Minshall and others (1989) and Christensen and others (1989) predicted that stream discharge, sediment loads, and nutrient input would increase in spring of the first postfire year because of reduced vegetative cover on burned watersheds, but would drop in the second year and gradually return to prefire levels as vegetation recovered (Prediction 10). These predictions were partially supported (Table 1). The peak in sediment load actually occurred in a window of 3 or 4 years, and was often associated with intense summer rainfall over bare slopes rather than spring runoff (Minshall and others 1997). Minshall and others (1989) also predicted a dramatic increase in stream primary production in the summer of the first year following the fire because of increased light and nutrient input, followed by a gradual decrease through years 2–10 (Prediction 11). The prediction of early increase was supported, but the timing and initial post-runoff responses differed from expected (Table 1). Standing crops of periphyton measured as chlorophyll *a* peaked earlier than predicted, in the fall of 1988 (Figure 7d), then fell to prefire levels where they have remained since (Minshall and others 1997, 2003). It is hypothesized that the negative influence of increased runoff and suspended sediment overrode the positive effect of increased light and nutrients (Hauer and Spencer 1998) on primary production in small streams, and studies (discussed above) indicated that postfire nutrient input to streams varied across the landscape in concordance with soil, vegetation, geology, topography, geomorphology, and postfire weather (Gresswell 1999).

Minshall and others (1989) predicted an early and sustained increase in stream insect biomass and changes in community composition (Prediction 12). These predictions generally were supported, although there was no change in richness, and some mechanisms differed from expectation (Table 1). Leaf litter and algae provide the primary food for lotic macroinvertebrate consumers in most streams. It was expected that leaf litter inputs would be low after the first postfire year because of the loss of riparian shrubs. However, as in upland areas, the roots of riparian shrubs generally survived and re-sprouted in the first postfire year, even where most aboveground biomass was consumed. Rapid shrub growth during subsequent years (Figure 8) resulted in high litter input that is expected to continue for many years (Figure 7e). Diatom community composition differed between streams in burned versus unburned watersheds, and differences were highly correlated with percent of catchment burned (Robinson and others 1994). As expected, there was a shift to a periphyton (autochthonous) food base in streams that were heavily affected by fire, and then 10 years later (1998), the food base was becoming similar to reference streams where allochthonous materials dominate the food base (Mihuc 2004; Mihuc and Minshall 1995). Median insect richness has been comparable between burned and reference streams, but stream communities in burned watersheds have greater dominance of disturbance-adapted taxa such as *Baetis* (Ephemeroptera) and Chironomidae (Diptera) and increased within- and between-year variance of community metrics (Minshall and others 2001, 2003).

Minshall and others (1989) also predicted an initial pulse of coarse wood input to streams during the first postfire year, as fire-killed snags fell, followed by a century or more of low input as burned forests gradually re-grew large trees (Prediction 13). Coarse wood affects channel morphology and the routing and storage of water and sediment, providing structure and complexity associated with habitat for numerous aquatic and riparian organisms (Reeves and others 1995). Postfire coarse wood patterns were more complex than initially predicted and varied with stream size and timing and magnitude of peak runoff (Minshall and others 1997). Amounts did increase immediately postfire, but not as much as expected, and the predicted postfire depletions differed from stream to stream over a period of several years depending on the specific year in which the heaviest runoff occurred. Also, wood recruitment from fire-killed snags was initially slower than predicted but then accelerated to reach its peak (which far exceeded prefire levels of wood input) around 20 years postfire. This pattern was best seen in small (generally 1st and 2nd order) streams, where the wood is more stable and its abundance depends on local supply (Figure 8). In larger streams, where bank-full widths considerably exceed the length of the wood pieces, the pattern is obscured because the greater wood mobility and complex interactions within and adjacent to the channel result in heterogeneous distributions in space and time (Marcus and others 2011). Most of the fire-killed trees along streams have now fallen and been replaced by rapidly growing conifers, sufficient to cast significant shade over small streams and provide dense cover and habitat for streamside animals.

