

Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA

Tania Schoennagel^{A,C}, Erica A. H. Smithwick^B and Monica G. Turner^B

^ADepartment of Geography, University of Colorado, Boulder, CO 80309, USA.

^BDepartment of Zoology, University of Wisconsin, Madison, WI 53706, USA.

^CCorresponding author. Email: Tania.Schoennagel@colorado.edu

Abstract. We characterised the remarkable heterogeneity following the large, severe fires of 1988 in Yellowstone National Park (YNP), in the northern Rocky Mountains, Wyoming, USA, by focussing on spatial variation in post-fire structure, composition and ecosystem function at broad, meso, and fine scales. Ecological heterogeneity at multiple scales may enhance resilience to large, severe disturbances by providing structural, biological and functional redundancy. Post-fire heterogeneity in stand age, coarse wood abundance, microbial and understorey communities reflected interactions between existing pre-fire patterns and fire severity at different scales, suggesting that environmental context plays an important role in successional responses to large fires. In response to these post-fire patterns, heterogeneity in carbon (C) and nitrogen (N) storage, N mineralisation, decomposition, and productivity was also evident at multiple scales and may confer resiliency to large fires. For example, at broad scales, C storage in YNP appears resistant to changes in age-class structure associated with large stand-replacing fires. In summary, the YNP landscape is recovering rapidly from the 1988 fires through natural mechanisms, owing to the abundance and spatial heterogeneity of post-fire residuals, but other systems with fewer biotic legacies may be less resilient to such large, severe fires.

Additional keywords: carbon, ecosystem processes, landscape ecology, lodgepole pine, nitrogen, *Pinus contorta*.

Introduction

As the size of individual forest fires and annual area burned in the western United States (USA) grow (Stephens 2005; Westerling *et al.* 2006; NIFC 2007), understanding the ecological consequences of large fires becomes increasingly important. In some areas, low resilience to large severe fires results in qualitative ecological changes, such as conversion from forest to non-forest or significant reduction in structural or biological diversity. For example, large severe fires are deleterious in some ponderosa pine (*Pinus ponderosa*) forests of the south-western USA where past fire suppression has contributed to an increase in fire severity (Covington *et al.* 1994; Savage and Mast 2005). In other forest ecosystems, including Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) and high-elevation spruce–fir (*Picea–Abies*) forests, large severe fires comprise the natural disturbance regime and are recognised as key determinants of ecosystem structure, function and composition (Turner *et al.* 1994; Noss *et al.* 2006). The ecological importance of such large infrequent disturbances (LIDs) has been appreciated for over a decade (e.g. Foster *et al.* 1998), and recent studies have shown that LIDs can create spatial heterogeneity, provide rare opportunities for recruitment of native species, and maintain critical ecosystem function (Turner *et al.* 2003; Dale *et al.* 2005; Romme *et al.* 2005).

Here, we synthesise the ecological consequences of the large severe fires of 1988 in Yellowstone National Park (YNP), Wyoming, USA. Specifically, we discuss how these natural wildfires created patterns at multiple spatial scales (i.e. extents)

and suggest that this multiscaled, post-fire heterogeneity has important effects on long-term dynamics and resilience of the YNP landscape. Ecological resilience refers to the ability of a system to withstand disturbances without converting to a wholly new state with different composition, structure and function (Webster *et al.* 1975). This fundamentally differs from the term resistance, which is the ability for individuals to survive fire. Spatial heterogeneity in post-fire patterns and processes provide ecological complexity and redundancy that promote ecological resilience. We describe post-fire structural and successional heterogeneity in lodgepole pine forests of YNP at three nested scales: broad (~10–100 km), meso (~0.1–10 km), and fine (~0.001–0.1 km) and address two questions: (1) How is post-fire ecological heterogeneity manifest at different scales following large fires in YNP? (2) How does this post-fire heterogeneity influence post-fire ecosystem function, specifically carbon (C) and nitrogen (N) cycling? Understanding landscape resilience to large, severe fires is important for predicting responses to future disturbances and informing the management of ecosystems most sensitive to large fires.

The YNP landscape is an excellent natural laboratory for studying fire, landscape heterogeneity and subsequent effects on ecosystem processes. YNP is dominated by fire-adapted lodgepole pine and has a long history of natural, stand-replacing fires that have occurred at ~100–300-year intervals (Romme and Despain 1989; Millsbaugh *et al.* 2000; Schoennagel *et al.* 2003). Lodgepole pine are obligate, non-sprouting seeders with thin bark that makes them sensitive to fire. Predominantly moist,

Table 1. Sources of ecological heterogeneity at multiple scales

Summary of the sources of ecological heterogeneity at multiple scales in relation to the large fires of 1988 in Yellowstone National Park. Across different spatial scales, elements of pre-fire heterogeneity interacted with patterns of fire severity in creating post-fire ecological patterns, which in turn affected spatial variability in important ecosystem processes

Scale	Extent (km)	Pre-fire heterogeneity	Post-fire heterogeneity	Post-fire ecosystem processes
Broad	10 to 100+	Fire history, abiotic gradients	Burned v. unburned areas, mosaic of age classes, coarse wood abundance, microbial and understorey diversity	Net C storage and N availability
Meso	0.1 to 10	Serotiny, tree density	Fire severity within the burn, abundance of tree regeneration and coarse wood, understorey vegetation	Aboveground net primary productivity and decomposition rates, inorganic N availability
Fine	0.001 to 0.1	Stand structure, coarse wood, understorey vegetation	Local fire severity, configuration of coarse wood, understorey cover and composition, microbial communities	Decomposition rates, net N mineralisation, N fixation

cool climate conditions support forests with abundant live fuels (e.g. dense conifer needles) that burn readily when sufficiently dry (Schoennagel *et al.* 2004a). Large fires occur during extreme drought conditions that occur infrequently (on the order of centuries), often during dry regional climate anomalies linked to variation in sea surface temperatures in the Pacific and Atlantic Oceans (Schoennagel *et al.* 2005, 2007; Sibold and Veblen 2006; Kitzberger *et al.* 2007). Although infrequent, the resulting large fires account for most of the area burned over an extended time (Johnson *et al.* 1998).

