


ARTICLE

Nucleation sites and forest recovery under high shrub competition

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Handling Editor: Carolyn H. Sieg**Abstract**

Forests currently face numerous stressors, raising questions about processes of forest recovery as well as the role of humans in stimulating recovery by planting trees that might not otherwise regenerate. Theoretically, planted trees can also provide a seed source for further recruitment once the planted trees become reproductive, acting as “nucleation” sites; however, it is unclear whether changing site conditions over time (e.g., through the growth of competitors like woody shrubs) influences establishment in the long term, even if seed availability increases. We tested the nucleation concept in a system where shrub competition is known to influence tree establishment and growth, performing an observational study of sites within and close to newly reproductive planted stands in yellow-pine (YP) and mixed-conifer ecosystems in the Sierra Nevada, California. We surveyed and then modeled both seedling occurrence and density as a function of distance to seed sources, competing woody vegetation, and other environmental characteristics. We found that proximity to a planted stand was associated with an increase in the probability of YP seedlings (species more likely to originate from the planted stand) from 0.33 at 35 m from the planted stand to 0.56 directly adjacent to the stand and 0.65 within the stand. However, we found no significant effect of proximity on YP seedling density. This proximity effect suggests that seed availability continues to be a driver of recruitment several decades postwildfire, though other processes may influence the expected density of recruits. Proxies for competitive pressure (shrub volume and shrub cover) were not significant, suggesting that competing vegetation did not have a major influence on recruitment. Though seedling presence and density appeared to be independent of shrub impacts, we did find that shrubs were significantly taller than seedlings. Therefore, we suggest that shrubs may not limit seedling establishment, but they may negatively affect seedlings’ ability to grow and serve as a seed source for further recruitment and forest expansion. Altogether, we find that planting may provide a statistically significant but small role in driving recruitment outside of the planted site.

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KEYWORDS

dispersal, forest management, nucleation, reforestation, wildfire

INTRODUCTION

Understanding patterns and drivers of forest recovery has become increasingly pressing as forests face mounting threats from deforestation, pests and disease, wildfires, and climate change broadly (Curtis et al., 2018; Kautz et al., 2018; Seidl et al., 2017; Wees et al., 2021). Given the array of ecosystem services that forests provide, reforestation and forest restoration have become key priorities in public, private, and social sectors (see initiatives cited in Holl & Brancalion, 2020 and Di Sacco et al., 2021). This enthusiasm for large-scale forest planting and management raises questions about scalability, potential scope, and long-term outcomes of these forest management interventions (e.g., Holl & Brancalion, 2020). We investigated some of these questions in the context of reforestation in the Western United States, focusing primarily on postwildfire systems that may prompt this kind of active forest management.

In semiarid pine-dominated and mixed-conifer systems of the Western US, successful conifer regeneration is influenced by interactions between seed production (masting), dispersal, precipitation patterns, and the availability of suitable substrates (Donato et al., 2009; Haffey et al., 2018; Keyes & Manso González, 2015; Stevens-Rumann & Morgan, 2019). Before fire exclusion beginning in the late-19th century, low- and moderate-severity burning was frequent and pervasive, and pine regeneration was promoted by the widespread availability of bare mineral soil and high light incidence at the soil surface (Safford & Stevens, 2017; van Wagendonk et al., 2018). Recently, however, stand densification and fuel accumulation driven by a century of fire exclusion, as well as anthropogenic climate change, have led to major changes in wildfire behavior, with fires growing larger and more “severe” (characterized as having a greater amount of change in vegetation or soils; see Morgan et al., 2014) on average (Parks & Abatzoglou, 2020). Large, contiguous areas of very high, fire-associated tree mortality have become common in much of the Western US (e.g., Steel et al., 2018); such high-severity patches are inimical to the regeneration of nonserotinous conifers because they contain very few, if any, surviving trees and unburned areas that might serve as seed sources for future generations. Accordingly, it is unclear whether tree regeneration in these landscapes will be sufficient to maintain forest cover in the future (Coop et al., 2020).

Planting trees effectively removes dispersal limitation and can enable tree establishment in the absence of

nearby surviving or unburned reproductive trees (“seed trees”). However, this strategy is difficult to implement at broad scales: appropriate genetic stock must be collected and grown in a nursery, sites must be accessible and safe for planting crews (e.g., close to roads, walkable terrain, clear of hazards—potentially including standing dead trees), and funding and staff must be available for all of these steps (Fargione et al., 2021; Tappeiner et al., 2007). In Region 5 of the Forest Service (principally California), for example, conifer planting over recent decades has rarely exceeded 12,000 ha (R. Rojas, US Department of Agriculture [USDA] Forest Service, personal communication), but the area of burned forest warranting planting intervention in recent years has often been five to 10 times greater. Given the scale of the need as well as the hurdles involved in widespread planting, one proposed alternative is to plant small “founder stands” to grow and eventually serve as seed sources for the surrounding region (North et al., 2019).

The idea of strategic planting to achieve broader landscape restoration is closely associated with the concept of applied nucleation that has been investigated in other ecological contexts. Nucleation describes the process by which early arriving individuals establish and serve as a focal point for other species to coalesce, eventually creating patches that expand and contract in size as successional processes proceed (Yarranton & Morrison, 1974). In an applied context, planting these “nuclei” can accelerate the establishment of a more heterogeneous forest or woodland ecosystem by attracting animal dispersers, serving as an aggregation point for wind-dispersed vegetation, or otherwise creating appropriate conditions for a more diverse set of tree species (Corbin & Holl, 2012; Rey Benayas et al., 2008). Though there exists empirical support for the use of planted nuclei to accelerate the creation of later-successional forest structure, it is less clear whether nuclei lead to a substantial expansion from the original site. Existing studies in tropical forest sites have found some recruitment in areas immediately surrounding planted stands (1 m: Zahawi & Augspurger, 2006; 6 m: Holl et al., 2020). In other studies that assessed recruitment farther from planted stands, recruitment extended fairly equally over a wider space—likely reflecting dispersal syndromes that promote travel outside of the immediate vicinity of the planted individual (e.g., lightweight, wind-dispersed seeds (Corbin et al., 2016) and heavier seeds dispersed by highly mobile animal dispersers (Corbin et al., 2016; Rey Benayas

et al., 2015)). Such cases may not apply to systems where distance is a strong predictor of regeneration success, such as in yellow pine and mixed-conifer forests (collectively, “YPMC”). We are not aware of any applied nucleation studies in this system.