Minshall and others (1989) predicted that the fires would have minimal impacts on fish communities (Prediction 14), and this prediction was supported (Table 1). Dead fish were observed in a few 2nd and 3rd order streams, but fish mortality was rare overall. Subsequent evaluations of the fisheries of six larger rivers in the park uncovered no detectable changes in the composition or structure of the fish assemblages, despite changes in the composition of the macroinvertebrate community in some rivers (Jones and others 1993).

Less is known about fire effects on lakes and ponds, but it appears that lakes were well buffered from the 1988 fires (Gresswell 1999), as had been predicted (Minshall and Brock 1991). An interesting but untested hypothesis prior to 1988 was that productivity in Yellowstone Lake had decreased during the 20th century because few fires had occurred in the lake's watershed and therefore nutrient input (notably N, a limiting nutrient in the lake) had been reduced. The 1988 fires burned approximately 28% of the lake watershed, prompting Gresswell (2004) to evaluate growth of native Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) before and after 1988. There was no evidence of change in growth related to the fire, and other research suggested that the primary source of N to Yellowstone Lake was winter precipitation and subsequent runoff—all unrelated to fire (Theriot and others 1997). Despite concerns about the possible influence of the 1988 fires on Yellowstone's lakes and ponds, it was the surreptitious introduction of nonnative lake trout (*Salvelinus namaycush*) into Yellowstone Lake, which occurred during the same period (Kaeding and others 1996; Munro and others 2005), that has had the greatest and potentially irreversibly negative consequences for the lake ecosystem (Varley and Schullery 1995; Gresswell 2009).

Regardless of changes in the physical template of aquatic systems, it appears that aquatic organisms generally are well adapted to disturbances associated with wildfire—except where conditions prevent access to potential colonizers (Gresswell 1999). Negative effects are greatest on individuals and local populations that are the least mobile, and re-colonization is directly related to mobility, stream connectivity, and distance to sources of surviving adults (Rieman and Clayton 1997; Gresswell 1999; Rieman and others 2003). Although species composition of aquatic macroinvertebrates may change somewhat, biomass generally remains near prefire levels (Minshall and others 2003). Increased insolation often results in a flush of primary production, and in cases where light was limiting under prefire conditions, growth of fish may actually increase with increasing water temperatures (Heck 2007). In fact, it is becoming increasingly apparent that periodic disturbances in stream systems are important for maintaining the heterogeneity of the physical habitat and associated biodiversity of the system (Reeves and others 1995).

BEYOND THE 1988 FIRES: GENERAL INSIGHTS FOR ECOSYSTEM RESEARCH

Did studies of the Yellowstone fires catalyze advances in ecology? We highlight several general insights that have emerged from studies to date. Common to these is recognition of the importance of the spatial and temporal scales at which phenomena are observed. Yellowstone is not the only ecosystem from which these ideas gained prominence, but studies of the 1988 fires played a key role in their emergence.

Importance of Spatial and Temporal Heterogeneity

Studies of the Yellowstone fires catalyzed recognition of the importance of large disturbances as key drivers of heterogeneity in terrestrial and aquatic ecosystems. Ecologists were genuinely surprised by the amount of heterogeneity observed within the perimeter of the 1988 fires, but numerous subsequent postfire studies have confirmed that heterogeneity is the rule, not the exception. For example, tree seedling densities varied over three orders of magnitude following recent fires in boreal forests (Greene and Johnson 1999; Johnstone and others 2004), and over five orders of magnitude after the 2002 Biscuit Fire in Oregon (Donato and others 2009a, b). Heterogeneity was also surprising and of ecological significance in the 1980 eruption of Mount St. Helens (Franklin and MacMahon 2000). Indeed, many disturbances are characterized by substantial and functionally important spatial heterogeneity (Foster and others 1998; Turner and others 1997b; Fraterigo and Rusak 2009; Turner 2010).

