

Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains

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Abstract: Large-scale wildfires ($\sim 10^4$ – 10^6 ha) have the potential to eliminate seed sources over broad areas and thus may lead to qualitatively different regeneration dynamics than in small burns; however, regeneration after such events has received little study in temperate forests. Following a 200 000 ha mixed-severity wildfire in Oregon, USA, we quantified (1) conifer and broadleaf regeneration in stand-replacement patches 2 and 4 years postfire; and (2) the relative importance of isolation from seed sources (live trees) versus local site conditions in controlling regeneration. Patch-scale conifer regeneration density (72%–80% Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)) varied widely, from 127 to 6494 stems·ha⁻¹. Median densities were 1721 and 1603 stems·ha⁻¹ 2 and 4 years postfire, respectively, i.e., ~ 12 times prefire overstory densities (134 stems·ha⁻¹). Because of the complex burn mosaic, $\sim 58\%$ of stand-replacement area was ≤ 200 m from a live-tree edge (seed source), and $\sim 81\%$ was ≤ 400 m. Median conifer density exceeded 1000 stems·ha⁻¹ out to a distance of 400 m from an edge before declining farther away. The strongest controls on regeneration were distance to live trees and soil parent material, with skeletal coarse-grained soils supporting lower densities (133 stems·ha⁻¹) than fine-grained soils (729–1492 stems·ha⁻¹). Other site factors (e.g., topography, broadleaf cover) had little association with conifer regeneration. The mixed-severity fire pattern strongly influenced the regeneration process by providing seed sources throughout much of the burned landscape.

Résumé : Les grands feux ($\sim 10^4$ à 10^6 ha) peuvent éliminer les sources de semences sur de vastes superficies et peuvent donc provoquer des dynamiques de régénération qualitativement différentes de celles qui résultent des feux de moindre importance. Cependant, la régénération qui s'établit après de tels événements a fait l'objet de peu d'études dans les forêts tempérées. À la suite d'un feu de sévérité variable qui a brûlé une superficie de 200 000 ha en Oregon, aux États-Unis, nous avons quantifié : (1) la régénération de conifères et de feuillus établie dans les parcelles de terrain où le feu avait complètement détruit la forêt, deux et quatre ans après le passage du feu et (2) l'importance relative de l'isolement par rapport aux sources de semences (arbres vivants) et des conditions locales de station pour l'établissement de la régénération. À l'échelle des parcelles, la densité de la régénération de conifères (composée de 72 à 80 % de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) était très variable, passant de 127 à 6494 semis·ha⁻¹. Deux et quatre ans après le passage du feu, la densité médiane était respectivement de 1721 et 1603 semis·ha⁻¹, ce qui correspond à environ 12 fois la densité du couvert dominant avant le passage du feu (134 tiges·ha⁻¹). À cause de la mosaïque complexe du feu, environ 58 % de la superficie où le feu avait complètement détruit la forêt était située à 200 m ou moins de la bordure d'une forêt (source de semences) et 81% de cette superficie était située à 400 m ou moins. La densité médiane de conifères était supérieure à 1000 semis·ha⁻¹ jusqu'à une distance de 400 m de la bordure d'une forêt et diminuait par la suite. L'établissement de la régénération était surtout influencé par la distance des arbres vivants et par le matériau d'origine du sol. Les sols squelettiques à texture grossière supportaient des densités moins élevées (133 semis·ha⁻¹) que les sols à texture fine (729 à 1492 semis·ha⁻¹). Les autres variables de la station (p. ex. la topographie et le couvert de feuillus) avaient peu d'impact sur l'établissement de la régénération de conifères. La sévérité variable du feu a fortement influencé l'établissement de la régénération en fournissant des sources de semences sur la majeure partie du territoire brûlé.

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Introduction

In many temperate forests, fires generate and maintain ecosystem structure, in part, by regulating tree establishment

(Agee 1993; Turner et al. 1997). Patterns of conifer regeneration after wildfire strongly influence future succession, plant community composition, and wildlife habitat. Postfire regeneration has thus been of basic interest to ecologists

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and land managers for decades (e.g., Franklin and Hemstrom 1981; Isaac and Meagher 1936; Shatford et al. 2007). Recent increases in the occurrence of large wildfires have heightened this interest (see GAO 2006), and considerable uncertainty exists regarding the capacity of forests to regenerate following fires that burn over large landscapes ($\sim 10^4$ – 10^6 ha).

Conifer regeneration is governed by the interaction between seed availability (supply-side control) and favorable microsites for germination and survival (site-factor control) (Bonnet et al. 2005; Galipeau et al. 1997). Seed availability for species with wind-dispersed seeds typically shows a negative exponential decline with increasing distance from seed source (Greene and Johnson 2000). For species reliant on regeneration from live-tree seed sources, this dispersal pattern leads to abundant regeneration near burn edges and less in patch interiors (Bonnet et al. 2005; Greene and Johnson 2000). Local site factors, including both abiotic (e.g., topography, soils, precipitation) and biotic (e.g., interspecific competition) conditions, act as a filter between seedfall and seedling establishment. For example, soil moisture is a highly important factor for regenerating seedlings, and water stress may reduce conifer establishment even if seedfall is abundant (Minore and Laacke 1992; Tappeiner et al. 1992).

Large wildfires have the potential to remove seed sources over broad areas because of their sheer size. Thus, seed supply may be the main limiting factor for regeneration in these burns. Lack of conifer regeneration could consequently alter successional patterns compared with those resulting from smaller fires (Romme et al. 1998; Turner et al. 1997). Although the occurrence of large fires has increased recently — with large fires now accounting for much of the area burned in North America — the historically low frequency of extremely large events (e.g., $> 100\,000$ ha) has made opportunities for study rare (Turner et al. 1998). Most research has been conducted in boreal regions, where large stand-replacing fires have predominated (e.g., Galipeau et al. 1997; Greene et al. 1999; Johnstone et al. 2004). Surprisingly few studies have quantified regeneration following such wildfires in temperate North America; examples of those that have include the 1933 Tillamook Burn in the Oregon Coast Range (Isaac and Meagher 1936) and the 1988 Yellowstone fires (Turner et al. 1997). Although a rich (and relevant) literature exists on postfire regeneration following small- to meso-scale events (e.g., Bonnet et al. 2005; Chappell and Agee 1996; Larson and Franklin 2005; Lyon and Stickney 1976; Shatford et al. 2007), little study has been conducted on how seed-supply versus site-factor controls may differ following very large ($> 100\,000$ ha) temperate wildfires.

An important aspect of many temperate forests is the mixed-severity fire regime (Agee 1993; Chappell and Agee 1996; Lentile et al. 2005; Schoennagel et al. 2004), which is among the most complex and poorly understood disturbance types. A mix of surface, torching, and running crown fire behavior within and among fires leads to complex patch structure at multiple scales. Mixed-severity fires often contain much more internal edge between live and dead vegetation than either high-severity (stand-replacement) or low-severity (surface) fires (Lentile et al. 2005). The resulting severity mosaic influences regeneration via the distribution

of postfire legacies, seed sources, and patch environments (Chappell and Agee 1996; Turner et al. 1998).

In 2002 the Biscuit Fire burned in a mosaic pattern over 200 000 ha of mixed-evergreen forest in the Klamath–Siskiyou Mountains, Oregon (USA), presenting an important opportunity to study regeneration following a large mixed-severity wildfire. Across a broad range of environmental conditions, we quantified regeneration of conifers and associated vegetation in stand-replacement patches 2 and 4 years after fire. We addressed the following research questions: (1) What are early patterns of density, distribution, and composition of conifers and associated vegetation in stand-replacement patches? (2) In the context of a large burn mosaic, what is the distribution of seed sources relative to stand-replacement areas? (3) What abiotic and biotic site factors are most important in predicting initial conifer abundance, and how important are these site factors compared with potential seed supply limitations? In addition to providing basic ecological insight, increased understanding of the factors controlling postfire conifer regeneration will aid land managers allocating limited resources to achieve reforestation objectives following large fires.