The 1988 fires affected ~36% (321 000 ha) of YNP, burning all ages of forest under conditions of severe drought and high winds (Renkin and Despain 1992). After more than three months, the fires were stopped by snow in mid-September. Such fires have occurred in Yellowstone throughout the Holocene (Millspaugh *et al.* 2000); however, misperceptions that the fires resulted from poor forest management or past fire suppression and that the forests would not regenerate were common (Smith 1996). We use the 1988 Yellowstone fires as a case study, but our findings have implications for ~8 million hectares of undeveloped lodgepole pine forests in the western USA (Theobald and Romme 2007), and provide a framework for considering effects of large fires in other forested systems.

Post-fire heterogeneity at multiple scales

Heterogeneity is a hallmark of natural disturbances. Large, severe disturbances are ecologically important because the imprint they leave on the ecosystem is spatially extensive and may persist for a very long time. Indeed, a large disturbance may be the dominant force structuring the system, creating the template on which subsequent ecological processes and interactions among species occur (Turner *et al.* 1998). Understanding the nature of the patterns created by large disturbances and the factors controlling them is essential for understanding and predicting ecosystem dynamics (e.g. the rate and pattern of energy flow, nutrient cycling) and for guiding natural resource management. Here, we characterise the spatial heterogeneity resulting from the 1988 Yellowstone fires at multiple scales in order to increase understanding of the relationship between pattern and process following large, severe fires (Table 1).

Broad-scale post-fire patterns across the landscape

At the broad scale (~10–100 km), large, stand-replacing fires create a coarse pattern of burned and unburned forests and establish a new mosaic of stand ages across the landscape (Fig. 1a). Prior to the 1988 fires, the Yellowstone landscape was dominated by conifer stands >150 years old (Romme 1982; Romme and Despain 1989). Although there were some small patches of younger forests from occasional fires earlier in the 20th century (e.g. fires in 1931 burned 8245 ha, and fires in 1981 burned 8342 ha; Balling *et al.* 1992), average stand age was relatively high in 1987, and patches of older forest were large and well connected. With the occurrence of the 1988 fires, nearly 36% of YNP was reset to a stand age of zero, substantially lowering the average stand age and reducing connectivity of the remaining older forests. Almost one-third of the forests within the burn perimeter remained unburned, and the sizes and shapes of the burned patches were quite variable. Spatial analysis of the burn mosaic revealed that 75% of the sites experiencing high-severity burns were within 200 m of green forest, indicating a complex spatial pattern of burned and unburned forest (Turner *et al.* 1994). Thus, the 1988 fires imposed a coarse-grained mosaic of burned and unburned patches that initiated a complex spatial pattern of stand ages distributed geographically across the landscape.

In general, large, stand-replacing fires change both the mean and variance of forest stand-age classes within a landscape. Spatial modelling of fire and succession in YNP over time revealed that the coefficient of variation of stand age across the landscape increased significantly in response to simulated large fires (Fig. 2; Schoennagel *et al.* 2006). This increase in stand-age variance occurs in natural fire systems with long return intervals because large, stand-replacing fires reduce the age of burned stands but leave many old stands unaffected.

The burn mosaic also influenced the broad-scale spatial pattern of standing and downed coarse wood (CW) abundance across the landscape. The 1988 fires created ~25 million metric tons of standing dead wood (Tinker and Knight 2001) and produced a significant pulse of downed wood during the subsequent two decades (Litton *et al.* 2004; Tinker and Knight 2004). Thus, post-fire stands in YNP harbour more CW than mature stands. For example, 13 years following the 1988 fires, average CW abundance was 3301 g C m⁻² in post-fire stands compared with