Postfire heterogeneity in structure and function can be observed at almost any spatial scale. For example, the abundance of downed coarse wood varied across the burned landscape with pre-fire tree density (Tinker and Knight 2000, 2004) and topographic setting (Romme and Lyons, unpublished data). The mass and arrangement of coarse wood also varied at fine scales (meters) within burned stands, and this structural variation in turn influenced local rates of decomposition and N cycling (Remsburg and Turner 2006; Metzger and others 2008). Measures of variability following disturbance provide insights that complement those derived from measures of central tendency (Fraterigo and Rusak 2009; Marcus and others 2011). Studies in Yellowstone that were motivated by understanding the space–time dynamics of forests contributed to this recognition and demonstrated that initial spatial variability in postfire forest structure and function persists for decades to centuries (Kashian and others 2005a, b; Smithwick and others 2005b).

Contingent Influences

Disturbance and recovery patterns in Yellowstone underscored the importance of contingencies in ecosystem response to disturbance. In contrast to deterministic controls that are constant and predictable (for example, substrate, topography), contingent influences vary in space and/or time and are less predictable. Contingent influences include the state of an ecosystem at the time of disturbance, stochastic spatial variation in disturbance severity, and temporal variation in post-disturbance conditions (for example, weather). As observed after the eruption of Mount St. Helens, contingent factors that influence the abundance and spatial distribution of survivors and propagules may largely determine initial successional trajectories (Franklin and MacMahon 2000, Swanson and others 2011). For the 1988 fires, pre-fire serotiny and fire severity determined postfire lodgepole pine sapling density, which largely determined ANPP and LAI in young post-fire stands. Relative to the 1988 fires, summer drought the year after fire may have led to 10-fold fewer lodgepole pine saplings following fires of summer 2000, given otherwise similar conditions (Romme and Turner, unpublished data). High elk mortality during the 1988–1989 winter was due, in part, to deep winter snows that made existing winter forage inaccessible to grazers (Singer and others 1989); modeling experiments also demonstrated that severe winter conditions would overwhelm fire effects (Turner and others 1994; Wu and others 1996). Postfire contingencies have also modified the effects of the 1988 fires on Yellowstone streams; tremendous changes were associated with three back-to-back years of record spring floods in 1995–1997 (Marcus and others 2011). Long-term effects of the 1988 fires on the elk population also have been confounded by unpredictable contingencies including the effects of hunting outside the park and the 1995 reintroduction of wolves. Wolves and hunter harvest have so dominated elk population dynamics since wolf reintroduction (Vucetich and others 2005; Wright and others 2006; Eberhardt and others 2007) that they have masked any signal of the 1988 fires in elk population data. Yellowstone studies unambiguously demonstrated the role of contingent influences on postfire dynamics.

Multiple Interacting Drivers

Although ecologists sometimes try to isolate the effects of individual drivers on parameters of interest, studies of the 1988 fires also clearly illustrated the importance of multiple, interacting drivers. Understanding the effect of the 1988 fires on aspen required also considering the effects of elk, wolves and climate. For the new aspen seedlings that established in the burned lodgepole pine forests, elk browsing was sufficiently high in many areas to suppress their growth or even kill them (Romme and others 2005). Anecdotal observations suggested that ''jackpiles'' of fallen fire-killed trees might protect the aspen seedlings and enhance growth and survival. Forester and others (2007) tested this hypothesis in the early 2000s—after wolves had been present in Yellowstone for almost a decade—and found that elk browsing on the aspen was still high, even when downed wood was abundant. Further study indicated that elk use of the dense postfire stands with heavy downfall had actually increased, apparently because those areas provided some protection from wolf predation (Mao and others 2005). Although aspen seedlings continue to be heavily browsed in many areas, some of the best survival and growth of the post-1988 seedling cohort is at higher elevations, far above the elk winter range and the pre-1988 range of aspen (Figure 4), where warmer temperatures and longer growing seasons during the past two decades may have enhanced aspen growth. Thus, effects of the 1988 fires on aspen must be evaluated in concert with multiple drivers. Similarly, the post-1988 carbon balance of the Yellowstone landscape must be evaluated in the context of changing climate and subsequent disturbance. Smithwick and others (2009) forecast increased productivity, net N mineralization, and C stocks in Yellowstone's lodgepole pine forests by 2100—unless fire frequency increased such that stands were re-burning before they could regain the C lost in the previous fire.