Methods

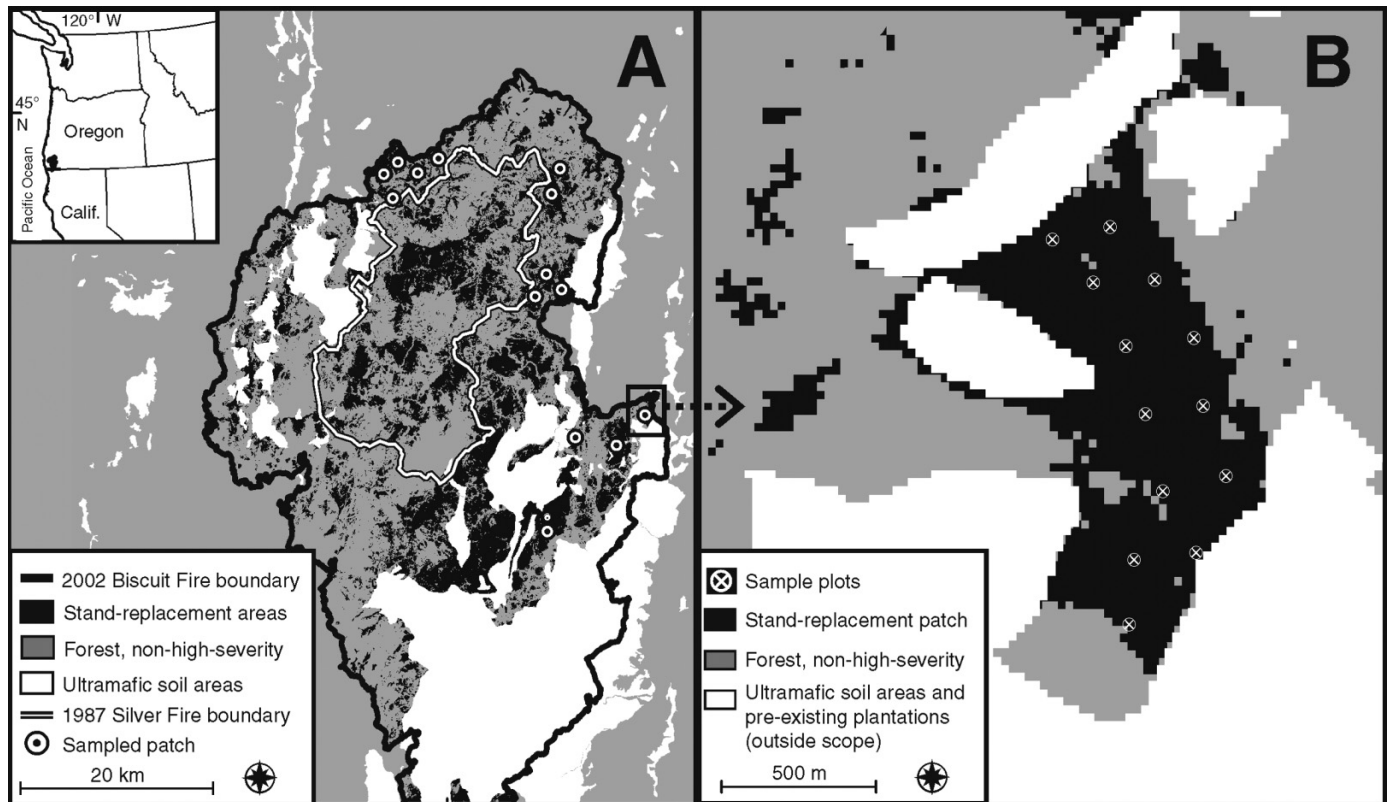
Study area

The Klamath–Siskiyou region of southwest Oregon and northern California comprises the most diverse forest flora of western North America (Whittaker 1960), due, in part, to sharp climatic and topoedaphic gradients. The region is characterized by a Mediterranean-type climate with warm, dry summers (mean max. July temperature: 27 °C) and cool, wet winters (mean min. January temperature: 2 °C); mean annual precipitation ranges from 140 to 500 cm over the burn area, less than 15% of which falls from May to September (Daly et al. 2002; <http://prism.oregonstate.edu>). Forest composition is characteristic of the mixed-evergreen and *Abies concolor* zones (Franklin and Dyrness 1973), dominated by conifers Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*); evergreen hardwoods tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), and canyon live oak (*Quercus chrysolepis*); and shrubs greenleaf manzanita (*Arctostaphylos patula*) and snowbrush (*Ceanothus velutinus*). Less common conifer species include the endemic weeping spruce (*Picea breweriana*), an Arcto-Tertiary relict restricted to cool, wet sites of low evaporative demand, and the fire-dependent, relatively short-lived knobcone pine (*Pinus attenuata*), which has been in decline in the region since the onset of fire suppression (~ 1940).

Regeneration mechanisms for local hardwood and shrub species include resprouting, in situ soil seed banks, and seed dispersal from off-site live sources; conifers regenerate primarily via wind dispersal of seeds from off-site live sources. In situ seed banks for conifers, either aerial (serotinous cones) or stored in soil, are important primarily for knobcone pine, though they may occasionally play a role for other species (see, e.g., Larson and Franklin 2005).

Major vegetation types in the Klamath–Siskiyou region (locally referred to as plant association groups) reflect gradients in precipitation and elevation and are often used as a

Fig. 1. (A) The 2002 Biscuit Fire burned over 200 000 ha of mixed-evergreen forest, imparting a complex mosaic of mortality and survivorship on the landscape. Regeneration was sampled in stand-replacement patches. Ultramafic soil areas and preexisting plantations were not examined. For regeneration data in the Silver–Biscuit overlap area, see Donato (2008). (B) Example of sampling layout in a typical stand-replacement patch. Plots were spaced at ~250 m intervals along elevational contours. Spatial data courtesy of Rogue River – Siskiyou National Forest; see USDA (2004).



stratification tool for regeneration management (Atzet et al. 1992). These vegetation types include low- to mid-elevation dry sites in the eastern portion of the burn (tanoak–oak and Douglas-fir associations, respectively), low- to mid-elevation wetter sites in the western portion of the burn (tanoak associations), and high-elevation sites distributed throughout the burn (white fir associations) (USDA 2004). Other distinct vegetation types occur on ultramafic (serpentine) soils, which cover ~23% (45 000 ha) of the burn area; these types have a unique ecology (Whittaker 1960) and are outside the scope of this study.

Fire history

Fire regimes in the Klamath–Siskiyou region are complex, typically described as low to mixed severity, with fire intervals ranging from 5–35 years in drier vegetation types to 50–200 years in higher elevation and wetter types (Agee 1991, 1993; Stuart and Salazar 2000; Taylor and Skinner 1998; USDA 2004; Wills and Stuart 1994). Variable fire intervals, extents, and severities lead to complex forest age structures and successional pathways. Even-aged overstory cohorts are generally attributed to past stand-replacement fire patches (Agee 1993; Wills and Stuart 1994). The frequency of large (>10⁴ ha) fires is not well quantified, but such fires are thought to have occurred historically (Agee 1993). The proportion of a burn area experiencing stand replacement is known to vary among fire events, vegetation

types, and topographic positions and has been reported as ~10%–30% (Taylor and Skinner 1998).

The Biscuit Fire, the largest forest fire on record for the state of Oregon and among the largest in modern United States history, burned for 4 months between July and November of 2002 over a wide range of vegetation, topography, and weather conditions. Varying degrees of surface, torching, and active crown fire behavior resulted in a complex spatial mosaic of tree mortality and survivorship (Fig. 1). Stand replacement (high severity) occurred in patches up to ~13 000 ha, with a skewed patch-size distribution (median patch sizes were ~100–300 ha depending on scale definition and aggregation) and highly variable patch shapes (US Forest Service GIS data; Fig. 1). Total stand-replacement area of the Biscuit Fire, which at times burned under extreme weather conditions and occurred after a 60 year period of effective fire suppression, was estimated at 84 000 ha (42% of 200 000 ha burn area) based on remotely sensed vegetation change, with an agency accuracy assessment of >90% (USDA 2004).

Sampling design

Scope

We sampled across a representative range of biotic and abiotic conditions within the Biscuit Fire (Table 1), with an approach similar to those of Isaac and Meagher (1936) and

Table 1. Sampled range of biophysical characteristics and relation to Biscuit Fire area.

Biophysical characteristic	Sampled range (mean)	Proportion of Biscuit Fire area within sampled range (%)	Source
Mean annual precipitation	178–381 cm (287 cm)	93	PRISM Group, Oregon State University, http://prism.oregonstate.edu
Soil types	Coarse-grained igneous, metasedimentary, metavolcanic	95	US Forest Service GIS data; USDA 2004; http://www.gis.state.or.us/data/alphalist.html
Plant association group	Tanoak moist, tanoak dry, Douglas-fir, white fir	98	Atzet et al. 1992; USDA 2004
Aspect	All	100	10 m DEM
Slope*	12°–41° (28°)	88	10 m DEM
Elevation†	490–1368 m (1004 m)	80	10 m DEM
Distance to contiguous seed source‡	≤552 m (240 m)	89	US Forest Service GIS data; digital orthoquad aerial photos; Fig. 3

Note: Statistics exclude areas of ultramafic soil and associated communities, which constitute ~23% (45 000 ha) of the Biscuit Fire area. Also omitted is the 4.7% (9400 ha) of the burn area in California (much of which is ultramafic as well) because of limited data availability. We make no inference to these areas. DEM, digital elevation model.

*Areas flatter or steeper than sampled range are primarily riparian or ridgetop (flatter), or nonstockable rocky cliffs (steeper).