In YPMC forests, distance to seed trees is a key predictor of regeneration success. This has been shown in several postfire studies, with conifer regeneration decreasing as distance to surviving seed trees increases in landscapes sampled within a few years postwildfire (Shive et al., 2018; Stevens-Rumann & Morgan, 2019; Welch et al., 2016). Dispersal kernels also have been evaluated in postharvest landscapes, where gap studies show that seed availability is correlated with proximity to forest edges (McDonald, 1980).

In addition to seed availability, changes in vegetation that occur in the years following disturbance have relevant associations with future regeneration and should be considered in nucleation or founder stand reforestation strategies. Depending on the environmental context and species mix, co-occurring shrubs can have facilitative or competitive impacts on seedlings. Facilitative relationships in particular have been found in lower-elevation, sun-exposed, and drier sites or years compared with higher-elevation, shaded, and wetter conditions (Gómez-Aparicio et al., 2004)—a finding that is consistent with theory that predicts more positive interspecific interactions under stressful abiotic conditions (Bertness & Callaway, 1994).

In YPMC forests, competition is the dominant paradigm used to explain seedling interactions, with the quick regeneration and recruitment of shrub species (such as *Arctostaphylos* spp. and *Ceanothus* spp.) after wildfires potentially inhibiting forest recovery (North et al., 2019). Shrub competition can reduce the growth and survival of trees, particularly among shade-intolerant pine species (Airey Lauvaux et al., 2016; McDonald & Fiddler, 2010; Tubbesing et al., 2020). When shrubs are among the first to establish, the effects can be long lasting: trees establishing later in chaparral patches can have persistent slow growth rates for 30 or more years until they emerge from the shrub canopy (Airey Lauvaux et al., 2016; Nagel & Taylor, 2005). Therefore, many silviculturists choose to plant trees only immediately after disturbances and then only in conjunction with the removal of competing vegetation (Tappeiner et al., 2007).

Given the important role of proximity to seed sources as well as the role of shrub competition, we investigated the relative importance of these factors in the context of applied nucleation or founder stand reforestation. We performed an observational study of sites that had been planted 25–27 years prior and where we could evaluate regeneration patterns associated with the stands. We focused on two hypotheses:

1. Dispersal limitation hypothesis: If seedling establishment is limited by seed availability, then we expected to observe greater densities of seedlings close to planted stands compared with areas outside of the planted stands’ seed shadow.
2. Competitive impacts hypothesis: If seedling establishment is limited by competing vegetation, then we expected to observe negative correlations between seedling density and shrub cover. Though under some conditions nontree woody vegetation can have a facilitative effect, we felt that existing empirical work in similar ecosystems favored a hypothesis that included negative interactions between plant forms.

These hypotheses evaluate both seed availability and one important axis of site suitability (interactions with other woody plant forms) as potential drivers of plant regeneration. In testing these, we aimed to evaluate a specific proposed land management practice, the application of nucleation concepts through the planting of “founder stands,” as well as develop insight into the relative role of these constraints in a period relatively late in the postdisturbance trajectory.

METHODS

Study design

To address our hypotheses, we characterized tree regeneration in plots that varied in distance to planted stands as well as in shrub competition. We surveyed plots in planted stands that were 25–30 years old—old enough to have been reproductive for several years to account for intra-annual variation in seed production, but young enough to ensure that the focal seedlings (those originating from planted trees) could be aged by counting bud scars (Hankin et al., 2018). We also sampled in areas that had a well-defined boundary between planted and unplanted areas, with planted areas visually identifiable because they contained a single-aged cohort in a grid configuration. We sampled in areas that did not have an observable difference in substrate that explained the planting perimeter: in one location (Sierra National Forest [SNF]), planting boundaries had been established for an unrelated research purpose rather than due to reforestation needs; the second location (Eldorado National Forest [ENF]) spanned an ownership boundary, with early reforestation on one side and no management on the other; and for a third location (Tahoe National Forest [TNF]), we determined through site visits that there was likely no difference between planted and unplanted areas. Two of the sites were planted postfire (SNF, ENF), and we included the TNF site because (1) there was a clear and seemingly arbitrary planting boundary that

was suitable for testing nucleation processes and (2) we believed, based on the presence of coarse woody debris and forest designations on available land-cover map products (US Forest Service, 2019), that the region historically supported trees. We also restricted sampling to locations that had a minimal number of nearby large trees because our aim was to characterize regeneration associated with planted trees specifically; we later confirmed through a relative delta Normalized Burn Ratio (RdNBR)-based severity analysis that all ENF plot areas and 94% of the SNF plot areas burned at high severity (Miller & Thode, 2007) and largely burned at high severity within 100 m of the plots. Table 1 and Figure 1 provide details on the location, climate, management history, and fire history of these sites. We analyzed 87 plots within these three locations.

Data collection

We sampled plots along transects that bisected the boundary between planted and unplanted areas: one plot center was located 15 m into a planted stand, the second

plot center was 10 m outside of the planted stand, and each subsequent plot center was 25 m farther out. We used a variable plot size, defaulting to sampling within a 10-m-radius circular plot but shrinking the sampling area to 8-, 6-, 4-, or 2-m-radius plots if regeneration was dense; we aimed to sample about 10 seedlings per species per plot. We subsampled on a species-by-species basis, and in most cases we sampled the full 10-m-radius plot. For all plots, we later multiplied counts by a multiplicative factor to express them per 10-m-radius plot and per hectare for comparison with other studies.