Looking Ahead and Coping with Environmental Change

Climate projections indicate that large fires, like those in Yellowstone in 1988, will become increasingly frequent in coming decades (IPCC 2007; Flannigan and others 2009; Westerling and others 2011). Indeed, an upswing in burning has already been documented during the past 20 years (Westerling and others 2006; Wotton and others 2010). Post-1988 research in Yellowstone has helped and will continue to help society cope with this major environmental change in at least two important ways: first, by changing society's perceptions and attitudes toward wildland fire and fire management, and second, by providing a strong foundation for predicting and testing the impacts of climate change on future fire regimes and fire effects.

Since 1988, the public has gained a far greater understanding of the importance of wildland fire, both ecologically—the role of fire as a natural ecological process—and socially—the inevitability of fire in many places and the need to proactively reduce fire hazard to communities and resources (J. Clement, personal communication, 2011). Community wildfire protection plans now are being developed throughout much of the West; these involve place-based thinking and learning with input from agencies and academics, but the process is driven primarily by local community members. Surveys reveal widespread support for fuel reduction via mechanical vegetation removal and prescribed fire, although prescribed fire is still viewed with caution because of the fear of escape (Jakes 2003; Brunson and Shindler 2004; McCaffrey and others 2008; Shindler and others 2009). Uncontrolled wildfire is also gaining acceptance in areas where human lives and infrastructure are not threatened. In the summer of 2008, when numerous fires were burning in and around the GYE, many people in the local town of Jackson, WY, criticized the U.S. Forest Service for what was perceived as overly aggressive fire suppression in backcountry areas (J. Clement, personal communication, 2011). The public also is becoming more engaged in decision-making about what should be done—or not done—for postfire rehabilitation (Olsen and Shindler 2010). Studies after the 1988 Yellowstone fires, which have demonstrated that fire can damage human structures but does not necessarily destroy nature, have helped provide the groundwork for the public's re-evaluation of fire and fire management.

We have learned from Yellowstone that large severe fires–in the right context–are not ecological catastrophes, but reflect instead a powerful natural process that has long shaped the biota and ecological functioning of the system. This message has been reinforced by studies of more recent large fires, notably those that burned in boreal and temperate mid- to high-elevation conifer forests. For example, after the 2002 Biscuit Fire in southwestern Oregon, which burned 200,000 ha of mixed conifer and broad-leaf forest, natural seedling establishment was sufficient to restock most burned stands within 4 years of the fire, native forbs and shrubs recovered rapidly via sprouting, on-site seed banks, and off-site seed sources (Donato and others 2009a, b), and bird diversity and abundance were not adversely affected even in areas of high-severity and short-interval burning (Fontaine and others 2009). In other ecosystems where fire had been excluded for many decades, recent uncontrolled fires have burned in a manner similar to historical fires and moved the systems closer to the historical condition (for example, Fulé and others 2004; Collins and others 2009).

Although these insights from the 1988 Yellowstone fires provide a necessary corrective to earlier notions that fires are merely destructive, it is important not to assume that all fires and all ecosystems are like Yellowstone. Fires like 1988 had occurred previously in Yellowstone and the biota were adapted to severe fire. However, in ecosystems such as dry southwestern pine forests where fires historically were frequent and predominantly low-severity, recent fire behavior and ecological effects have exceeded the historical range of variation (Strom and Fulé 2007). A century of fire exclusion allowed development of fuel structures conducive to higher-severity burning which, in combination with recent severe droughts, has resulted in greater extents of stand-replacing fire than was typical of the several centuries prior to 1900 (Covington and Moore 1994). Some recent fires, uncharacteristically severe for these particular ecosystems, have led to qualitative changes in vegetation structure. For example, some of the ponderosa pine forests burned in Arizona's 2002 Rodeo-Chediski Fire appear to have been converted to shrublands or grasslands that will not re-forest naturally but will persist indefinitely as non-forest vegetation (Savage and Mast 2005; Strom and Fulé 2007). It is increasingly recognized that there is a variety of "natural" fire regimes, and that fires need to be interpreted within the framework of the relevant historical fire regime (Karr and others 2004; Schoennagel and others 2004).