†Nearly all of the unsampled remainder is at 200–490 m elevation, primarily along the lower Illinois and Chetco rivers.

‡Percentage based on stand-replacement portion only to avoid influencing estimate with areas of substantial canopy survival. If all severities are included, estimate is ~96%.

Turner et al. (1997). In this study, sampling was carried out in conjunction with a study of postfire management, and the particular patches sampled were identified a priori by the Biscuit Fire Recovery management plan (USDA 2004). These sites captured much of the range in major biophysical gradients and conditions within the Biscuit Fire (Table 1). Thus, we expect they provide a reasonably representative picture of regeneration in much (but not all) of the burn area and most importantly afford analysis of how regeneration varies across these gradients.

Study areas were upland slopes covered in mature to old-growth conifer-dominated forest (generally >100 years old; see Agee (1993); Thornburgh (1982) for developmental-structural descriptions) that experienced stand-replacement fire — defined as ≥75% overstory conifer mortality (USDA 2004), top-kill of all understory and surface layer vegetation, and combustion of most ground layer organic matter. We excluded extremely steep rocky areas, riparian zones, ultramafic soil areas, and preexisting plantations and shrub fields. For conifer regeneration in the Silver-Biscuit “reburn” area, see Donato et al. (2009).

Annual climatic variation, especially for precipitation, may be large and thus can strongly influence a study’s scope of inference. Regenerating conifers require sufficient moisture for flower development, seed and cone maturity, germination, and early growth and survival. To relate the years we sampled to the long-term climate record, we summarized precipitation patterns using local climate data (Daly et al. 2002; PRISM Group, Oregon State University, <http://prism.oregonstate.edu>) for the five growing seasons from 2002 to 2006 (Appendix A). Precipitation during the period was generally within a characteristic envelope (27 of 30 months were within one standard deviation of the 30 year mean) but overall was relatively dry, with 24 of 30 months below average, and no year with >1 wet month except for the spring of 2005 (Appendix A).

Sampling

We sampled regeneration in 11 stand-replacement patches in the Biscuit Fire (identified a priori based on agency management plan; range of patch sizes 15–13 000 ha, median ~180 ha), surveying 60 plots (1–12 per patch, mean 5.5). These patches represented ~40% of the nonserpentine high-severity burn area. Within each burn patch, sample plots were located systematically at 250 m intervals along elevational contours beginning from a random start point. Burn patches were saturated with sample plots, notwithstanding constraints of patch size, remote or unsafe access, and the presence of conditions outside the study scope (Fig. 1).

To best assess spatial variability in conifer regeneration, sample plots were surveyed using two complementary approaches. In every plot, conifer seedlings were measured in a central 5 m radius circular subplot. In approximately every fifth sample plot, conifer seedlings were also measured in four 75 m × 0.5 m rectangular subplots radiating from plot center in the subcardinal directions. Plots were chosen to receive additional sampling based solely on their proximity to proposed logging units (as these plots served as controls for an associated study on management effects) and were not systematically different from the rest of the burn patch in terms of stand characteristics (Donato 2008). The single circular subplot, based on regional regeneration survey protocols (USDI 2003), affords an efficient way to assess frequency (i.e., presence-absence or stocking) at the burn-patch scale via widely dispersed sample plots. The supplementary long rectangular subplots more effectively capture heterogeneity in microsites and obtain a more precise estimate of plot-scale seedling density (Elzinga et al. 1998). We verified that rectangular subplots yield higher precision (mean coefficient of variation (CV) 62%) than four circular subplots (mean CV 80%) with highly similar point estimates between the two methods (paired *t* test: $t_{23} = 0.73$, $P = 0.47$, mean ratio of estimates = 1.07).

Sampling and analysis were focused primarily on 2006 data, 4 years postfire. These data represented the largest sample size ($n = 60$ plots across 11 burn patches) and the latest year of measurement and thus stand establishment. A smaller set of plots ($n = 25$ across 11 burn patches) was measured in 2004, 2 years postfire; these data were used to augment the 2006 data by quantifying early patterns of establishment. Not all 2004 plots were in common with the 2006 sample because postfire logging between sampling years eliminated 14 of 25 plots from suitability for this study. Thus, in terms of comparability, the two sampling years do not represent an identical population tracked between years, rather they provide a measure of broad-scale temporal regeneration patterns after the fire.

For each seedling encountered we recorded species, height, age by whorl count, and rooting substrate. Concurrent measurements in each plot (site factors) included percent cover, height, and canopy volume of all hardwoods and woody shrubs by species; percent cover of all forbs and low (suffrutescent) shrubs by species; percent cover of ground substrates (litter, exposed mineral soil, rock >1 cm diameter, woody detritus, moss-lichen); and density, diameters (DBH), and species of all fire-killed conifers and hardwoods >10 cm DBH as a measure of prefire stand condition. Environmental parameters recorded for each plot included elevation, slope, aspect, soil parent material (USDA 2004), plant association group (Atzet et al. 1992), and estimated mean annual precipitation (Daly et al. 2002). Aspect was mathematically folded about the southwest-northeast axis so that southwestern slopes were assigned the highest (warmest) value and northeastern slopes, the lowest (coolest) value; then aspect was combined with slope to create one continuous variable estimating potential annual solar heat load for each plot (<http://oregonstate.edu/~mccuneb/radiation.htm>).

To assess patch-scale regeneration distribution (frequency-stocking), we recorded whether each seedling fell within a 3.6 m radius inner circle (allowing an estimate of occupancy at smaller scale of 0.004 ha or 1/100 acre; USDI 2003). For plot-scale distribution, we quantified spatial pattern — uniform, clumped, or random — via the spatial C-statistic, which is based on field-measured nearest-neighbor distances (subplot center → nearest seedling → nearest next seedling beyond) (see USDI 2003).

Seed source data

Potential seed source availability was assessed for each plot by recording the distance to the nearest contiguous patch of live mature conifers (>25% overstory survival over area >1 ha) using 2003 digital orthoquad aerial photos, geospatial data, and field checking. We also recorded whether the patch was above or below the plot in elevation. Isolated remnant trees and small patches could not be reliably identified with the available data but are an inherent feature of stand replacement as commonly defined (i.e., 70%–90% overstory mortality and therefore up to 10%–30% survival). Therefore, the metric we used is a measure of isolation in a stand-replacement patch relative to surrounding areas of contiguous live trees (hereafter, “live-tree edge”).

We also used Forest Service GIS data to perform a landscape analysis on the isolation of stand-replacement portions

of the Biscuit Fire relative to areas of surviving trees, similar to the approach of Turner et al. (1994). We identified areas of potential seed source, defined as medium- to large-sized conifer-dominated forest with substantial survivorship (i.e., low to moderate fire effects per the fire severity layer, <75% mortality). We then estimated the Euclidean distance from each 30 m pixel of stand replacement to the nearest edge of the seed source layer. Finally, we constructed a cumulative frequency diagram of these distances for the entire stand-replacement portion of the Biscuit Fire. Ultramafic soil areas and the combined 6% of the burn in California or on Bureau of Land Management land (insufficient spatial data) were excluded, with the conservative assumption that these areas provided no seed source for dominant tree species in the remainder of the burn.

To augment the agency accuracy estimate of >90% for the fire severity layer (USDA 2004), we further validated both the fire severity and seed source layers via cross-referencing with digital orthoquad aerial photos (sample of 80 random points yielded similar accuracy of >90%), additionally checked via opportunistic field surveys from road, trail, and off trail. Nonetheless, spatial data over large heterogeneous domains such as the Biscuit landscape will typically contain inaccuracies for fine-scale entities such as small, isolated patches of surviving trees. We therefore developed a range of estimates, one based on original Forest Service data and a second more conservative estimate based on adjustments that excluded seed sources <1 ha in size (to eliminate possibility of false positives for small seed sources) and stand-replacement patches <10 ha in size (to eliminate edge influence of very small patches).

Data analysis

We investigated seed-source versus site-factor controls on conifer regeneration density using mixed effects regression models evaluated within an information theoretic framework (Burnham and Anderson 2002). Analysis was conducted using data collected 4 years postfire. To account for the lack of spatial independence among plots within each patch, we used hierarchical mixed linear regression models with penalized quasi-likelihood to determine parameter estimates for the influence of each variable on seedling density. These models penalize estimated standard errors for dependence within groups (i.e., patches), making them appropriate for the analysis of clustered, spatially dependent data. Groups were allowed to vary randomly, and all other variables were treated as fixed effects. Analysis was implemented in R version 2.5.1 (<http://www.R-project.org>, accessed October 2007) using the `glmmPQL` function in the `MASS` package (Venables and Ripley 2001). Because conifer seedling densities were typically positively skewed, data were $\log_e(x + 1)$ transformed to better meet distributional assumptions (Larson and Franklin 2005; Ramsey and Schafer 2002). We also accounted for positive skew by reporting patch-scale seedling densities as median values. Residuals and model fits were checked using residual versus fit diagnostics described by Ramsey and Schafer (2002).