At each plot, we characterized regeneration by identifying each conifer tree to species, measuring its current height and prior year's height (seedlings, saplings), measuring its diameter at breast height (dbh; only for trees), and counting terminal bud scars to estimate age (all). We categorized trees as individuals >3 cm dbh, saplings as individuals <3 cm dbh but taller than 1.4 m, and seedlings as individuals <1.4 m height. Several of our plots had a fairly broad range of seedling ages due to natural regeneration from existing large trees (e.g., trees that survived the wildfire). Though we attempted to sample in

TABLE 1 Locations for data collection, along with site, vegetation, and management characteristics.

Location and coordinates	Elevation (m)	Vegetation ^a	Most recent wildfire	Site history				No. transects
				Burn severity within plot area		Burn severity within 100 m of plots		
				Moderate (%)	High (%)	Moderate (%)	High (%)	
Eldorado National Forest: 38.7872, -120.4308	1409–1437	Ponderosa Pine, Montane Chaparral	Cleveland Fire (1992)		100 ^b	6	94	6
Sierra National Forest: 37.2150, -119.2572	1593–2301	Jeffrey Pine, Ponderosa Pine, Sierran Mixed Conifer, Montane Chaparral, White Fir	Big Creek Fire (1994)	6	94	11	89	11
Tahoe National Forest: 39.4028, -120.0661	1930–1960	Eastside Pine, Sierran Mixed Conifer, Montane Chaparral	Unknown; no fire apparent; likely planted ca. 1990 ^c					6

^aDominant vegetation is characterized using the California Wildlife Habitat Relationship (WHR) classification scheme as reported in the US Department of Agriculture Forest Service's EVeg map product (US Forest Service, 2019).

^bFire severity is characterized according to methods published in Miller and Thode (2007) and with severity map products published by the US Forest Service (2018).

^cTrees in this area were almost exclusively *Pinus jeffreyi* and followed a grid pattern typical of planted stands. Management records indicate that the area received a "release" treatment typical of early plantations in 1991 ("Forest Service Activity Tracking System [FACTS]," 2018).

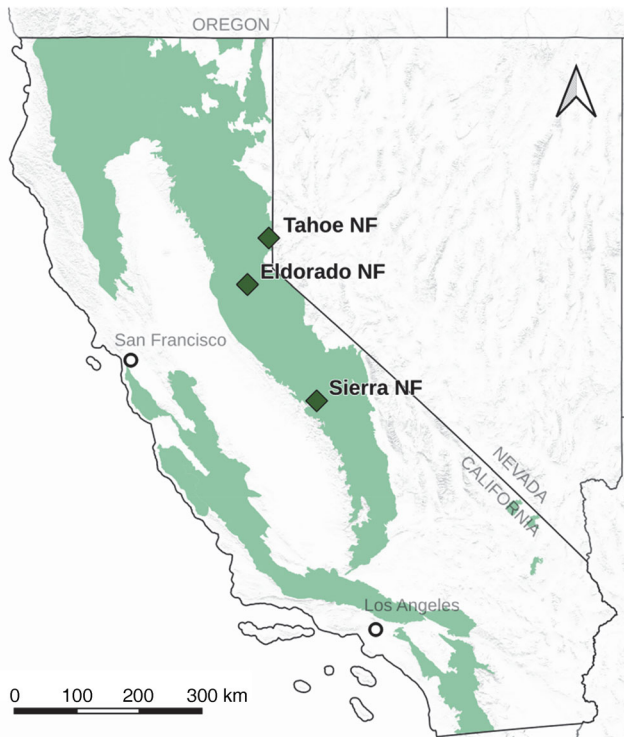


FIGURE 1 Locations for data collection, produced using a US Geological Survey shaded relief base map (US Geological Survey - National Geospatial Program, 2020) and overlaid with a vegetation range map that includes California Wildlife Habitat Relationship classes found at the study sites and as reported in the US Department of Agriculture Forest Service’s EVeg map product (US Forest Service, 2019). Montane chaparral was excluded because it extends to much lower-elevation sites and likely is not representative of the potential range of our focal conifer species. NF, National Forest.

areas that had few large seed trees (e.g., high-severity areas in postfire regions; see Table 1 for fire severity summaries), such trees were still present in the broader landscape and potentially contributed seed rain to all plots. Hereafter, we refer to them as “large tree seed sources” (LTSS). We focused our analysis on trees that were 10 years old or younger in light of the potential influence of natural regeneration, thereby evaluating the establishment patterns of seedlings that plausibly could have come from the planted stand (based on expected ages of reproductive maturity). Hereafter and particularly for the statistical analysis and results, we refer to these as seedlings and the older individuals as “other natural regeneration”. We were unable to assess prior year’s height or bud scar age for *Calocedrus decurrens* due to its morphology; however, we did not observe this species in any of the planted stands and therefore did not consider it to be a focal species for our research question.

To evaluate the role of seed dispersal, we estimated proximity to seed sources from the center of the plot. First, the distance to planted trees was accounted for in the plot

placement. Based on the dispersal patterns of the tree species common to YPMC—and particularly *Pinus ponderosa* and *Pinus jeffreyi* (hereafter aggregated as “yellow pine” [YP]), which accounted for most of the planted trees—we expected seed rain to occur in the plot within the planted stand and just adjacent to the planted stand. This expectation was informed by the height of the planted trees (average height of YP: 9 m; data not shown) and prior work showing that most seed fell within 1.5 times the height of the average dominant tree (in this case, within 13.5 m) (McDonald, 1980). However, we continued to sample farther from this expected range to account for potential longer-distance dispersal. Second, we accounted for the distance to LTSS. From each plot, we used a laser rangefinder to measure the distance to the nearest three individuals or clumps of trees for each species, up to a distance of 500 m (corresponding to the technical limits of our rangefinder). We then aggregated these by multiplying the inverse of the distance by the number of individuals at that distance, and then we summed across the three individuals or clumps; this index represents the potential seed rain by species in that higher values indicate more seed potentially arriving at the site, and it accounts for the potential of seed rain from multiple sources. Last, we accounted for natural regeneration that was functionally similar to planted trees (hereafter “natural regeneration seed source” [NRSS]). These trees were of similar size and age to planted trees but were inconsistent with the regular grid or planting boundary that characterized the planted stand; we assume that they likely germinated as natural regeneration from nearby large trees. We used the same index method to account for the potential seed contribution of these trees.