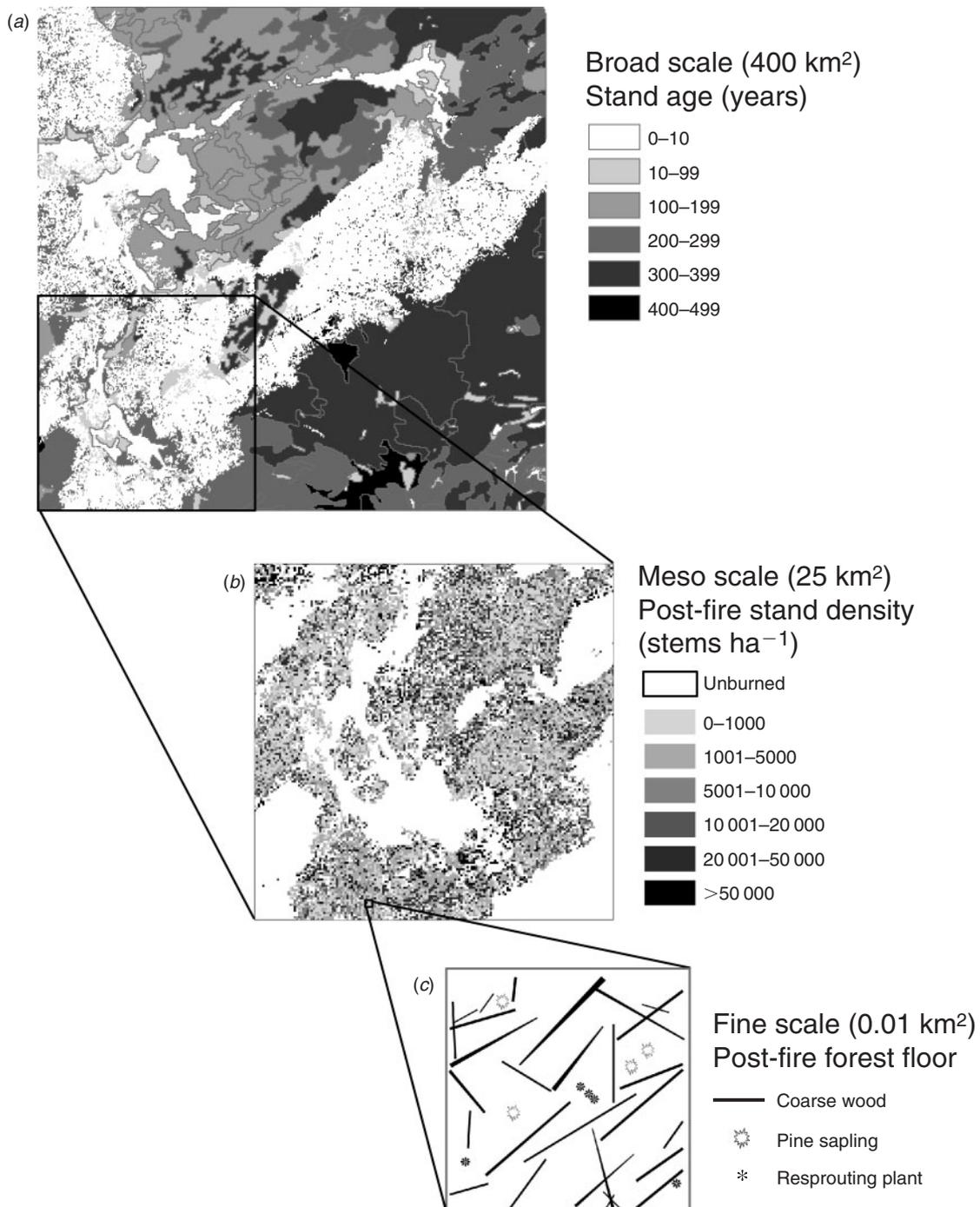


Fig. 1. Patterns of heterogeneity at multiple nested scales following the large fires of 1988 in Yellowstone National Park. Spatial variation in (a) stand age at the broad scale (Romme and Despain 1989); (b) stand density at the meso scale (Kashian *et al.* 2004); and (c) coarse wood, pine saplings and resprouting understorey plants on the forest floor at the fine scale (Turner *et al.* 1999; Tinker and Knight 2001). Plant size not to scale in (c).

2543 g C m⁻² in mature stands (Litton *et al.* 2003). Therefore, the broad-scale pattern in stand age created by large fires was also associated with landscape variation in CW abundance.

The post-fire stand-age mosaic interacts with environmental gradients to affect broad-scale distributions of biotic (vegetative

and microbial) communities. Recently burned patches have greater understorey cover and plant species richness than mature forests (Taylor 1973), but abiotic gradients are also important. In YNP, vegetative cover and species richness increase with elevation and soil fertility, with andesite and lacustrine-derived soils

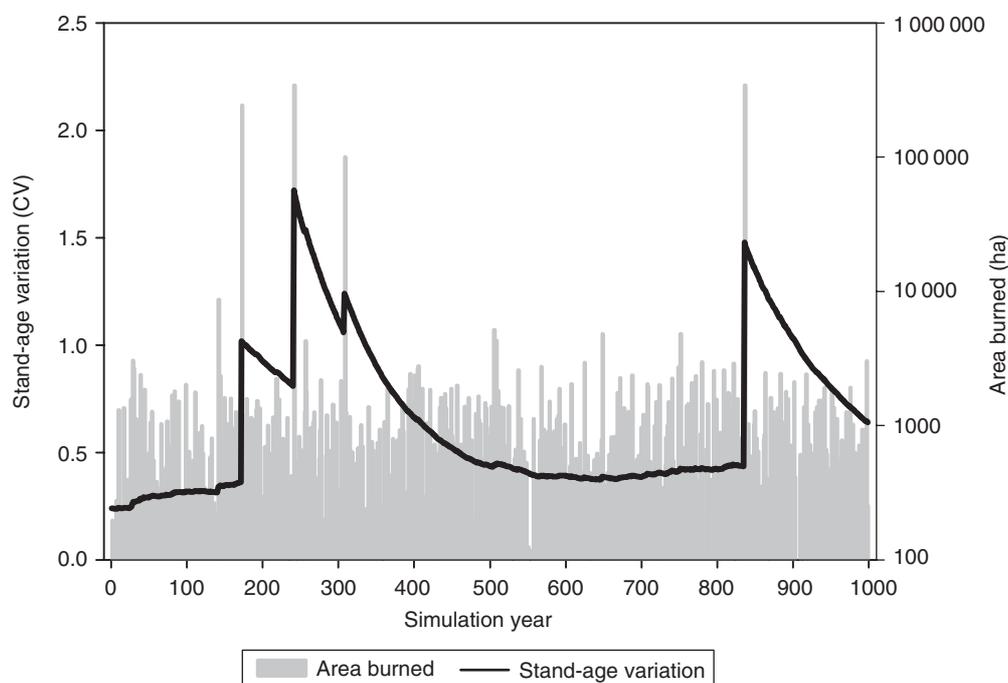


Fig. 2. Output from a 1000-year run produced by a landscape simulation model developed for Yellowstone National Park showing annual changes in the coefficient of variation of stand age across the landscape in relationship to annual area burned. Variation in stand age across the landscape increases dramatically in response to large fires. Adapted from Schoennagel *et al.* (2006).

supporting higher understorey diversity and cover (Turner *et al.* 1997; Schoennagel *et al.* 2004b). Microbial communities are also known to vary at broad spatial scales with stand age and abiotic conditions (Merila *et al.* 2002b; Douglas *et al.* 2005; Smithwick *et al.* 2005b; Fierer and Jackson 2006). In YNP, soil microbial communities varied both with stand age (ranging from 50 to 350 years) and abiotic variables such as pH and soil organic matter quantity (Smithwick *et al.* 2005b). Microbes respond directly to fire, with mortality increasing with fire severity but differing among functional groups. However, relatively little is known about how spatial patterns of recovering microbial and vegetation communities develop through successional time (Hart *et al.* 2005). In sum, large, stand-replacing fires create a broad-scale mosaic of stand ages that is associated with landscape patterns of CW and biotic communities.