Our approach was to assess the importance of distance to nearest live-tree edge relative to 11 site-factor variables (Table 2). The latter comprised local factors affecting germination substrate, water, light, and nutrient resources for re-

Table 2. Predictor variables assessed in regression analyses.

Variable	Units
Supply side	
Distance to nearest live-tree edge (seed source)	m
Site factors	
Biotic	
Forb – low-shrub cover	%
Hardwood – woody shrub cover	%
Crown-scorch indicator (vs. crown consumed)	1–0
Standing-dead basal area	m ² ·ha ⁻¹
Abiotic	
Slope	degrees
Annual solar heat load index (aspect proxy)	unitless
Elevation	m
Estimated mean annual precipitation	cm
Substrate	
Surface cover of exposed mineral soil	%
Surface cover of rock	%
Coarse-grained igneous soil indicator	1–0

generating seedlings (see Isaac and Dimock 1960 and references therein). We included an indicator variable for soil originating from coarse-grained igneous parent materials; these soils are typically skeletal (>40% rock fraction), very well-drained, and experience prolonged drought during the growing season (other soils within the study area are typically more loamy and derived from finer grained metasedimentary and metavolcanic materials) (see USDA 2004, <http://nrcs.gov>). Because the number of variables was large relative to sample size, we performed the analysis in two steps. First, univariate regression models of seedling density versus each of the 11 site variables were ranked based on their model weights (weight of evidence supporting a particular model given the data and model set; see Burnham and Anderson 2002). Second, the top six site variables were then tested against the seed source variable using an all subsets approach to give equal consideration to all variables. Models with more than five predictors (in addition to the intercept), or interaction terms, were excluded from analysis because of modest sample size, resulting in a set of 120 candidate models.

Models were evaluated using an information theoretic framework, in which the relative support in the data for hypotheses (in the form of models) was assessed with the Akaike information criterion (Burnham and Anderson 2002). We applied the small sample size correction (AIC_c) to all AIC calculations (see Burnham and Anderson 2002). Conditional parameter estimates and 95% confidence intervals for each predictor were computed for each model. These estimates, coupled with relative importance (RI) values obtained by summing weights (w_i) of the models containing each predictor, were used to rank the importance of the predictors on regeneration density (Burnham and Anderson 2002).

Results

Overall density, distribution, and composition

Across both sample years, conifer regeneration density in individual plots ranged over five orders of magnitude, from 0 to 12 987 stems·ha⁻¹. Median density within each burn

patch ($n = 11$) ranged from 303 to 4190 stems·ha⁻¹ 2 years after fire and from 127 to 6494 stems·ha⁻¹ 4 years after fire (Table 3). Averaging these median values across all patches yielded a study-wide mean of 1721 and 1603 stems·ha⁻¹ in 2004 and 2006, respectively — approximately 12 times the mean prefire overstory density of 134 stems·ha⁻¹ (Table 3).

Regeneration was detected in all sampled patches (Table 4). Within patches, a mean of 90% (range 60%–100%) of plots were occupied; this parameter adjusts to 69% (29%–100%) if only trees >20 cm height are considered (Table 4). Within plots, spatial distribution of seedlings was random rather than regular or clumped (Table 4).

Regeneration composition was similar to prefire overstory composition, dominated by Douglas-fir (72%–80% in 2004–2006), followed by white fir and sugar pine (2%–10%) (Table 3). The primary exception was knobcone pine, which constituted ~14% (mean) of regeneration but was rarely detected in the survey of prefire stems (Table 3). No weeping spruce seedlings were detected (survey of prefire stems showed three patches with weeping spruce prior to fire). Species present at low frequency included incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), and red fir (*Abies magnifica* var. *shastensis*). Most plots contained one to three conifer species (Table 3); a maximum of six were detected in one 5 m radius plot.

By 2 years postfire, hardwoods and woody shrubs combined attained a mean cover of 25% (range 9%–49%), and forbs and low shrubs combined attained 34% mean cover (4%–85%) (Table 3). By 4 years, hardwood–shrub cover averaged 33% (4%–63%), and forb – low-shrub cover averaged 48% (5%–197%). Grouped by vegetation type (management bins; Table 5), wetter associations had higher forb – low-shrub cover (42%–53%) but less hardwood–shrub cover (21%–37%) than drier types (14%–19% and 46%–51%, respectively). Broadleaf species were taller than conifers in all types (Table 5), suggesting their likely dominance during early succession; this differential was greatest in west-side low-elevation associations and slightest in high-elevation associations.

Regeneration timing and early survival

Regeneration was a continual process, occurring all 4 years after fire (Fig. 2). However, the second year after fire, 2004, was by far the major year of conifer establishment (Fig. 2). This pattern was driven by Douglas-fir and white fir, while the serotinous-coned knobcone pine regenerated primarily in the first year. Age structure in the first 4 years was hump-shaped rather than the J-shape typical of annual-turnover populations (Fig. 2). Data from plots measured in both sample years indicated a mean survival rate for the main cohort of 67% between postfire years 2 and 4. This relatively low mortality rate, coupled with continued seedling establishment, kept overall densities high (Fig. 2, Table 3).

Seed source distribution and relations

The complex burn mosaic resulted in potential seed sources distributed throughout most of the burn (Figs. 3–4). The range of estimates indicated that 46%–70% of stand-replacement burn area was within 200 m of a live-tree edge, and 71%–90% was within 400 m (excluding serpen-

Table 3. Patch-scale abundance and composition of conifers and associated vegetation, before and 2–4 years after the Biscuit Fire.

Time point	Conifers (trees·ha ⁻¹)	Plot-scale conifer species richness	Conifer composition (% of total density)				Hardwood- shrub abundance	Hardwood-shrub composition (% of total abundance)				% cover forbs and low shrubs*
			Douglas-fir	White fir	Sugar pine	Knobcone pine		Tanoak	Madrone	Canyon live oak	Chinquapin	
Prefire	134 (64-208)	2.2 (1-3)	82 (29-100)	5.4 (0-17)	10 (0-54)	0 (0-0)	198 (0-540) stems·ha ⁻¹	31 (0-80)	25 (0-88)	15 (0-79)	26 (0-100)	18 (12-25)
2 year postfire (2004)	1721 (303-4190)	2.3 (1-4)	72 (32-100)	3.8 (0-26)	9.2 (0-28)	15 (0-59)	25 (9-49) % cover	36 (18-61)	6.8 (0-28)	22 (0-56)	2.7 (0-14)	34 (4-85)
4 year postfire (2006)	1603 (127-6494)	1.7 (1-3)	80 (46-100)	5.7 (0-28)	1.6 (0-17)	13 (0-49)	33 (4-63) % cover	31 (0-68)	6.8 (0.2-44)	13 (0-40)	6.3 (0-14)	48 (5-197)

Note: Data are means (range) of patch-scale means, except conifer densities, which are from patch-scale medians to account for positive skew. Prefire densities are for overstory conifers >30 cm DBH and hardwoods >10 cm DBH. Postfire hardwood–shrub abundance is reported in percent cover because of highly coppiced postfire resprouts that render stem densities less meaningful. Other conifer species present in minor amounts include ponderosa pine, incense-cedar, and red fir. Other hardwood–shrub species present include snowbrush, deer brush (*Ceanothus integerrimus*), and manzanita spp.

*Unburned forb and low-shrub data from Donato (2008).

tine areas) (Figs. 3–4). Thus, of a 200 000 ha fire only 13 000–23 000 ha of nonserpentine area were farther than 200 m from surviving trees, and only 4200–12 000 ha were at distances exceeding 400 m.

Regeneration density was high across most of the measured range of distance to live-tree edge (62–552 m) (Fig. 5). Although the upper bounds of the data showed a negative exponential decline with increasing distance (Fig. 5), median densities declined only gradually, remaining above 1000 seedlings·ha⁻¹ with a threshold at 400 m, beyond which densities were below 300 seedlings·ha⁻¹ (Fig. 5 inset). Of the unoccupied plots, 75% were >400 m from live-tree edge. Elevation differential of the nearest potential seed source was not a major factor (Fig. 5). The overall pattern of density versus distance was driven by Douglas-fir, since it constituted the majority of seedlings. Only one seedling of the heavier seeded white fir was detected beyond 220 m distance. Sugar pine and knobcone pine were detected at all distances and did not show strong trends with distance.