We also characterized competing vegetation and other site characteristics at the plot scale. For shrub competition, we assessed the percentage cover and modal height of all woody, nontree species, and we generated species-level estimates for the three most abundant species and any species with >10% cover. In our analysis, we tested the effect of shrub percentage cover as well as an index of shrub volume, which we computed by summing the percentage cover multiplied by height across shrub species meeting our threshold (“shrub volume”). To account for tree competition, we assessed the percentage cover and height of overstory trees within the plot. In our analysis, we also accounted for intraseedling/sapling competition by controlling for the density of individuals older than 10 years in each plot (“other natural regeneration”). We accounted for the availability of suitable substrate by estimating percentage cover for the following ground cover categories: large rocks and bedrock (>0.5 m in shortest dimension); cobbles and stones (75–500 mm); litter, bare soil, and small rocks (<75 mm); basal vegetation; and woody debris. We also collected data on elevation, slope, and aspect at the plot scale.

Statistical analyses

We fit a binomial generalized linear mixed model to predict whether seedlings would occur in a given plot, and we used a negative binomial generalized linear mixed model to predict the densities at each plot. We analyzed these data in R version 3.6.3 using the glmmTMB (Brooks et al., 2017) and lme4 packages (Bates et al., 2015). We fit a minimum model that included hypothesized mechanisms driving seedling establishment (seed rain from planted and surviving trees, as well as shrub competition) and a random intercept to account for the nested plot structure within transects. We added other explanatory factors (ground cover, overstory cover, abiotic site characteristics) if they improved the model fit based on a corrected Akaike information criterion (AIC_c) comparison.

We focused our analysis on the YP species (*P. ponderosa* and *P. jeffreyi*) because the vast majority of trees planted were of these species. Though we observed single planted individuals of other species (e.g., *Pinus lambertiana*, *Pseudotsuga menziesii*) within some of the planted stands, there were not enough individuals—and not close enough to the planted edge—for us to assess seed rain from those particular species. However, we also analyzed the regeneration of all species aggregated together in order to evaluate whether proximity to planted stands engendered a broader edge effect in terms of enabling recruitment from large surviving trees.

RESULTS

We analyzed the presence and density of conifer seedlings as associated with proximity to seed sources—stratified across distances to nearby, reproductive planted stands—and as associated with other potential drivers of regeneration success such as shrub competition, competition from other seedlings and saplings, and environmental characteristics (Table 2). Seedling counts were very low in most plots, with

median counts of 0 or 1 in all three locations but with counts as high as 375 at our highest-density plot. Table 3 provides summary statistics for seedling counts, shrubs, and LTSS.

Distance effects

We found that the probability of observing a YP seedling in a plot was negatively correlated with distance from the planted edge, with the mean model-predicted probability going from 0.65 within the plantation to 0.56 just adjacent to the plantation to 0.33 at a distance of 35 m from the planted stand edge (Figure 2). We did not observe a significant effect of distance on the density of YP seedlings. YP density (but not probability of occurrence) was also positively correlated with the density of other (larger) natural regeneration, likely reflecting plots that had a generally high amount of seed rain from large, surviving trees.

Shrub effects

We did not observe a significant effect of shrub percentage cover or shrub volume in either of our models, though we did find that higher shrub volume was marginally associated with a decline in seedling density. For all models, we tested the effect of shrub percentage cover as well as shrub volume. We found that they had very comparable effects in the models (data not shown), and therefore we retained the shrub volume estimate because it accounted for shrub height as well as horizontal spread.

Nonfocal seedlings

We also analyzed the presence and density of seedlings of all conifer species (except *Calocedrus decurrens*; see *Methods*) in addition to our YP-only analysis. The

TABLE 2 Model results for probability of observing (“presence” columns) and density of yellow pine seedlings.

Predictors	Presence (YP) ^a		Density (YP) ^b	
	Log odds	<i>p</i>	Log mean	<i>p</i>
(Intercept)	0.64 (−0.30 to 1.57)	0.183	0.48 (−0.26 to 1.21)	0.201
Distance from planted stand (m)	−0.04 (−0.07 to −0.01)	0.011	−0.01 (−0.03 to 0.01)	0.383
Shrub volume	−0.29 (−1.03 to 0.46)	0.452	−0.63 (−1.31 to 0.04)	0.067
Other natural regeneration (density)	0.93 (−0.22 to 2.09)	0.113	0.86 (0.25 to 1.47)	0.006
Large tree seed source (index)	0.53 (−0.23 to 1.28)	0.172	0.35 (−0.18 to 0.89)	0.199
Natural regeneration seed source (index)	−0.10 (−0.69 to 0.49)	0.748	−0.08 (−0.55 to 0.38)	0.721

Note: Coefficients that are significant at $p < 0.1$ are bolded for emphasis. This table and Table 4 were generated using the sjPlot package in R (Lüdtke, 2021). Abbreviations: ICC, intraclass correlation coefficient; YP, yellow pine.

^aObservations = 87. Marginal $R^2 = 0.361$. Conditional $R^2 = 0.511$. Random effects as follows: $\sigma^2 = 3.29$; $\tau_{00} = 1.01_{\text{transect}}$; ICC = 0.24; $N = 23_{\text{transect}}$.