Meso-scale post-fire patterns among stands

Heterogeneity was also manifest at finer scales within the area burned by the 1988 fires and the even-aged stands that subsequently developed. This meso-scale variation (~0.1–10 km) reflects patterns of post-fire tree density (Fig. 1b), CW and understorey cover that were largely determined by spatial variation in fire severity and its interaction with pre-fire vegetation. Field studies conducted in 1989 and 1990 identified three categories of fire severity that were related to post-fire vegetation (Turner *et al.* 1999). These included (1) light surface fires, where canopy trees were scorched but not killed by the fire,

and understorey vegetation, soils and the litter layer were minimally affected; (2) severe surface fires, where stand-replacing fires killed the canopy trees but did not consume needles or fine fuels in the canopy; and (3) crown fires, where stand-replacing fires consumed the needles and fine fuels of the overstorey trees (Turner *et al.* 1999). The litter layer was consumed in both classes of stand-replacing fires (severe surface and crown fires), exposing mineral soil throughout.

There were a variety of plant community responses to fire severity (e.g. relative abundance of different species and functional groups, seedling recruitment, species richness and community composition; Turner *et al.* 1997, 1999), but most notable was the high post-fire density of lodgepole pine seedlings associated with severe surface fires (Turner *et al.* 1997, 1999). Post-fire stand density also reflected pre-fire levels of lodgepole pine serotiny (Anderson and Romme 1991; Turner *et al.* 1997). Lodgepole pine bears serotinous cones (Koch 1996), but not all lodgepole pines are serotinous, and the abundance of trees with serotinous cones varies at different spatial scales across the landscape (Tinker *et al.* 1994; Schoennagel *et al.* 2003). The percentage of trees bearing serotinous cones in YNP is greatest for older trees (Lotan 1975; Koch 1996; Schoennagel *et al.* 2003) at lower elevations (Tinker *et al.* 1994) and appears to be associated with the shorter fire intervals (~170 years at elevations <2300 m) that characterise these warmer and drier locations (Schoennagel *et al.* 2003).

The spatial variation in serotiny interacted with fire severity to produce tremendous heterogeneity in lodgepole pine recruitment

following the 1988 fires (Turner *et al.* 1997). Post-fire stand densities ranged from zero to $>500\,000$ stems ha^{-1} (Kashian *et al.* 2004; Turner *et al.* 2004), with the highest densities observed at lower elevations where pre-fire serotiny was high, and the lower densities at high elevations where pre-fire serotiny was low and fire-return intervals approached 300 years (Schoennagel *et al.* 2003). Spatial analyses of lodgepole pine sapling densities in 1998 mapped from colour infrared aerial photography revealed a pattern of high-density patches interspersed within a matrix of low-density patches (Fig. 1b; Kashian *et al.* 2004). This initial variation in post-fire stand densities can persist for almost 200 years, converging to ~ 1200 stems ha^{-1} by 175–200 years (Kashian *et al.* 2005b).

Interactions between burn severity and pre-fire stand density influenced the abundance of downed and standing CW within the burn perimeter. Measurements made between 2002 and 2003 throughout the areas burned by the 1988 fires revealed substantial among-stand heterogeneity in CW abundance (Remsburg and Turner 2006; Forester *et al.* 2007). Coarse wood densities measured in 64 stands, all burned in 1988, ranged from 100 to 2134 logs ha^{-1} (mean = 744.15, s.d. = 379.45) and was greatest where pre-fire stand density was high (Forester *et al.* 2007). However, there was also wide variation (from 0 to 98%) in the percentage of fire-killed trees that had fallen, with the greatest treefall rates recorded at the lower elevations (W. H. Romme and H. D. Lyons, unpubl. data). Thirteen years after the 1988 fires, newly fallen CW comprised between 21 and 68% of above-ground woody biomass, indicating wide variation among stands (Litton *et al.* 2003).

Early successional post-fire plant communities were also characterised by among-stand variation associated with fire severity as well as patch size and shape. Specifically, the relative abundance of different species and functional groups, recruitment of seedlings, and species richness all displayed significant responses to these meso-scale factors (Turner *et al.* 1997, 1999). For example, *Epilobium angustifolium* and *Carex rossii* were more abundant in areas of crown fire, whereas *Lupinus argenteus*, *Vaccinium scoparium*, *Carex geyeri* and *Arnica cordifolia* were more abundant in areas of severe surface fire. These understorey responses appeared to be relatively ephemeral, diminishing within 15 years as the influence of broad-scale environmental gradients became increasingly evident (Turner *et al.* 2003; Schoennagel *et al.* 2004b). However, Schoennagel *et al.* (2004b) also documented a negative relationship between post-fire lodgepole pine density and understorey cover, suggesting that meso-scale patterns in plant abundance could persist through stand maturity. In sum, within the extent of the large 1988 fires, we have documented substantial spatial heterogeneity in stand density, CW abundance, and understorey plant communities. The fires not only created a landscape mosaic of stand age but also a mosaic of stand structure within the burn perimeter.

Fine-scale post-fire patterns within stands

Post-fire heterogeneity was also apparent at fine scales (0.001–0.1 km) within the 1988 burn mosaic. For example, local variation in the depth to which soil charred was pronounced within stands and affected the survival of individual understorey plants and soil microbial communities. The mean depth to which soil

charred within areas of crown fire was only 13.6 mm, but measurements ranged from 0 to 39.2 mm among 117 sampling points (100 m separation) from which this mean was calculated (Turner *et al.* 1999). At an even finer scale, the depth of soil char measured at four points within a 50-m² circular plot ranged from 0 to 50 mm. Thus, there was substantial local heterogeneity in fire effects on soils, as has also been observed in other stand-replacing fires (Smithwick *et al.* 2005a).

