



Benefits of thinning and burning for understory diversity vary with spatial scale and time since treatment



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ABSTRACT

Fuel-reduction treatments have been used effectively in dry, fire-adapted forests to reduce risk of high-severity crown fire, but it is less certain whether they achieve ecological objectives such as promoting understory diversity. Using long-term data from a fuel-reduction experiment, we tested how conclusions about treatment effectiveness are related to the spatial and temporal scales over which ecological responses are evaluated. We modeled the richness of herbs and shrubs at smaller (1–50 m²) and larger (1000 m²) spatial scales as functions of pre-treatment richness, thinning intensity, burning, and time since treatment (2–3 vs. 10–13 years). Pre-treatment richness was the strongest predictor of post-treatment richness, reflecting high rates of species survival, irrespective of treatment. Richness was enhanced by burning and, to a lesser extent, by thinning, although the timing and strengths of these effects varied with spatial scale. Among herbs, annuals showed an early and persistent increase after burning at the larger scale, but a lagged response at the smaller scale—the latter enabled by limited competition from perennial herbs and shrubs. In contrast, perennials showed lagged responses to thinning at smaller scales and to burning at larger scales, suggesting slow recruitment via seed or vegetative spread. Non-natives were unresponsive to treatments but were also uncommon before treatment, suggesting limited propagule pressure from the surrounding landscape. Rates of colonization were unrelated to pre-treatment richness; thus, the potential for understory enrichment was not constrained by initial diversity. The low cover and lagged responses of woody and herbaceous perennials suggest that further enrichment is possible, particularly at smaller spatial scales. Our results illustrate that uncertainty about the ecological effectiveness of fuels treatments can relate to the spatial and temporal scales over which responses are measured. They underscore the value of long-term, multi-scale assessments in defining the spatial and temporal contexts of ecological outcomes, and in evaluating the necessity for, or timing of, further intervention.

1. Introduction

Dry forests that historically experienced frequent fire have been substantially altered by decades of fire exclusion, selective logging, and livestock grazing (Agee, 1993; Harrod et al., 1999; Merschel et al., 2014). Increases in overstory density and amount and continuity of fuels have heightened the risks of high-severity wildfire and insect outbreaks, reduced the diversity and productivity of native understory vegetation, and degraded the habitat qualities and ecosystem services of these forests (Everett et al., 2000; Hessburg et al., 2000b). In Oregon and Washington, it has been estimated that 40% of dry forests require restoration to lower risks and enhance ecological functioning (Haugo

et al., 2015). Recognizing this need, land managers are using mechanical thinning and prescribed burning to reduce fuel loads and restore the structure that characterized these forests historically (Brown et al., 2004; Martinson and Omi, 2013).

Although fuel-reduction treatments are effective at reducing the likelihood of high-severity fire (Fulé et al., 2012; Martinson and Omi, 2013; Stephens et al., 2012), it is less clear that they meet ecological objectives such as enhancing the diversity of native understory species. Recent reviews and meta-analyses highlight the lack of predictability in understory responses to thinning and burning (Abella and Springer, 2015; McIver et al., 2013; Schwilk et al., 2014; Willms et al., 2017). In this paper, we examine how the spatial and temporal scales over which

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responses are measured can contribute to this uncertainty. Both factors have been examined individually, but typically over short time frames (2–5 years; [Abella and Springer, 2015](#); [Willms et al., 2017](#)). Rarely have they been considered together using multi-scaled, longitudinal designs of sufficient duration to assess the longevity of short-term effects, the potential for lagged effects, or the consistency of temporal responses as spatial scales of observation change.

In addition to reducing fuel loads, restoration treatments in dry forests are often designed to enhance resource availability and habitat heterogeneity. Both objectives can be achieved by thinning from below (removing smaller stems) and retaining larger trees in patches to approximate the historical size distributions and spatial structures of these forests ([Harrod et al., 1999](#); [Larson and Churchill, 2012](#)). Patterns of tree removal thus generate patchy ground disturbance and increase the amount and heterogeneity of light and soil resources ([Grayson et al., 2012](#); [Sprugel et al., 2009](#)). Low-severity prescribed burning, alone or in combination with thinning, is used to consume fine fuels and kill smaller trees ([Brown et al., 2004](#); [Fulé et al., 2012](#); [Neary et al., 2005](#)). However, effects can vary with the continuity of fuels and the intensity or duration of heating ([Neary et al., 2005](#); [Wan et al., 2001](#)). This variation in the magnitude and spatial distribution of disturbance and resource change may, in turn, play a role in the timing and spatial scale of understory response to both types of treatments ([Abella and Springer, 2015](#)).

Vegetation responses to disturbance, whether positive or negative, can vary over time. By altering substrate conditions, light, and/or below-ground resources, mechanical thinning and prescribed burning are likely to cause changes in understory structure and diversity. Initially, these disturbances can reduce diversity by damaging, burying, or consuming plants. Alternatively, they can increase diversity by creating open space, stimulating germination, or enhancing resource availability ([Gundale et al., 2005](#); [Halpern, 1989](#); [Pyke et al., 2010](#)). The longevity of these effects can vary, in part, with disturbance severity or post-disturbance processes that are time-dependent (e.g., litter accumulation, seed dispersal, or vegetative regrowth). As a result, responses to thinning or burning may differ in the short and long term.