Supply-side versus site-factor associations

The six site variables selected by analysis step 1 (univariate regressions) were the coarse-grained igneous soil indicator, rock cover, forb – low-shrub cover, hardwood–shrub cover, slope, and standing-dead basal area (see Appendix B for full outputs). When these variables were combined with seed source distance in an all-subsets analysis, the top-ranked model was (intercept + distance to live-tree edge + coarse-grained igneous soil) with a model weight of 0.13 (Table 6). The most important predictors by far were distance to live-tree edge (RI = 0.95) and the coarse-grained igneous soil indicator (RI = 0.88), both of which had negative parameter estimates and were the only variables with 95% confidence intervals (CIs) that excluded no effect (Table 6). Based on 95% CIs within the top models (Table 6), each metre of distance to live-tree edge was associated with a reduction in seedling densities of 0.1%–1%, and coarse-grained igneous soils had 5%–74% of the seedling densities occurring on other soils. Most of the explanatory power attained by this analysis was contained in this model ($R^2 = 0.45$); other variables added little. Hardwood–shrub cover and rock cover ranked as moderately important (RI = 0.47 and 0.40, respectively); both parameters were negative but had confidence intervals that included no effect (Table 6). Relatively unimportant correlates with seedling density were (decreasing order of importance) forb – low-shrub cover, slope, standing-dead basal area, mean annual precipitation zone, mineral soil cover, solar heat load index (aspect), elevation, and crown scorching (see Appendix A).

Discussion

Early density, distribution, and composition

Despite the large size of the burn, we observed abundant but spatially variable conifer regeneration following the Biscuit Fire (Table 3). Thornburgh (1982) suggests that in the Klamath–Siskiyou region where Douglas-fir establishes immediately after fire it will develop codominantly with resprouting broadleaf vegetation, and where seedling establishment is delayed or sparse, Douglas-fir will develop

Table 4. Mean ($\pm$ standard error, with range in parentheses) spatial pattern and frequency of conifer regeneration 4 years after stand replacement in the Biscuit Fire.

No. of patches	No. of plots within patches	Spatial C statistic*	% patches occupied	% plots occupied within patches	% plots occupied within patches (by trees ≥ 20 cm ht.)
11	5.5 $\pm$ 1.0 (1–12)	0.51 $\pm$ 0.03 (0.37–0.62)	100	90 $\pm$ 5.1 (60–100)	69 $\pm$ 8.6 (29–100)

Note: Occupancy is defined at minimum density of 250 stems·ha⁻¹ (see USDI 2003).

*Spatial distribution metric based on field-measured nearest-neighbor distances. Range 0–1 (0, uniform; 0.5, random; 1, highly clumped).

more slowly until emerging above broadleaf canopies. Given the wide variability in patch size, initial conifer density, and broadleaf cover after the Biscuit Fire (Fig. 4; Tables 3, 5), both pathways will likely operate in different portions of the burn. Many factors will influence stand development over time (e.g., competition, repeat fire); however, these data suggest these processes will act on a template of existing heterogeneity, formed early in the establishment phase. This fire-induced heterogeneity may contribute to the renowned biodiversity of the Klamath–Siskiyou region (Whittaker 1960).

Comparable regeneration has been reported after other large wildfires. In a Douglas-fir ecosystem in the Oregon Coast Range, Isaac and Meagher (1936) reported that 69% of sampled areas had natural conifer densities exceeding 1235 stems·ha⁻¹ 2 years after the 100 000 ha Tillamook Fire. After the $\sim$ 400 000 ha 1988 Yellowstone Fires, Turner et al. (1997) reported mean lodgepole pine (*Pinus contorta*) densities of $\sim$ 60 000 stems·ha⁻¹ (range 0 to >100 000), with high spatial variation in occupancy. Following large fires in mixedwood boreal forests (6000–17 000 ha), Greene and Johnson (1999) reported jack pine and black spruce seedling densities of $\sim$ 500 to >100 000 stems·ha⁻¹, depending on prefire conspecific basal area. In the latter two regions, cone serotiny in dominant species including lodgepole pine, jack pine (*Pinus banksiana*), or black spruce (*Picea mariana*) provides rapid in situ recolonization across large burned areas. Notably, nonserotinous conifers such as white spruce (*Picea glauca*) have also persisted for millennia in boreal regions under a regime of large-scale crown fires (Galipeau et al. 1997; Greene and Johnson 2000). By contrast, dry ponderosa pine forests of the interior United States often exhibit sparse regeneration in severe burns except near edges (e.g., Bonnet et al. 2005; Lentile et al. 2005). Heavy seeds and a general adaptation to smaller patch sizes, coupled with compositional changes due to fire exclusion (Agee 1993), likely contribute to lower seed availability in large burns in ponderosa pine forests. Thus, regeneration following large-scale fire is more expected in wetter forest types with longer fire-return intervals.

Within the Klamath–Siskiyou region, our observations are consistent with reports of conifer regeneration following several smaller wildfires (Shatford et al. 2007), as well as with several fire history studies reporting regeneration of distinct age cohorts following past stand-replacement fires (Agee 1991; Stuart and Salazar 2000; Taylor and Skinner 1998; Wills and Stuart 1994). Although regional heavy seed crops for Douglas-fir occur only every 3–11 years (Isaac and Dimock 1960), postfire regeneration is not solely tied to this

cycle, since establishment occurs across years of variable seed crops (Shatford et al. 2007). Conifers of the region possess advantageous reproductive and autecological traits for fires of both high and low severity (e.g., well-dispersed seeds, germination on mineral soil, thick bark, etc.) and are thus well suited to the mixed-severity fire regime of the region.

Early patterns indicate high temporal continuity in conifer species composition through fire (Table 3). Douglas-fir will likely continue to be the most abundant conifer in the majority of sites. This continuity may simply reflect the relative availability of seed sources for each species at the time of fire, or it may indicate that overstory composition in many mature forests was determined in large part by past fires. One notable change in species composition was the major establishment of knobcone pine, which had been in decline in the area since the onset of fire suppression. This fire-dependent species regenerates from serotinous cones (in situ aerial seed bank) and would be expected to increase after fire. Because of rapid growth and relatively short life-span, knobcone pine will be an important component of early- and mid-seral communities along with evergreen shrubs.

Regeneration timing and survival

Timing: relevance to seed source

Seeds for postfire conifer regeneration generally come from two potential sources: in situ seed banks (either in soil or in serotinous cones of fire-killed trees) or dispersal from residual live trees in and around a burn. These two sources may produce very different age structures because in situ seed banks are only viable for a short time — only 1 year for Douglas-fir seeds (Isaac and Dimock 1960) — while live trees can produce seed over several postfire years. The peak we observed in Douglas-fir regeneration during the second year (Fig. 2) indicates that most areas were seeded by live trees producing seed in 2003, rather than by in situ sources, which would have produced a peak in the first post-fire year. Conversely, knobcone pine regenerated primarily in the first postfire year, largely from an in situ canopy seed bank.

Early survival

This early cohort is the first in a larger continual dynamic of establishment and mortality over time (Shatford et al. 2007). The lack of a J-shaped age structure (Fig. 2) indicates establishment and early survival of a main cohort rather than successive annual pulses of regeneration with high turnover. The 2004 cohort had been present for three growing seasons at the time of 2006 sampling. Mortality of

Table 5. Plot-scale conifer regeneration and associated vegetation characteristics 4 years after the Biscuit Fire, by vegetation type.

Vegetation type*	Total conifer seedlings (stems·ha ⁻¹)	Proportion (%) of plots occupied at ≥250 stems·ha ⁻¹	Conifer regeneration composition†					Conifer seedling height (cm)	Shrub–hardwood cover (%)	Shrub–hardwood height (cm)	Forb – low-shrub cover (%)
			% Douglas-fir	% white fir	% sugar pine	% knobcone pine					
White fir associations (high elevation)	1401 (127–12987)	96	69 (0–100)	11 (0–67)	0 (0–1)	20 (0–100)	18 (8.2–41)	21 (2.5–71)	61 (20–160)	42 (1.5–197)	
Douglas-fir associations (mid-elevation, dry)	334 (0–1146)	75	75 (46–100)	0 (0–0)	2.6 (0–7.7)	23 (0–46)	13 (8.1–17)	46 (36–65)	139 (99–160)	19 (7.0–51)	
Tanoak–oak associations (low elevation, dry)	700 (0–2674)	88	79 (0–100)	0 (0–0)	5.0 (0–38)	14 (0–100)	16 (9.7–40)	51 (32–67)	125 (74–170)	14 (4.5–31)	
Tanoak associations (low to mid elevation, wet)	1146 (0–3565)	83	97 (58–100)	0.4 (0–3.8)	0 (0–0)	3.1 (0–42)	21 (13–47)	37 (0–75)	155 (90–204)	53 (1–101)	

Note: Data are means (range) of plot values, except for total conifer seedlings data, which are medians (range) of plot values.

*Vegetation type is based on super plant association groups (see USDA 2004).

†Other conifer species present in minor amounts include ponderosa pine, incense-cedar, and red fir.