The position of CW within a given stand was another source of fine-scale heterogeneity, introducing substantial variation in physical structure (Fig. 1c). The fallen, fire-killed trees created horizontal and vertical complexity in CW abundance, condition and spatial configuration. Trees could have fallen onto the forest floor, but they often fell onto each other and created piles of CW >1 m deep (Forester *et al.* 2007). Adding to the structure created by the newly fallen wood was the persistence of legacy wood that survived the fire. A relatively small proportion of the pre-fire CW in the forest was actually consumed by the 1988 fires (8%; Tinker and Knight 2000), so a large pool of residual downed wood in various decay stages remained within the stands. Collectively, these diverse structures created a wide range of microsites within young post-fire stands and were associated with fine-scale variation in soil temperature and moisture (Remsburg and Turner 2006).

The fine-scale patterns in the depth of soil charring and position of CW interacted with pre-fire vegetation and species' life-history traits to influence post-fire understorey vegetation. Resprouting followed by new seedling recruitment was a dominant mechanism of plant re-establishment within the burned areas. Thus, the spatial patterns of residuals (surviving roots, rhizomes and propagules) were key determinants of post-fire vegetation patterns at fine scales. Interestingly, we observed minimal colonisation of burned areas by exotic, invasive species (Turner *et al.* 1997, 2003); the vigorous resprouting of surviving plants resulted in abundant seed sources for native species within the burned area. The presence and position of CW also appeared to affect local vegetation patterns; in 1989, we often observed new *Pinus contorta* seedlings establishing in the drip line below fallen trees (M. G. Turner and W. H. Romme, pers. obs.). Dispersal capability also contributed to local variation. Wind-dispersed annuals (e.g. *Gayophytum diffusum*) or perennials (e.g. *Epilobium angustifolium*) established widely within burned stands, but heavier-seeded species such as *Lupinus argenteus* (a nitrogen fixer) remained localised and patchy in distribution, with newly established seedlings located near reproductive individuals. For a few species (e.g. *Arnica cordifolia*, *Vaccinium scoparium*), there was no post-fire seedling establishment 12 years after fire; all post-fire individuals of these species resprouted following fire and spread vegetatively.

Although we did not characterise microbial communities following the 1988 fires, we hypothesise substantial fine-scale variation exists in microbial populations in response to soil charring, understorey vegetation, litter quality and quantity, and microclimate, based on other research (Parkin 1993; Ettema *et al.* 2000; Mabuhay *et al.* 2006). One year after stand-replacing fire in Alaska, we observed bacteria to be more common in more severely burned microsites (high mineral soil, ash and burned litter), whereas fungi were more common in less severely burned microsites (high depth of the organic layer, total cover, and

percentage shrubs) (Smithwick *et al.* 2005a). In sum, the interaction between local fire severity and pre-fire stand structure created complex patterns of CW arrangement and understorey vegetation at fine scales within patches burned in 1988.

Effects of post-fire heterogeneity on C and N cycling at multiple scales

In the previous section, we characterised post-fire heterogeneity at three key scales. We now explore the functional consequences of this variation, focussing on C and N cycling. Spatial patterns of C and N cycling are important from local to regional scales (Robertson *et al.* 1988; Gross *et al.* 1995; Schimel *et al.* 1996), and understanding how disturbance influences spatial patterns of ecosystem function has emerged as a key ecological question (Fraterrigo *et al.* 2005; Turner 2005). Understanding the scales of variation that underlie patterns of C storage may help define trajectories of response to future climate change in temperate and boreal forests that experience stand-replacing fire (Harden *et al.* 2000; Kashian *et al.* 2006; Monserud *et al.* 2006). In addition, primary productivity in YNP is limited by N availability (Fahey and Knight 1986), which depends on the quantity of ammonium (NH_4^+) and nitrate (NO_3^-) that is available in soil solution for plant uptake. N mineralisation, the conversion of organic forms of N to these inorganic forms typically through the activities of microbial organisms, has been considered a limiting step in the N cycle (but see Schimel and Bennett 2004). Thus, identifying the effects of post-fire successional and structural variability at different scales on C and N dynamics may lend insight into mechanisms that promote functional resilience to large severe fires. We review ongoing and published studies that explore the linkages between post-fire patterns and ecosystem processes at broad, meso and fine scales in YNP.

Broad-scale variation in C and N cycling

Because variation in ecosystem structure and function is often linked to changes in successional age (Kurz and Apps 1999; Kashian *et al.* 2005a; Smithwick *et al.* 2005b), the broad-scale patterns of stand age produced by the 1988 fires are likely to influence productivity and biogeochemistry across the landscape. Indeed, landscape patterns of aboveground net primary production (ANPP) in YNP were associated with the stand-age mosaic (Fig. 3a; Hansen *et al.* 2000). When fires burn, a pulse of C is released to the atmosphere as organic matter is consumed. Atmospheric C is subsequently sequestered as the forest regenerates, but C released through decomposition may exceed that gained via production, resulting in negative net ecosystem productivity for several years following a fire (Janisch and Harmon 2002; Wirth *et al.* 2002; Bond-Lamberty *et al.* 2003). Thus, although net carbon balance will be zero when integrated over the entire post-fire successional sequence (Harmon 2001; Chapin *et al.* 2006; Smithwick *et al.* 2007), the post-fire stand-age mosaic alters C flux in the near term (i.e. years to decades; Fig. 3a) (Kurz and Apps 1999; Amiro *et al.* 2000; Smithwick *et al.* 2007). The balance of C production *v.* loss at the landscape scale is dependent on the fire-created patch mosaic, which may qualitatively shift the landscape from a sink to a source of C to the atmosphere for decades to centuries (Kurz and Apps

1999; Amiro *et al.* 2000). However, C storage across the YNP landscape appears to be remarkably resistant to changes in fire frequency owing to relatively small losses of C from combustion (primarily small fuels such as needles, litter, and fine branches are consumed, and <10% of large CW), the large storage of C in CW, and the large storage of C in soils (Kashian *et al.* 2006). Changes in the average age-class structure of the landscape or mechanisms of post-fire regeneration would have to be extreme (e.g. a change in mean stand age by >150 years) for there to be a substantial effect, either negative or positive, on net C storage across the YNP landscape.