^bObservations = 87. Marginal $R^2 = 0.479$. Conditional $R^2 = 0.648$. Random effects as follows: $\sigma^2 = 1.35$; $\tau_{00} = 0.65_{\text{transect}}$; ICC = 0.32; $N = 23_{\text{transect}}$.

TABLE 3 Summary statistics of field data, grouped by location and distance to planted stand.

Location and distance to the planted stand (m)	YP seedlings (count)		All seedlings (count)		Shrub % cover (mean SD)	Shrub volume (mean SD)	YP prefire trees, index (mean SD)	Prefire trees, index (mean SD)
	Mean (SD)	Median	Mean (SD)	Median				
	ENF							
0	2.2 (2.4)	2	3.3 (3.4)	3	44.7 (34.4)	313.7 (316.7)	0.008 (0.002)	0.008 (0.002)
10	0.5 (1.2)	0	1.2 (1.6)	0.5	95 (8.4)	1199.5 (598.5)	0.009 (0.002)	0.009 (0.002)
35	0.6 (0.9)	0	1.2 (2.2)	0	100 (0)	1200.4 (483.2)	0.011 (0.002)	0.011 (0.002)
60	0.2 (0.4)	0	0.2 (0.4)	0	99 (2.2)	1202.8 (394.6)	0.013 (0.003)	0.013 (0.003)
SNF								
0	4.8 (4.7)	3.9	22.6 (54.6)	6	15.7 (16.3)	67 (72.4)	0.094 (0.077)	0.166 (0.172)
10	23.5 (42.7)	1.9	96 (129.5)	28.6	35.8 (32.8)	169.2 (213.4)	0.029 (0.052)	0.088 (0.14)
30–35	9.5 (23.8)	0	45.5 (63.3)	1	54.7 (31.9)	283.3 (232.9)	0.039 (0.049)	0.125 (0.159)
50–70	9.2 (16.8)	0	19.3 (25.7)	5.7	58.7 (33)	303.7 (219)	0.051 (0.057)	0.131 (0.164)
TNF								
0	1.2 (1.2)	1	1.2 (1.2)	1	50 (7.1)	149 (47.7)	0.159 (0.087)	0.192 (0.101)
10	1.2 (1.2)	1	1.3 (1)	1	65.8 (9.2)	171.5 (64.2)	0.113 (0.051)	0.172 (0.067)
35	0 (0)	0	0 (0)	0	59 (23)	159.4 (82.3)	0.102 (0.018)	0.183 (0.103)
60	0 (0)	0	0 (0)	0	58.3 (16.1)	181 (96.6)	0.133 (0.064)	0.165 (0.084)

Abbreviations: ENF, Eldorado National Forest; SNF, Sierra National Forest; TNF, Tahoe National Forest; YP, Yellow pine.

purpose of the all-conifer analysis was to assess whether the presence of a planted stand could influence recruitment aside from being a seed source (e.g., provide edge effects like shelter or shading or serve as habitat for seed dispersers or seed predators). We found largely similar effects compared with the YP-only model (Table 4). First, both the probability and density of seedlings were correlated with proximity to the planted stand, with the probability going from 0.97 within the planted stand to 0.93 just adjacent to the stand to 0.62 at a distance of 35 m from the planted stand edge (Figure 3). Both the presence and density of seedlings were correlated with the density of older natural regeneration. Shrub competition, as indicated by the percentage cover or the volume of shrub species in the plot, was not significant in these models. Including the percentage ground cover of litter also improved our density model, reflecting a positive correlation between available substrate and seedling establishment.

Disturbance history

We performed all analyses on all data as well as without TNF plots, as the latter were not postfire and therefore had a different disturbance history. All significant variables had coefficients within 20% and with the same slope direction in both data sets; the only exceptions were

the non-focal-seedling intercepts, which was expected given our random intercept model structure, and ground cover in our nonfocal density model. Model comparisons are included in Appendix S1.

DISCUSSION

We surveyed conifer recruitment in the context of newly reproductive planted stands in order to evaluate the role of dispersal limitation and shrub competition in controlling seedling establishment. Our data provide some support for the dispersal limitation hypothesis: YP seedlings were largely found within the immediate vicinity of planted stands and dropped off substantially as distance from the stand increased, suggesting that planted trees can serve as a seed source for future generations within a certain radius of the planted area. We observed this pattern in models of seedling presence but not density. It is possible that density is correlated with factors outside the scope of this study, such as the availability of microsites or the presence of animal dispersers, and thus was too variable to detect a significant relationship with proximity to a planted stand (Stevens-Rumann & Morgan, 2019). Though we focused on species that are known to be primarily wind- and gravity-dispersed, secondary dispersal may also play a role in this system, particularly for

P. jeffreyi (Vander Wall, 2008). When we included other conifer species in our model (*Abies* spp., *Pinus lambertiana*, *Ps. menziesii*), we found that both presence

and density were positively correlated with proximity. We interpret these findings to suggest that planted stands not only can serve as a seed source but also may increase site suitability for seedlings of other species. Existing literature suggests that sites closer to forest edges may have more moderate microclimates (e.g., Baker et al., 2014),