Fig. 2. Conifer seedling establishment by year after the Biscuit Fire, based on age structure from whorl counts 4 years postfire (mean ± SE; median indicated by the black dot). Data represent the net balance of germination and mortality for each cohort as of year 4. Patch-scale median cumulative density by year four was 1603 ± 542 stems·ha⁻¹.

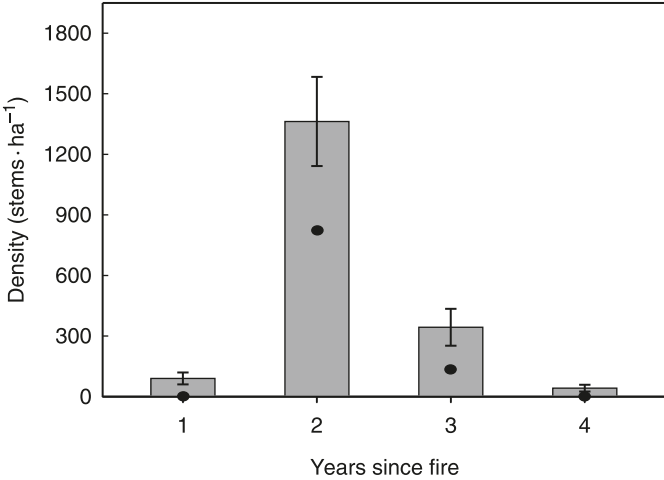
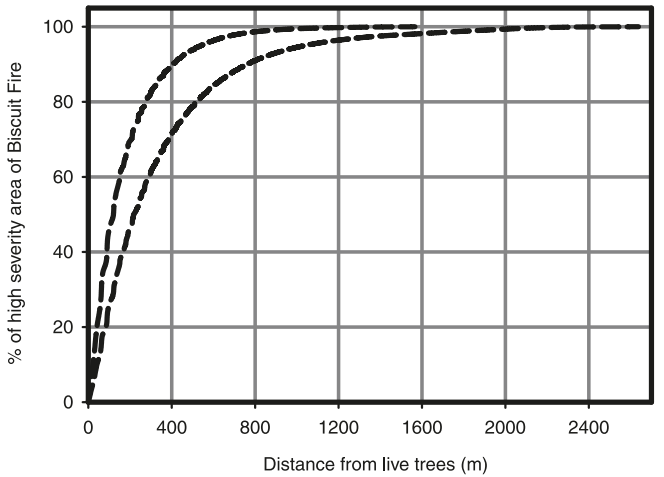


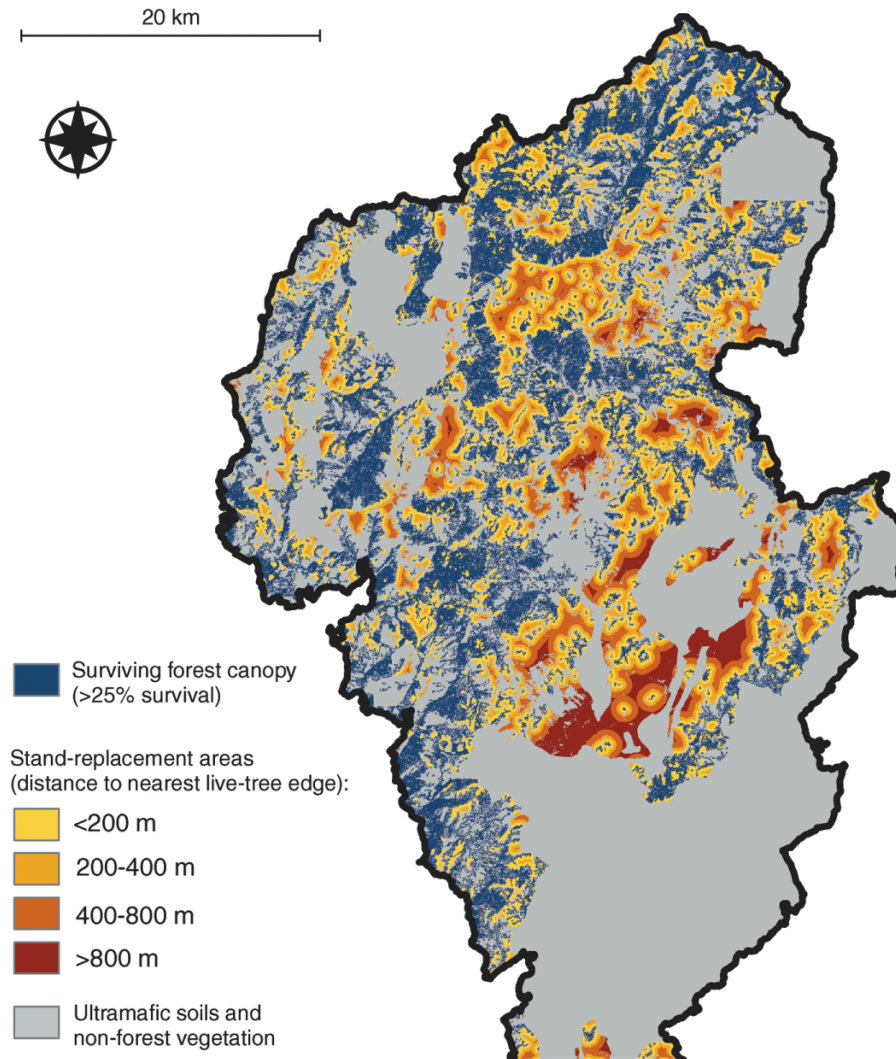
Fig. 3. Cumulative frequency diagram for distance of Biscuit stand-replacement area from patches of surviving trees. Range of estimates based on US Forest Service data using two different data treatments: upper curve was derived from original data; lower curve is a conservative estimate derived by excluding very small patches of surviving trees (<1 ha) and of stand-replacement burn (<10 ha), which eliminated the possibility of false positives for small seed sources and edge effects of small burn patches. Ultra-mafic soil areas were excluded from analysis.



natural seedlings is generally concentrated in the first growing season, leveling off by year 3 (e.g., Minore and Laacke 1992). Thus, the period of very high initial mortality has likely passed.

Interestingly, even during the first growing season for the major cohort (2004), seedling survival was high despite below-average precipitation that year (Appendix A). (High spring precipitation in 2005 may have contributed to second-year survival but is not likely to explain overall survivorship rates.) This observation differed from low

Fig. 4. Map of Euclidean distance between stand-replacement areas of the Biscuit Fire and adjacent patches of surviving trees (potential seed source). Ultramafic soils, nonforest vegetation, and areas with insufficient data (small areas in south and northeast corners) were excluded. Of the stand-replacement area, ~58% was within 200 m of a live-tree edge, and ~81% was within 400 m.



seedling survival in this region following timber harvests, which has been addressed by years of silvicultural research (Tappeiner et al. 1992 and references therein). Several reasons could explain high postfire survival. First, postfire environments are likely ideal for seedling establishment and survival given the evolutionary history of local conifers. Examples include increased light, nutrients, and mineral soil seedbeds; a period of reduced hardwood–shrub leaf area; and mycorrhizal associations between conifer seedlings and resprouting hardwoods (Borchers and Perry 1990). Second, postfire sites contain abundant snags lending “dead shade”, which, by reducing direct solar insolation and evaporative stress, increases seedling survival (Minore 1971). Third, past reforestation research in southwest Oregon has typically focused on sites most difficult to regenerate (e.g., hot, dry slopes at low elevation); the Biscuit Fire comprises a full range of site conditions including large portions in higher elevation and mesic areas. By this measure, conditions in the Biscuit Fire are broader than the scope of those studies. Fourth, naturally regenerated conifers allocate much of their initial growth below-

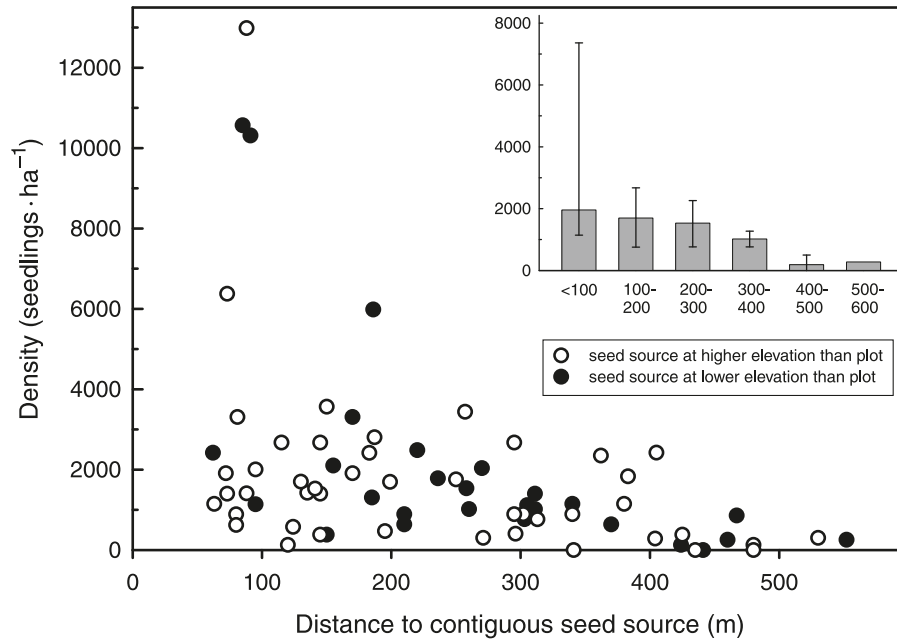
ground: at 2 years old, seedlings typically have root:shoot length ratios of 5:1 and taproot lengths of 50–100 cm (Stein 1978). These deep roots access soil layers in which summer moisture deficits are less severe.