Although surprisingly little is known about the effects of stand-replacing fire on N cycling in forests (Wan *et al.* 2001; Certini 2005; Smithwick *et al.* 2005a), N availability is expected to respond to fire (Boerner 1982; Boerner *et al.* 2004; DeLuca *et al.* 2006) and vary with stand age (Merila *et al.* 2002a; Yermakov and Rothstein 2006). Recent fires provided opportunities to study N cycling processes across a range of post-fire intervals in YNP. We studied inorganic N mineralisation following fires in 1996, 2000 and 2003 and identified some intriguing patterns in N availability related to stand age. For example, microbial uptake of NH_4^+ was quite high immediately following severe fire (Turner *et al.* 2007), which is consistent with general patterns in N availability in other cold, temperate, fire-prone ecosystems (Vitousek *et al.* 1989) and may help minimise N losses. Nitrogen availability, particularly NO_3^- , was higher for several years after fire relative to mature stands in the same area (Romme and Turner 2004; Smithwick *et al.* 2005b). However, elevated N availability was observed for only a short period of time (~4 years) and was largely assimilated by microbial organisms and plants. For example, foliar N concentrations in many plant species were significantly higher 2 years after the fires of 2000 compared with nearby unburned forest (Metzger *et al.* 2006). Broad-scale conservation of N is also suggested by the low concentrations of nitrate and ammonium in surface waters. Nitrate and ammonium concentrations in stream water and snowmelt in burned areas of YNP were negligible (Romme and Turner 2004), and nutrient concentrations in lakes were not elevated after the fires of 1988 (Lathrop 1994).

Thus, broad-scale patterns of fire severity, which created a mosaic of burned *v.* unburned stands following the 1988 fire, affected patterns of both C and N. Recently burned patches experience substantial immobilisation of ammonium, elevated nitrification, and higher foliar N concentrations. In contrast, mature forest patches have higher ammonium availability, negligible rates of nitrification, and lower foliar N concentrations. Taken together, our studies to date suggest that the Yellowstone landscape is resistant to major changes in both C and N cycling dynamics at broad scales, even when fires are as large and severe as those that burned in 1988.

Meso-scale variation in C and N cycling

At the meso scale, post-fire variation in stand density and CW within the areas burned by the 1988 fires was associated with spatial patterns of ANPP (Fig. 3b), decomposition and N availability. ANPP increased with stand density, which explained most of the variation in ANPP, and was inversely related to elevation (Turner *et al.* 2004). In 1999, ANPP averaged $2.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$ but