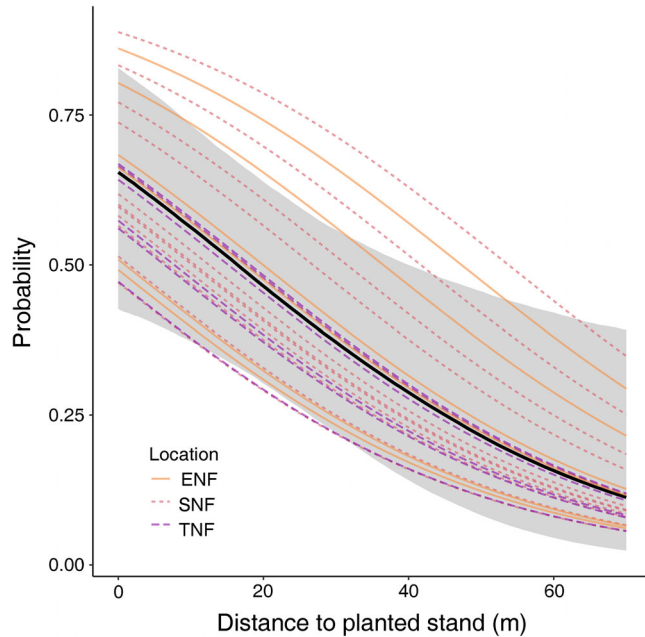


FIGURE 2 Predicted probability of yellow pine (YP) seedling presence, based on distance to planted stand and with all other variables held constant at their mean observed value. Relatively high seedling probabilities at relatively large distances from the planted stands (>40 m) likely reflect either long-distance dispersal from the planted stand or dispersal from alternate seed sources (large tree seed sources [LTSS] and natural regeneration seed source [NRSS]). Predicted probability is in black, with a 95% confidence interval in gray. Transect-level predictions are included in color and varying line types to demonstrate variation between locations. ENF, Eldorado National Forest; SNF, Sierra National Forest; TNF, Tahoe National Forest.

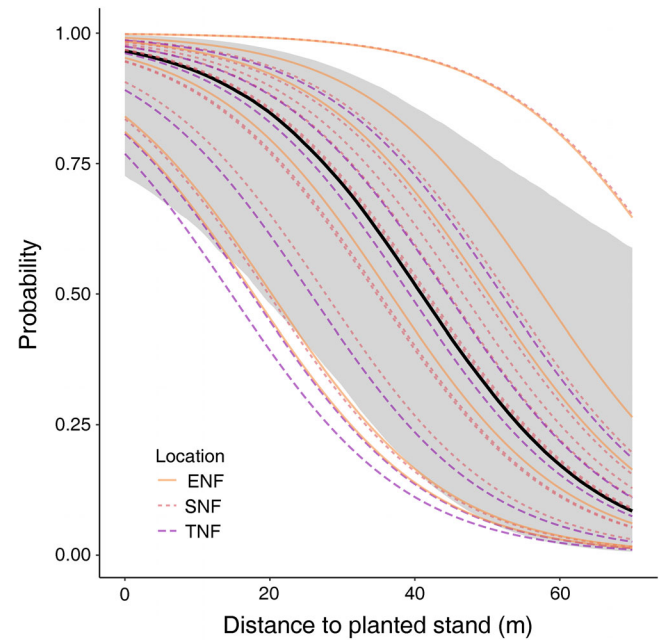


FIGURE 3 Predicted probability of seedlings (except *C. decurrens*), based on distance to planted stand and with all other variables held constant at their mean observed value. Predicted probability is in black, with a 95% confidence interval in gray. Transect-level predictions are included in color and varying line types to demonstrate variation between locations. ENF, Eldorado National Forest; SNF, Sierra National Forest; TNF, Tahoe National Forest.

TABLE 4 Models results for probability of observing (“presence” columns) and density of all conifer seedlings (except *Calocedrus decurrens*).

Predictors	Presence (all species) ^a		Density (all species) ^b	
	Log odds	<i>p</i>	Log mean	<i>p</i>
(Intercept)	3.35 (0.96 to 5.74)	0.006	0.98 (0.07 to 1.89)	0.034
Distance from planted stand (m)	-0.08 (-0.14 to -0.03)	0.003	-0.02 (-0.03 to -0.00)	0.021
Shrub volume	0.15 (-0.81 to 1.11)	0.760	-0.43 (-0.95 to 0.08)	0.101
Other natural regeneration (density)	4.46 (-0.23 to 9.16)	0.063	0.65 (0.27 to 1.02)	0.001
Large trees seed source (index)	0.93 (-0.49 to 2.34)	0.199	0.22 (-0.33 to 0.77)	0.429
Natural regeneration seed source (index)	0.58 (-0.49 to 1.65)	0.288	0.10 (-0.25 to 0.46)	0.569
Ground cover: litter (pct)			0.37 (0.05 to 0.68)	0.022

Note: Coefficients that are significant at $p < 0.1$ are bolded for emphasis.

Abbreviation: ICC, intraclass correlation coefficient.

^aObservations = 87. Marginal $R^2 = 0.761$. Conditional $R^2 = 0.893$. Random effects as follows: $\sigma^2 = 3.29$; $\tau_{00} = 4.01_{\text{transect}}$; ICC = 0.55; $N = 23_{\text{transect}}$.

^bObservations = 87. Marginal $R^2 = 0.223$. Conditional $R^2 = 0.844$. Random effects as follows: $\sigma^2 = 0.88$; $\tau_{00} = 3.48_{\text{transect}}$; ICC = 0.80; $N = 23_{\text{transect}}$.

which may be especially important for shade-tolerant species like *A. concolor* and *C. decurrens*. Applied nucleation theory would also suggest that animal dispersers may be attracted to forest patches, thereby providing a mechanism for dispersing species not common in the planted stands; however, this is unlikely given that the species found are primarily gravity- and wind-dispersed.

We also found that the density of older natural regeneration was positively correlated with YP seedling density, highlighting the importance of large trees, such as those that survive wildfires or are present at wildfire edges—or other remnant trees from much older cohorts in a nonwildfire context. Large trees generated seed rain for decades prior (the older natural regeneration) and likely continued to enable the establishment of seedlings within the focal age range. Though we attempted to control for seed availability from large trees by measuring distances to these trees, our model did not capture a significant relationship with this term. One limitation of our study was that we could only measure distances to standing trees, whereas seed sources for older natural regeneration could have fallen in the interim. This is especially possible given the high amount of drought- and beetle-driven pine and fir mortality in this region in the 5 years prior to our field surveys (Restaino et al., 2019; Young et al., 2017). Given this or simply due to the high context dependency of dispersal and establishment processes, it may be that the density of other natural regeneration provided a more direct estimate of seed rain from these trees—or microsite suitability—and was therefore a better explanatory variable.