Broadleaf vegetation interactions

Over longer time periods in this mixed-evergreen region, interactions between conifers and evergreen broadleaf species will have a major influence on forest development (Atzet et al. 1992; Tappeiner et al. 1992). Resprouting broadleaf vegetation can strongly compete with conifers for growing space and water resources over annual to decadal time scales. In some sites, such as tanoak associations with especially rapid broadleaf recovery (Table 5), only a portion of the early conifer cohort will eventually emerge to canopy dominance. Coupled with recurrent low-severity fires (Agee 1993), this competition may be an important factor thinning the extremely high regeneration densities toward the low densities characteristic of mature – old-growth forests (Table 3).

Interactions between conifers and broadleaf vegetation are

Fig. 5. Postfire seedling density as a function of distance to nearest contiguous (≥ 1 ha) patch of surviving trees, and whether seed source was above or below plot in elevation. Inset shows median and 25th–75th percentile of same data, by 100 m distance class. Distances < 50 m were not sampled. Regression analysis after log transformation (which effectively linearized the relationship) indicated that each metre of distance to live-tree edge was associated with a reduction in seedling densities of 0.1%–1% (see Table 6 for regression model outputs).



not solely competitive in nature. Facilitative interactions through shade provision, nitrogen fixation, and mycorrhizal associations can be important (Borchers and Perry 1990; Gomez-Aparicio et al. 2004), particularly over long time scales (Busse et al. 1996). These effects, and the observation that Douglas-fir in southwest Oregon is capable of growth in just 7% of full sunlight (Emmingham and Waring 1973), may explain observations of high postfire conifer survival and growth in spite of dense broadleaf cover (Shatford et al. 2007). Further study is needed on how facilitative and competitive interactions influence stand development over time scales measured in fire cycles.

Seed source distribution and relations

Extremely large burns are often expected to lack seed sources over broad areas. However, as Isaac and Meagher (1936) stated, “Contrary to the general belief that the Tillamook Burn contained a great many large clear-burned areas devoid of seed trees, relatively few [such areas] were found”. Our findings are consistent with this observation (Figs. 3–4). Similarly, Turner et al. (1994) concluded that 75% of severely burned areas of the Yellowstone fires were within 200 m of a live-tree edge. Greene and Johnson (2000) reported average distances of 150 m between burn edges and random points in large burns (5000–13 000 ha). In mixed-severity fires, the spatial arrangement of residuals reflects the complex nature of fire behavior and effects, resulting in highly intermixed patches and convoluted edges. With respect to conifer regeneration, large mixed-severity fires can often be described as a collection of smaller stand-replacement patches in a matrix of surviving canopy, rather than vice versa (Lentile et al. 2005; Turner et al. 1998).

Regeneration densities are generally expected to decline

rapidly with distance to live-tree edge, such that conifer regeneration would be minimal beyond 100–200 m (e.g., Greene et al. 1999). Our observations on the Biscuit Fire were largely inconsistent with this expectation in that regeneration densities were high out to 400 m from live-tree edges before declining (Fig. 5), a finding that is similar to those of other empirical postfire studies (e.g., Galipeau et al. 1997; Shatford et al. 2007). There are several possible reasons for this pattern. First, negative-exponential seed dispersal models tend to underpredict long-distance seed flights that occur as a result of, among other things, wind updrafts (Greene and Johnson 1995; Isaac and Dimock 1960). For example, Douglas-fir seed may regularly carry to 400 m in prevailing winds (Isaac and Dimock 1960 and references therein). In complex mountain terrain with strong local temperature fluctuations, updrafts and elevational gradients may further increase dispersal distances. Second, isolated remnant trees throughout stand-replacement areas very likely serve as local seed sources (Greene and Johnson 2000; Isaac and Meagher 1936). This mechanism is generally difficult to study (Greene and Johnson 2000), and spatial data were not available to quantify this reliably. We know, however, that most Biscuit stand-replacement areas retained scattered live conifers and that many of our sample plots had live trees closer than the nearest contiguous live-tree edge. Third, secondary seed dispersal after initial deposition, especially over snow surfaces, can also be an important mechanism (Greene et al. 1999; Thoreau 1861). Fourth, soil seed banks or aerial seed banks on fire-killed trees can provide regeneration throughout a stand-replacement patch (Greene et al. 1999; Larson and Franklin 2005). However, in the Biscuit Fire this mechanism appeared important only for the serotinous-coned knobcone pine (see above).

Supply-side versus site-factor controls

Both seed supply and local site factors were important controls on early regeneration density. Similar to the observations of Galipeau et al. (1997), who studied a boreal fire >10⁶ ha, most predictive ability came from two variables: distance to live-tree edge and soil parent material (Table 6). Median densities in the Biscuit Fire were relatively flat between 0 and 400 m from live-tree edges, but the seed source predictor was still important, since densities declined sharply beyond 400 m and were occasionally very high at short distances (Fig. 5). Thus, even though seed sources were well distributed across much of the burn, wide variation in patch size and distance to edge was still a highly important influence on regeneration density (Table 6; Turner et al. 1998).

Soil parent material (coarse-grained igneous vs. others) ranked much higher in importance than surface cover of exposed mineral soil or rock (Table 6). Skeletal coarse-grained igneous soils, which cover ~5% of the burn (USDA 2004), supported much lower regeneration densities than metasedimentary and metamorphic–volcanic soils. We also found that regeneration occurred preferentially on exposed mineral soil (see supplementary material²), a finding that is consistent with results from other studies (Greene et al. 1999; Larson and Franklin 2005). However, mineral soil seed beds were generally abundant (i.e., not limiting) following fire. Thus, our data suggest that ground surface cover was less important than the properties of the underlying soil matrix.

Much of the variation in regeneration density is still unexplained by the variables we assessed (Table 6). For example, the relatively low influence of most abiotic and biotic site factors (e.g., local precipitation regime and interspecific competition) indicates that if these factors are to influence regeneration, the effects have yet to manifest themselves. In addition to uncertainties in predicting seedling densities due to (for example) the heterogeneous nature of the process, inherent sampling error, and difficulties in quantifying isolated seed sources, several other unmeasured processes may be important. For example, seed and (or) seedling predation by small mammals may affect Douglas-fir regeneration (Isaac and Dimock 1960). In an exploratory analysis, Fontaine (2007) found a strong negative correlation between deer mouse (*Peromyscus maniculatus*) abundance and seedling density (Spearman $r = -0.73$, $n = 6$ plots).

Reconstructive (tree-ring) studies in old-growth Douglas-fir forests have identified a wide range of early establishment patterns, from rapid and dense to slow and sparse (Franklin and Hemstrom 1981; Larson and Franklin 2005; Poage and Tappeiner 2002). Mechanisms behind this variation are poorly understood, usually speculated to be some combination of seed availability, germination conditions, broadleaf competition, or repeat fires after the initiating disturbance. Early regeneration patterns in the Biscuit Fire suggest that both the slow and rapid routes may occur within a single large burn. Areas very distant from live-tree edges (>400 m) or on poor soils (i.e., dry, coarse-textured, etc.) may take a slow pathway partly because of seed source lim-

itations and low germination and (or) juvenile survivorship. Other areas, which may include significant portions of even large burns, are not limited in terms of seed availability or suitable substrate, leading to dense early regeneration. If the latter areas are found to exhibit slow recruitment over time, it could be inferred that later conditions such as interspecific competition, rather than early factors, are driving long-term recruitment rates.

Conclusions and management implications

Despite the large size of the Biscuit Fire, we observed abundant but variable conifer regeneration in most stand-replacement areas, and it is likely that these early cohorts are but the first of several (Shatford et al. 2007). Abundant regeneration was directly associated with the mixed-severity fire pattern, which resulted in well-distributed seed sources throughout much of the burn. In this way, a large mixed-severity fire may be described as a collection of smaller stand-replacement patches in a matrix of surviving canopy, rather than vice versa (see Lentile et al. 2005). Coupled with variable soil properties, distance to seed source was an important control on early conifer density. Thus, variation in burn patch size may be a key mechanism underlying heterogeneity in regeneration, successional pathway, and forest structure, thereby contributing to the globally renowned biodiversity of the Klamath–Siskiyou region.