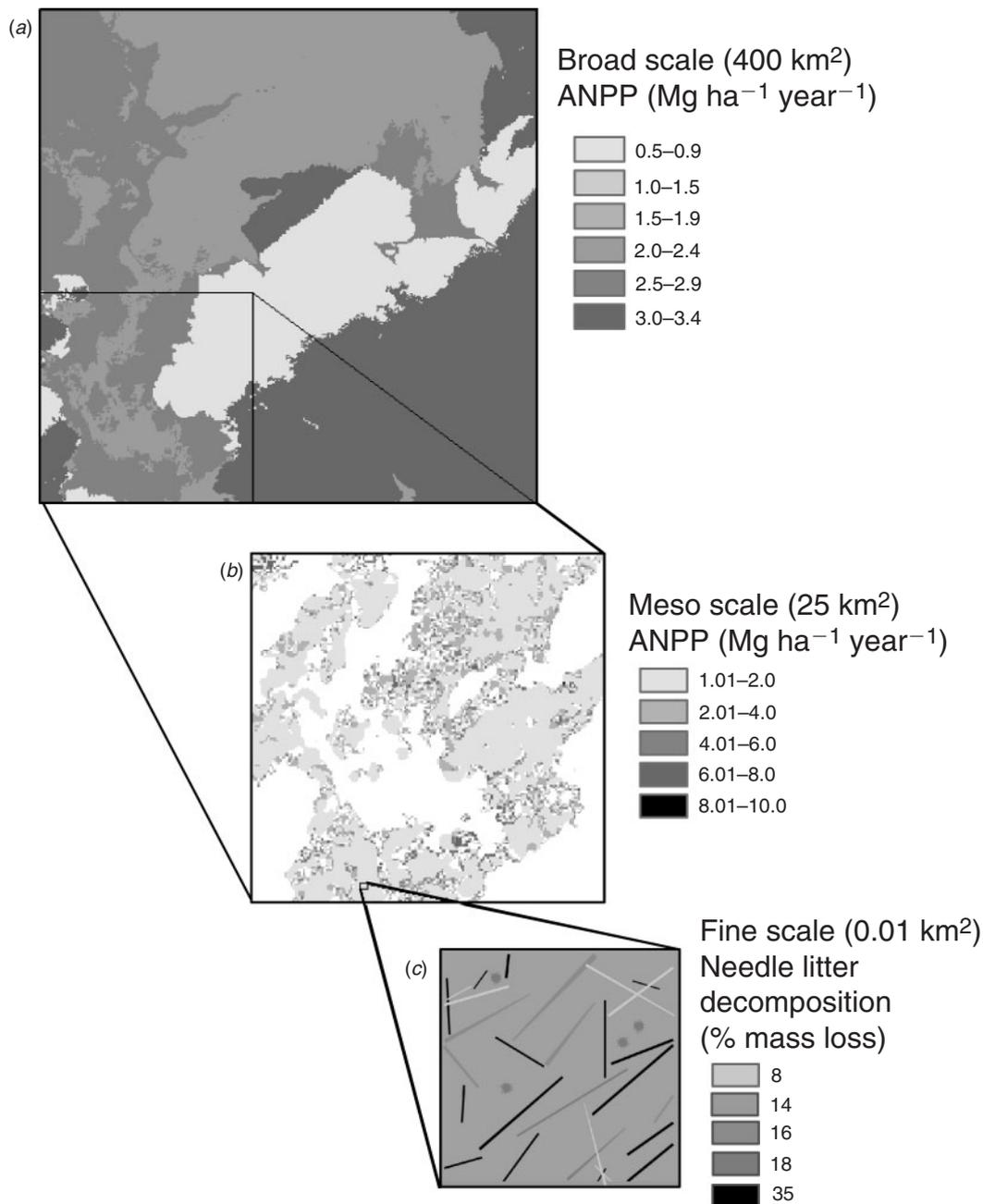


Fig. 3. Post-fire spatial heterogeneity in ecosystem processes at multiple nested scales Yellowstone National Park. Spatial variation in (a) aboveground net primary productivity (ANPP) at the broad scale (Hansen *et al.* 2000); (b) ANPP at the meso scale (Turner *et al.* 2004); and (c) rates of needle decomposition at the fine scale (adapted from Remsburg and Turner 2006).

ranged from 0.04 to 15.12 Mg ha⁻¹ year⁻¹. This variation was all within stands of the same age, yet it is comparable with the range of variation observed through successional time (Turner *et al.* 2004). The initially high spatial variation in ANPP rates diminishes through successional time in response to changes in stand structure, but appears to persist for up to two centuries (Kashian *et al.* 2005b).

Among-stand variation in CW abundance was associated with differences in decomposition rates within the young post-fire

stands (Remsburg and Turner 2006). Decomposition rates of herbaceous, pine needle and woody litter were inversely related to the abundance of CW elevated above the ground (i.e. the piles of fallen trees). This reduction in decomposition may be a mechanism by which C losses are lessened during early succession, and may be one means by which the systems returns to a zero or positive C balance more rapidly.

Post-fire soil N availability also varied spatially within areas burned in 1988, largely in response to post-fire patterns of stand

density. Twelve years after fire, Litton *et al.* (2004) reported lower inorganic N availability in high-density lodgepole pine. At 17 years after fire, Levitt (2006) measured inorganic N availability in 25 stands that varied in lodgepole pine density from 200 to 430 500 stems ha^{-1} . Net N mineralisation varied from 0.87 to 13.30 $\mu\text{g N bag}^{-1} \text{ day}^{-1}$ and showed a strong inverse correlation with lodgepole pine density (Levitt 2006). These relationships presumably reflect greater uptake of soil N in denser stands, which in turn sustains greater C accumulation.

Taken together, the initial post-fire variability in the abundance of pine saplings and downed CW among stands was associated with substantial differences in the rates of productivity, decomposition and soil N availability at meso scales. The high spatial variability in C and N cycling of early post-fire stands diminishes over successional time as stands infill or thin, minimising differences caused by initial variation in post-fire stand density.

Fine-scale variation in C and N cycling

At the fine scale, the arrangement and composition of CW following fire contributes to within-stand variation in surface and belowground ecosystem function, namely decomposition (Fig. 3c) and N mineralisation. Remsburg and Turner (2006) examined how fine-scale variation in the position (elevated *v.* contacting the soil), decay class (killed in the most recent fire *v.* legacy logs from the pre-fire stand), and quality (C:N ratios) of CW affected litter decomposition rates. Decomposition of herbaceous and needle litter was slowest under elevated logs and greatest under legacy wood, indicating that the downed trees were associated with significant within-stand functional variation. In addition, Metzger *et al.* (2008) found that annual *in situ* net N mineralisation under elevated logs was half as much as in open (i.e. exposed) mineral soil, and laboratory assays indicated that ammonium consumption (presumably largely due to microbial immobilisation) exceeded gross production of ammonium under all wood features. Differences in extractable organic C and microbial community composition may cause local variation in net N mineralisation rates, consistent with other work indicating that CW inputs of C to underlying soil may be significant (Spears and Lajtha 2004; Hafner and Groffman 2005). Because wood decomposition is relatively slow in these forests, the pulse of CW generated by the fires will remain a conspicuous source of structural heterogeneity within stands for decades (Wei *et al.* 1997; Tinker and Knight 2000), thus having a persistent influence on N mineralisation, which may be tightly controlled at the fine scale.

Fine-scale spatial patterns of understorey vegetation and microbial communities can also alter rates of C and N cycling at fine scales. A major influence on N cycling within post-fire stands is the location and abundance of N-fixing vegetation, i.e. plants capable of using atmospheric N, thereby bypassing the soil pool and increasing the total pool of N in the ecosystem. The most common symbiotic N-fixing plant in YNP is a species of lupine (*Lupinus argenteus*). The natural abundance values of N isotopes (used to identify the source of N used by the plant) in lupines were close to zero following stand-replacing fire ($-0.07 \pm 0.19\%$, per mil), indicating atmospheric N as the sole N source (E. A. H. Smithwick and K. L. Metzger, unpubl.

data). Fifteen years following the 1988 fires, lupines were found to have natural abundances characteristic of N-fixing behaviour ($0.13 \pm 0.17\%$), whereas a structurally similar plant (*Solidago* spp.) did not ($3.0 \pm 0.49\%$). In other ecosystems, N-fixing plants can form a continuous cover and contribute substantially to N inputs immediately following fire (e.g. Busse 2000). However, in YNP it appears that N inputs from N-fixing vegetation may be heterogeneous owing to the patchiness of individual plants. In sum, decomposition, mineralisation rates, and the location of N-fixers appear to govern C and N cycling at fine scales in YNP. The length of time that this fine-scale heterogeneity persists is unknown, but it is likely to be present until structural changes in CW or understorey communities have occurred.