Similarly, responses to treatments can vary with the spatial scales at which they are observed. For example, species richness is scale-dependent, as are the mechanisms that regulate it ([Palmer and White, 1994](#); [Preston, 1962](#)). At local scales (e.g., the sizes of individual plants), dispersal and competition for resources may limit the number of species and the ability of new species to establish ([Huston, 1999](#); [Tilman, 1997](#)). At larger spatial scales, other mechanisms become important. Larger areas typically encompass greater habitat heterogeneity or resource (niche) diversity, and thus support a greater diversity of species ([Chesson, 2000](#); [Rosenzweig, 1995](#)). Larger areas also increase the probability of establishment and decrease the likelihood of extinction ([MacArthur and Wilson, 1967](#); [Preston, 1962](#)). The ways in which fuels treatments mediate these scale-dependent processes will affect the spatial scales at which treatment responses are detected. For example, burning may increase richness at smaller scales by creating open space and reducing competition, promoting recruitment from the local species pool and greater ‘species packing’ ([Fig. 1](#), scenario 1). Conversely, burning may increase richness at larger scales by increasing habitat heterogeneity, allowing species with different regeneration requirements to colonize from the regional species pool (scenario 2). Alternatively, burning may increase richness at both spatial scales, either concurrently, or over time, depending on the proximity of seed sources (scenario 3).

Species’ responses to disturbance are shaped by their life histories, growth forms, and physiological traits ([Halpern, 1989](#); [McIntyre et al.,](#)

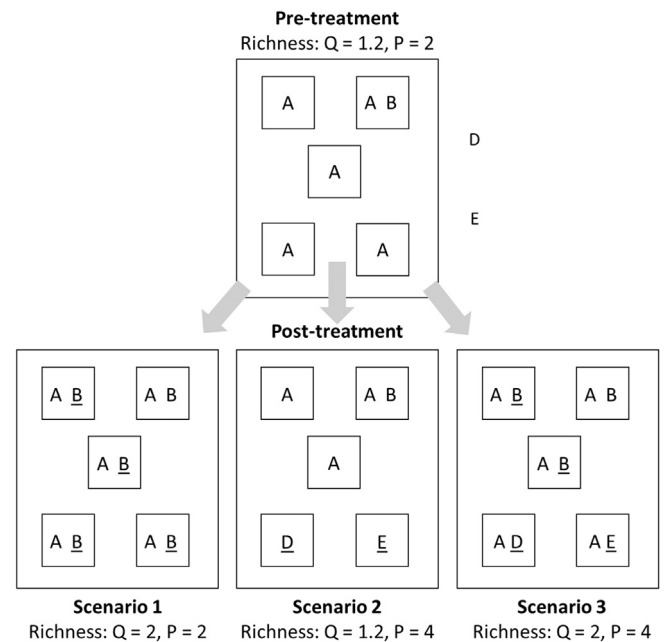


Fig. 1. Three scenarios in which prescribed burning enhances richness at different spatial scales via colonization (or loss) from the local or regional species pool (e.g., D and E). Spatial scales are ‘small’ quadrats (Q) and ‘large’ plots (P). Letters are different species; underscore indicates a colonization event. In scenario 1, small-scale richness (mean of quadrats) increases through local dispersal, but large-scale richness (cumulative number of species) does not. In scenario 2, small-scale richness does not change, but large-scale richness increases via dispersal from the regional species pool. In scenario 3, richness increases at both spatial scales.

1995; [Noble and Slatyer, 1980](#); [Pyke et al., 2010](#); [Rowe, 1981](#)). Persistence through thinning or burning requires that species can tolerate physical damage or burial, high temperature or prolonged heating, or abrupt changes in microclimate ([Flinn and Wein, 1977](#); [McLean, 1969](#); [Nelson et al., 2007](#); [Pyke et al., 2010](#)). Following damage by thinning or fire, many forest perennials can resprout from buried stems, roots, or rhizomes ([Rowe, 1981](#); [Sobey and Barkhouse, 1977](#)), thus stabilizing diversity through disturbance. However, colonization by new species requires a seed source (and the ability to germinate and survive in the post-treatment environment) or traits that promote vegetative spread. The reproductive traits of annuals—high fecundity, long-distance dispersal, and maintenance of a seed bank—confer an advantage in newly disturbed environments ([Halpern, 1989](#); [Pyke et al., 2010](#); [Zouhar et al., 2008](#)). However, as litter accumulates and competition from perennials increases, annual reproduction from seed may become a liability.

Non-natives (typically annuals) may be particularly responsive to disturbance, thus able to compete with natives for space and resources ([D’Antonio, 2000](#); [Hobbs and Huenneke, 1992](#); [Zouhar et al., 2008](#)). As a consequence, invasion by non-natives is a common concern in dry forest restoration ([Keeley, 2006](#); [Willms et al., 2017](#)). Whether non-natives are able to establish or spread in newly disturbed environments may depend on numerous factors: propagule availability, the novelty of species’ life-history traits ([Hamilton et al., 2005](#); [Vitousek et al., 1987](#)), characteristics of the resident community (e.g., biotic resistance; [Huston, 1999](#); [Tilman, 1997](#)), resource availability or heterogeneity ([Davies et al., 2005](#); [Levine and D’Antonio, 1999](#)), and how disturbance disrupts or alters these local and larger-scale controls ([Belote et al., 2008](#); [Fridley et al., 2007](#)). If restoration treatments promote invasion

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