Yellowstone studies provide a foundation for predicting the impacts of climate change on future fire regimes and fire effects, as well as a benchmark for evaluating whether the ecological impacts of ongoing climate change exceed those of historical episodes of climate change. Extensive paleoecological data from the Yellowstone area provide some of the best understanding available for any region about the magnitude and direction of climatic and ecological changes that have occurred in the past. During the transition from glacial to Holocene conditions (ca. 14,000–9,000 years ago), temperatures rose at least 5–7°C and new plant communities formed as species expanded their range from multiple small glacial populations (Whitlock 1993; Shafer and others 2005; Jackson and others 2009a, b; Gugger and Sugita 2010). Less dramatic but nevertheless substantial climate variation also occurred from the early Holocene until the present. Holocene climate variation was associated with shifts in species distributions as well as substantial variation in fire frequency, with more fire occurring during warmer and drier periods (Meyer and others 1995; Millspaugh and others 2000, 2004; Meyer and Pierce 2003; Whitlock and others 2008; Higuera and others 2010).

How well does this understanding of past relationships among climate, fire, and ecosystems enable us to predict the future of mountainous regions like Yellowstone? If future climate conditions, fire regimes, and ecological relationships remain within the range of variation represented by the Holocene, then we can expect small changes—for example, younger forest age class distributions with shorter fire intervals—but no change in the fundamental character of the GYE even as the climate changes and fires become more frequent. Indeed, one of the strongest conclusions from the post-1988 Yellowstone studies is that the system is very resilient to fire. However, given the current rate of climate change, it is possible that the magnitude of ecological disruption and reorganization will be greater than occurred at any time in the Holocene or even during the glacial to Holocene transition. Climate change is gradual, but it can trigger rapid changes in disturbance regimes, including fire. A recent analysis of future climate projections and fire-climate relationships in the GYE indicates that fire rotations (the time required to burn an area equal to the landscape area) could be reduced from the historical rotation (100–300 years) to less than 30 years by the middle of the 21st century (Westerling and others 2011). Some current vegetation types probably would not be able to persist under such frequent burning, and a host of associated ecological processes would likely be altered.

The ecological effects and responses associated with the 1988 Yellowstone fires—which have been documented in detail—probably represent typical fire effects and responses during the period from the early Holocene to the recent past, that is, they characterize the historical fire regime. So long as the ecological effects and responses to future large fires are similar to those of 1988, then the system probably remains within the historical condition. However, if future fire effects are substantially different from the 1988 benchmark, then we will know that we have entered uncharted territory.

CONCLUSIONS

So, how did scientists do back in 1988 when they made their predictions about the ecological consequences of the Yellowstone fires? Considering the state of knowledge at the time, we think they did pretty well. Several of their predictions proved to be incorrect or only partially correct, but all had heuristic value—and much was learned when the a priori predictions failed. The rapid initiation of the postfire empirical data collection was key, and similar campaigns will be needed following future disturbances (Lindenmayer and others 2010).

Looking ahead, it is reasonable to ask how lessons learned from the 1988 Yellowstone fires may apply in the future. Given the complexities of heterogeneity, contingency, and multiple interacting drivers, predicting future ecological change is an immense challenge (Jackson and others 2009a, b). Yellowstone's ecosystems recovered rapidly from the 1988 fires with little human intervention; however, climate has continued to warm since 1988, and the frequency of large fires has increased throughout the Rocky Mountain region. Thus, the well-documented resilience of post-1988 Yellowstone ought not lull scientists and managers into a false sense of security if the ''rules of the game'' change qualitatively. The wealth of data collected following the 1988 fires may provide an unexpected benchmark from which the dynamics of fire-prone ecosystems will be evaluated in the future. By carefully documenting a wide array of postfire responses, the foundational studies of the 1988 Yellowstone fires may leave unanticipated but incredibly valuable legacies for future progress in ecosystem and landscape ecology.

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