Discussion

In response to our first question (*How is post-fire ecological heterogeneity manifest at different scales following large fires in YNP?*), we have shown that the large, stand-replacing fires of 1988 created remarkable ecological heterogeneity at multiple scales. These post-fire patterns reflected the interaction between existing pre-fire patterns and fire severity, suggesting that environmental context plays an important role in responses to large fires (Agrawal *et al.* 2007). At broad scales, these interactions were manifest in patterns of stand age (living trees) that reflected burned and unburned patches on the landscape, and patterns of structure (dead wood on the ground) that reflected pre-fire stand structure. At meso scales, most remarkably, the interaction between pre-fire serotiny and fire severity resulted in a mosaic of post-fire tree density that ranged five orders of magnitude across the landscape. At fine scales, the interaction between pre-fire stand structure and fire severity resulted in complex patterns of CW arrangement and understorey composition.

In response to our second question (*How does this post-fire heterogeneity influence post-fire ecosystem function, specifically C and N cycling?*), we have shown that these structural patterns resulted in equally heterogeneous patterns of C and N storage, N mineralisation, decomposition, and productivity at multiple scales. Given that the patterns in ecosystem function that we have observed largely correlated with patterns in post-fire stand structure (e.g. CW abundance and arrangement, stand density, stand age), these patterns are likely to persist until patterns in stand structure converge, which may take more than 175 years (Kashian *et al.* 2005b). As a group, these findings suggest a complex story of post-fire ecosystem dynamics. Specifically, in YNP, there appear to be multiple trajectories of ecosystem dynamics following severe fire, even within relatively definable ecological units such as age-classes, burned patches, or individual stands. Understanding this multiscaled variation in ecosystem C and N cycling requires understanding both intrinsic (e.g. biotic) and extrinsic (e.g. abiotic) patterns at each scale.

Interestingly, the multiscaled responses of ecosystem processes to structural patterns may provide a certain degree of resiliency to the YNP landscape following fire. At broad scales, C storage in YNP appears resistant to changes in age-class structure without extreme changes in fire interval or post-fire regeneration. At meso scales, the inverse relationship between N supply and post-fire lodgepole pine density within burned areas implies one possible mechanism by which convergence in stand structure

is governed (i.e. low soil N supply in dense stands may constrain future production, whereas larger N supplies in sparse stands may facilitate infilling). Ultimately, limitation of other resources (light, water) is likely to be equally constraining but will likely follow similar inverse relationships with lodgepole pine density. At fine scales, it is unclear whether hotspots of resource availability will confer resiliency, although experimental studies suggest that resource heterogeneity may increase biodiversity (and potentially, resilience) (Tilman *et al.* 2006), but this has not been tested in YNP. More generally, the notion that cross-scale interactions may either accelerate or dampen rates of change is receiving more attention (Peters *et al.* 2004), and landscapes with natural large fire regimes may offer opportunities for studying such dynamics.

Whether large fires result in unpredictable consequences for ecosystem structure and function and whether post-fire intervention is needed depends, in part, on post-fire heterogeneity and the biotic response capacity of the system (Turner *et al.* 1998). The YNP landscape appears to be recovering rapidly from the 1988 fires through natural mechanisms, but other systems may show different responses. The 2002 Hayman fire, the largest fire on record in Colorado (USA) provides a counter-example that demonstrates the importance of biotic legacies. On 9 June 2002, the fire burned 43% of the total area (24 215 ha) in a few hours under very extreme weather conditions (Romme *et al.* 2003). Thirty-seven percent of the forest within the fire perimeter experienced high-severity fire in which post-fire tree regeneration was very low, and there are still few signs of imminent tree regeneration (Romme *et al.* 2003). The dominant trees (*Pinus ponderosa* and *Pseudotsuga menziesii*) are not serotinous, so post-fire seed sources were relatively few and from unburned forests only. Compared with YNP with its abundance of serotinous trees, biotic residuals of the dominant trees were fewer and the Hayman post-fire landscape was more spatially homogeneous (although persistent openings contribute to structural heterogeneity across the broader forested landscape). Persistent treeless openings represent a state change from the pre-fire forest condition to a non-forest habitat; conversion of forest stands to meadows has been observed in other ponderosa pine forests following severe fires (Savage and Mast 2005). Active management may be necessary if a rapid return to forest conditions is deemed desirable; however, spatial, genetic and functional heterogeneity should remain an important management guide if resilience is an important goal. In contrast, the capacity for Yellowstone forests to regenerate following large severe fires was largely a product of abundant post-fire residuals, and management activities to restore forest cover were not needed (Dale *et al.* 1998). Such ecological resilience observed in Yellowstone may apply to other crown-fire ecosystems where (1) spatial complexity of the burn provides opportunities for seeds to disperse from surviving individuals relatively quickly throughout the burned area, and (2) variation in fire severity within the burn perimeter contributes to variation in post-fire biotic residuals (owing to resprouting or fire-resistant seed storage).

Large high-severity fires play a significant and unique ecological role in remote areas where ecological values are paramount, and threats to human communities are low. Post-fire management such as salvage logging, tree planting, and seeding of non-native grasses is often implemented but may not be needed for

ecological restoration or recovery (Turner *et al.* 2003; Lindenmayer *et al.* 2004; Romme and Turner 2004; Noss *et al.* 2006). Post-fire management can inhibit ecological recovery and may compromise the important spatial heterogeneity in stand and landscape structure, species composition and ecosystem function. Biologically rich and ecologically important, large unmanaged post-fire landscapes are relatively rare yet provide an important source of ecological heterogeneity.

In conclusion, large severe fires are important in that they shape the age-class structure of the landscape and create the template on which biotic processes play out for decades to centuries. Our findings suggest that post-fire heterogeneity at multiple scales may confer resilience within this landscape, promoting recovery and maintaining system integrity in the wake of a large, infrequent perturbation (Romme and Turner 2004). The 1988 Yellowstone fires introduced substantial and ecologically significant spatial heterogeneity at multiple scales, which promoted variability in species, structure and function that can increase redundancy, complexity and resilience to large severe disturbances (Franklin 2005).

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