Conifer establishment is typically a management goal after large wildfires (e.g., USDA 2004) but often receives limited funding (GAO 2006). Given limited resources for tree planting, postfire management may benefit greatly by using natural regeneration where possible. These data suggest that in mesic forest types experiencing mixed-severity fire natural regeneration may be a viable management option over more of a large burn than generally expected. Natural postfire succession, which has operated in the Klamath–Siskiyou region for millennia, may include prolonged periods of dominance by early-seral hardwoods and shrubs (Agee 1993; Thornburgh 1982). Using natural regeneration will thus require flexibility regarding spatial variation and timing of conifer establishment, with the recognition that periods of broadleaf dominance benefit landscape wildlife diversity (Fontaine 2007).

Assessing the distribution of seed sources could be an essential tool for prioritizing tree planting actions. In the Biscuit Fire, natural seedling densities and stocking rates were at or above prescribed levels (250–500 stems·ha⁻¹, USDA 2004) in small to medium burn patches and edges of larger openings (to ~400 m) (Fig. 4). However, sparse regeneration was measured in areas distant from live-tree edges (interiors of large burn patches, such as in the central portion of the Biscuit Fire (Fig. 4)). These areas are more likely to be continually dominated by resprouted hardwoods and shrubs. Where this vegetation is inconsistent with management objectives, such areas could be prioritized for conifer planting. Broad-scale seed source maps (Fig. 4) are a potential tool for predicting planting needs and successional path-

²Supplementary data for this article are available on the journal Web site (<http://cjfr.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3924. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 6. Top-ranked models and parameter estimates (95% confidence intervals in parentheses) from mixed-effects regression of conifer seedling density as a function of seed source and site variables 4 years after the Biscuit Fire.

Model diagnostics				Parameter estimates*						
AIC _c	ΔAIC _c	w _i	R ²	Distance to live-tree edge (m)	Coarse-grained igneous soil (1–0)	Hardwood–shrub cover (%)	Rock cover (%)	Forb – low-shrub cover (%)	Slope (°)	Standing-dead basal area (m ² ·ha ^{–1})
RI [†]				0.95	0.88	0.47	0.40	0.22	0.22	0.20
Model rank										
1	179.95	0	0.13	0.994 (0.990–0.998)	0.182 (0.059–0.561)	—	—	—	—	—
2	180.39	0.44	0.11	0.994 (0.990–0.998)	0.223 (0.070–0.709)	0.985 (0.962–1.007)	—	—	—	—
3	181.03	1.08	0.08	0.995 (0.991–0.999)	0.235 (0.075–0.738)	0.982 (0.960–1.005)	0.985 (0.963–1.008)	—	—	—
4	181.12	1.17	0.08	0.995 (0.991–0.999)	0.185 (0.060–0.569)	—	0.987 (0.965–1.010)	—	—	—
5	182.08	2.14	0.05	0.994 (0.990–0.998)	0.207 (0.061–0.704)	—	—	—	0.979 (0.909–1.054)	—
6	182.24	2.29	0.04	0.994 (0.990–0.998)	0.194 (0.060–0.631)	—	—	1.004 (0.987–1.021)	—	—
7	182.45	2.50	0.04	0.994 (0.990–0.998)	0.178 (0.052–0.611)	—	—	—	—	0.999 (0.984–1.015)

Note: AIC_c, corrected Akaike information criterion; w_i, model weight. All models with ΔAIC_c ≤ 2.50 are shown. All models had structure: $y \sim \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k$. Other site variables analyzed (not shown) are listed in Table 2; these were excluded from all subsets regression by analysis step 1 (site variable elimination step; see text) because of lower importance and weaker effect sizes than variables shown here (see Appendix B).

*Multiplicative effect, obtained via back-transformation from analysis of $\log_e(x + 1)$ data. A value of 1 indicates no effect.

†Relative importance (RI) value provides a measure of strength of association with seedling density, calculated by summing Akaike weights across a ll models in which a variable appears.

ways, but their reliability should be assessed for a given forest type and field validated to the extent possible.

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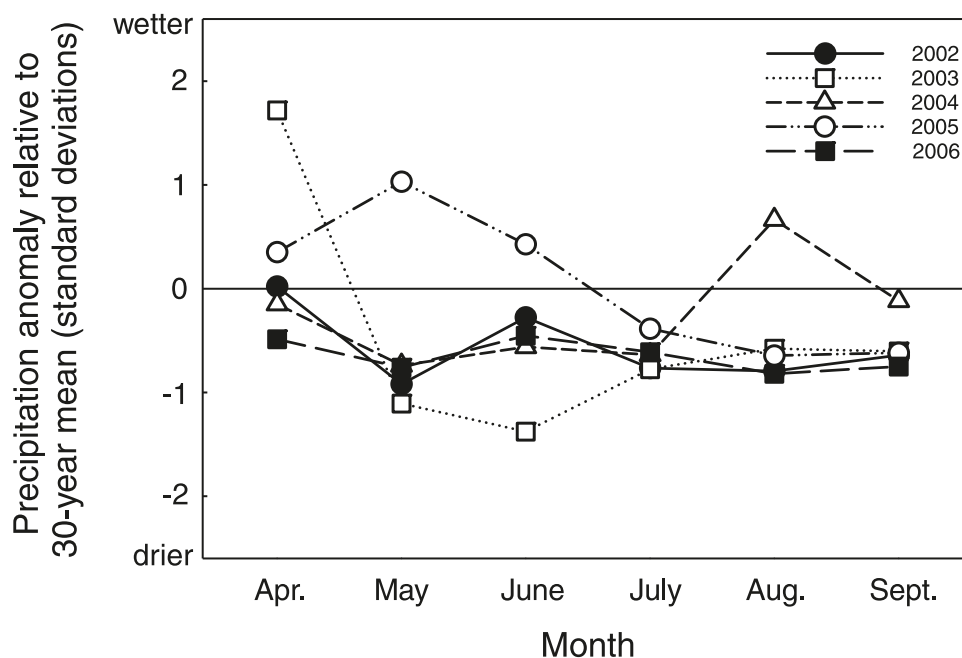
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Appendix A. Growing season precipitation patterns in study area for period 2002–2006

Fig. A1. Monthly precipitation patterns, in standard deviations (SD) above or below the 30 year mean, for the five growing seasons of 2002–2006. Twenty-seven months of 30 months were within 1 SD of the mean (all 30 months ≤ 1.7 SD); 24 of 30 months were drier than average. Computations were derived from PRISM climate data (Daly et al. 2002; PRISM Group, Oregon State University, <http://prism.oregonstate.edu>, accessed 7 November 2006).



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Appendix B. Analysis step 1 (univariate regressions for site-factor ranking)

Table B1. Model ranks and parameter estimates from mixed-effects regression of conifer seedling densities as a function of each of 11 site variables 4 years after the Biscuit Fire (analysis step 1).

Model rank	Variable	AIC	Δ AIC	w_i	Parameter estimate* (95% CI)
1	Coarse-grained igneous soil (1–0)	187.63	0	0.69	0.085 (0.028–0.259)
2	Rock cover (%)	190.80	3.17	0.14	0.971 (0.947–0.996)
3	Forb – low-shrub cover (%)	193.93	6.30	0.03	1.017 (0.996–1.038)
4	Hardwood–shrub cover (%)	194.10	6.47	0.03	0.977 (0.948–1.007)
5	Intercept only	194.11	6.48	0.03	na
6	Slope (°)	195.01	7.38	0.02	0.947 (0.862–1.040)
7	Standing-dead basal area (m ² ·ha ⁻¹)	195.12	7.49	0.02	1.010 (0.993–1.026)
8	Mean annual precipitation (cm)	195.30	7.67	0.01	0.981 (0.946–1.018)
9	Soil cover (%)	196.17	8.53	0.01	1.010 (0.970–1.050)
10	Annual solar heat load (index)	196.27	8.64	0.01	0.742 (0.130–4.22)
11	Elevation (m)	196.32	8.69	0.01	0.999 (0.996–1.003)
12	Crown scorched vs. consumed (1–0)	196.40	8.76	0.01	0.967 (0.209–4.483)

Note: For step 2, the six top variables here were combined with distance to live-tree edge in an all subsets regression analysis (see text). AIC, Akaike information criterion; w_i , model weight. All models had structure: $y \sim \beta_0 + \beta_1 x$, except the intercept-only model ($y \sim \beta_0$).

*Multiplicative effect, obtained via back-transformation from analysis of $\log_e(x + 1)$ data. A value of 1 indicates no effect.