We did not find a significant relationship between shrub competition and seedling establishment; therefore, our competitive impacts hypothesis was not supported based on these data. One potential explanation is that our sample size was too small. In fact, we did find that shrub volume had a marginally significant negative effect on seedling density for both YP-only and all-seedling models. This is suggestive of a true effect, though additional data collection would be required for statistical confirmation. Another potential explanation is that shrub cover may affect a different part of the life cycle than the one we were observing. We focused on germination and early establishment and therefore modeled seedling presence and density; however, it may be that seedling and sapling growth will continue to be impacted by shrub competition (Werner et al., 2019) and slow the transition to forest cover.

It is also possible that we observed a net neutral observed effect because both facilitative and competitive processes were operating in this system. Observational studies have suggested that shrubs can be positively correlated with tree regeneration (e.g., Collins & Roller, 2013; Downing et al., 2019; Shatford et al., 2007), though

this pattern is hard to disentangle from a scenario where productivity—rather than facilitation—drives increases in both plant forms. Experimental studies generally have shown negative or neutral shrub effects: one study demonstrating generally facilitative interactions among planted shrub-tree pairs in Spanish ecosystems facing similar climatic patterns (e.g., heat stress and lack of water availability during the growing season) also found that this effect was not significant among higher-elevation pines—the species mix most resembling our focal species (Gómez-Aparicio et al., 2004). Other empirical work in YPMC systems suggests that depending on environmental conditions, shrubs may play a competitive or facilitative role with regard to the survival of young pine seedlings (Legras et al., 2010; Werner et al., 2019), but they consistently have negative effects on growth (Werner et al., 2019). Further, the negative effect of shrubs on seedling growth rates may contribute to higher YP mortality (Tubbesing et al., 2020). Thus, it might be reasonable to expect that (1) environmental heterogeneity led to a variety of interactions across plots, obscuring a directional pattern, or (2) negative interactions might be increasingly influential once seedlings are established.

The potentially contingent nature of tree–shrubs interactions highlights a major limitation of our study: a single-year snapshot observation of tree regeneration is unable to capture the nuances between seedling life stages. We observed only seedlings that survived long enough to be observed and as a result are not able to disentangle germination rates from survival—and whether facilitation and competition might operate at either or both of these stages. Thus, our inferences come from a relatively narrow band in tree life stages: seedlings that have initially survived but whose long-term growth and viability may be impacted by shrubs.

In fact, shrub heights vastly exceeded seedling heights in most of our plots (Figure 4), calling into question how quickly these seedlings will be able to grow under these circumstances. It is likely that these seedlings will grow much slower and may even have reduced survival under these conditions (Airey Lauvaux et al., 2016; Tubbesing et al., 2020; Werner et al., 2019), and it may take several decades before they are able to overtop shrubs and capture the resources needed for more rapid growth (Airey Lauvaux et al., 2016). If this is the case, then the second cohort of trees in the zone surrounding the planted stand may be delayed in contributing seed for further expansion, and early expansion may be limited to longer-distance dispersal from the original planted cohort or other seed sources distributed in the landscape. This could limit the potential for planting to accelerate a shift from montane chaparral landscapes to forest cover across a broad landscape.

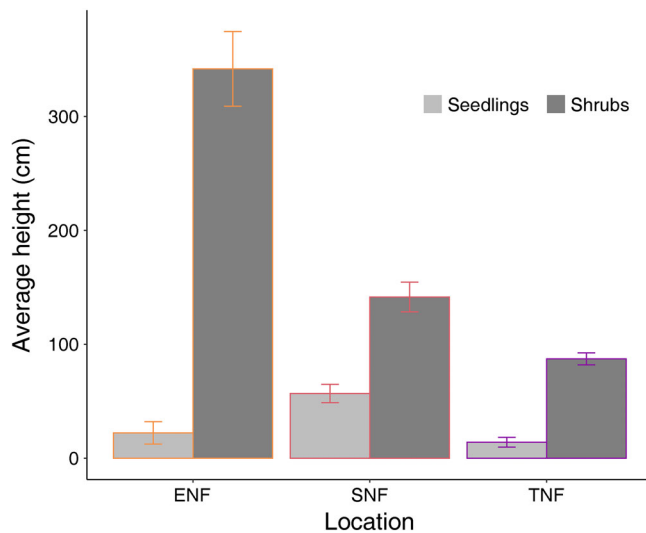


FIGURE 4 Mean and standard error of shrub and seedling heights, summarized for all plots across the three study locations. ENF, Eldorado National Forest; SNF, Sierra National Forest; TNF, Tahoe National Forest.

Applications

Though we found that planted trees could serve as seed sources for further establishment, there are some limitations to the extent to which this finding can be applied for landscape restoration, as implied by the nucleation and founder stand frameworks. Notably, we found only a 65% probability of observing YP seedlings directly within a planted stand, with this probability dropping substantially as we move away from the stand. In areas directly adjacent to a planted stand, we observed average YP seedling densities to be commensurate with 46 (18) trees per hectare (acre). This amount is within the range of historical densities of adult trees (Collins et al., 2015; Stephens et al., 2015), but it may not reflect a suitable density for seedlings. USDA Forest Service silvicultural guidelines specify a target stocking rate of about 500–740 trees per hectare in these forest types, indicating that the observed levels may not be considered sufficient by forest managers. Even outside the context of agency-specific guidelines, typical seedling densities in unburned areas may be closer to 750 individuals per hectare (Welch et al., 2016).

The low probability of occurrence and density of seedlings within and adjacent to seed sources may indicate that site suitability continues to be a key factor limiting establishment, though we were unable to attribute it to any one specific biotic or abiotic driver. We can infer, based on comparing shrub and seedling heights, that competitive dynamics may limit seedling growth. Under these ecological conditions, forest managers wanting to accelerate the transition from shrub cover to forest cover often may

consider it worthwhile to remove competing vegetation (McDonald & Fiddler, 2010) or otherwise prepare sites for recruitment near planted sites (North et al., 2019); however, this may not be feasible in the remote circumstances that necessitate the nucleation or founder stand strategy in the first place. However, planting founder stands may be a realistic option in cases where management is limited for other reasons—for example, to limit soil disturbance (such as near archeological sites) or where other management goals conflict with reforestation objectives. In these cases, planted founder stands may provide a critical source of seed rain to areas unable to be replanted directly, though land managers should not expect seedling density or vigor to be comparable to those of actively replanted areas.

Site productivity, the disturbance context, and land-use histories are also likely to be important considerations when using nucleation strategies. Though we did not find that the inclusion of unburned sites with postfire sites substantially changed our model results, we did observe that regeneration at TNF was quite low (Table 3), potentially a result of being a higher-elevation, lower-productivity region. We interpret this as a signal that the overall effect of planted nuclei may be similar among locations, but the landscape-level impact in terms of tree densities may differ based on local conditions. Given the pace of climate and other global change, it will be important to consider whether site conditions are able to support both the pace of planted tree growth as well as associated seedling growth in order to meet density targets.

Forest managers may wish to consider modifying the species composition of planted stands to favor shade-tolerant species or species with a long dispersal range. Though planting practices often prioritize species that are shade-intolerant or have a short dispersal range in order to achieve establishment that may not otherwise occur, as well as to steer forest composition toward a fire-adapted species mix that reflects prefire suppression conditions, planting for nucleation purposes may benefit from a more diverse species mix. In YPMC forests, for example, *Abies concolor* seedlings are able to survive and grow slowly even when overtopped by shrubs (Oakley et al., 2006), particularly in comparison with co-occurring pine species (Tubbesing et al., 2020). *A. concolor* also has small seeds relative to co-occurring pines, corresponding to a larger dispersal range (Safford & Stevens, 2017). Including *A. concolor* and species with similar traits in the planting mix could be a “bet hedging” strategy that increases the likelihood and range of forest expansion in the long term.

Our models also captured the importance of older natural regeneration in predicting younger seedling establishment, indirectly pointing to the role of surviving LTSS in driving recruitment. This pattern suggests that

large trees could play a significant role relative to planted trees, especially given that propagule pressure scales with tree size (Clark et al., 1999; Greene & Johnson, 1994). This would be consistent with findings across many ecosystems that large remnant or “scattered” trees can have a dramatic impact on the surrounding land, including serving as seed sources for regeneration (Manning et al., 2006). Our surveys did not stratify across distances to LTSS (and in fact tried to minimize the influence of these trees), but we suggest that a rigorous investigation of the relative contributions of remnant trees versus planted trees to multigenerational recruitment would be a fruitful avenue for further research. Depending on these relative contributions, land managers may find it worthwhile to invest significantly more in management practices that protect tree stands from mortality (“green forest management”) to obviate the major expenses—and higher uncertainty—associated with active postmortality planting—and particularly if planting is focused on spatially expanding the forest stand. The efficacy of nucleation treatments will also likely depend on dispersal syndromes and management objectives. Our study focuses on species that are primarily wind- or gravity-dispersed; however, many nucleation applications pertain to zoochorous plants and the important role of planted nuclei in terms of attracting dispersers and, therefore, increasing biodiversity across multiple trophic levels (see Guevara et al., 1986, as well as Holl et al., 2020, for a more complete review). Our study took a limited approach in terms of only considering the impact of nuclei on additional regeneration, and this may have ignored some of the other ecological impacts of planted nuclei. Even within the context of stimulating regeneration, the role of shrubs may differ based on ecological context. For example, shrubs may facilitate regeneration if they attract animal dispersers or favorably modify abiotic conditions, but this positive interaction may change over different life stages and may not apply to wind-dispersed seeds (Holl, 2002). Given these nuances, land managers will need to consider the specific dispersal strategies and shrub interactions of their ecosystem as they decide whether nucleation is likely to succeed.

CONCLUSION

The scale of high-severity wildfire in the Western US has raised concern over the possibility of forest recovery over broad regions that now experience limited dispersal from surviving or unburned trees (e.g., North et al., 2019)—a concern that echoes questions globally about whether forests will recover after land conversion, pest outbreaks, and

other stressors that can lead to the widespread mortality of seed trees (Peñuelas et al., 2017; Safford & Vallejo, 2019). These questions have prompted a reckoning over the role of reforestation and other management practices to accelerate forest recovery (and linked ecosystem service and conservation goals; Kemppinen et al., 2020; Staples et al., 2020). However, it remains unclear whether planting can have predictable and continued effects outside of the immediate planting zone and therefore at the landscape scale. We found that planting mostly wind- and gravity-dispersed trees could lead to subsequent regeneration outside of planted stands, but that this regeneration was limited in scale (low probability, potentially low density) and may have limited vigor or long-term survival; thus, the continued outward expansion from planted stands may occur over a much longer time horizon than desired by forest managers or permitted by the current (or future) fire regime. In systems with increasing fire frequency and the potential for short-interval reburns and where shrub-dominated vegetation may decrease seedling growth and increase future fire severity (Coppoletta et al., 2016), forest recovery will depend on whether regeneration and tree growth can keep pace with mortality from wildfire events. This scenario characterizes the contemporary YPMC ecosystem in much of the Western US. Our empirical study provides estimates of expected recruitment that can aid in projecting the likelihood of forest recovery in YPMC-type forests, particularly over the mid to long term following disturbance. These estimates may differ from other ecosystems, but they suggest that expectations for recruitment and forest recovery should generally reflect not only seed availability but also whether site conditions enable tree growth rates that can keep pace with disturbance trends.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Ursell, 2022a) are available in Dryad at <https://doi.org/10.25338/B80341>. Code (Ursell, 2022b) is available in Zenodo at <https://doi.org/10.5281/zenodo.5799734>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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