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A Mixed-Effects Heterogeneous Negative Binomial Model for Postfire Conifer Regeneration in Northeastern California, USA

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Many western USA fire regimes are typified by mixed-severity fire, which compounds the variability inherent to natural regeneration densities in associated forests. Tree regeneration data are often discrete and nonnegative; accordingly, we fit a series of Poisson and negative binomial variation models to conifer seedling counts across four distinct burn severities and three forest types 10 years after the 23,000-ha Storrie Fire, a large mixed-severity fire in northern California. Despite the accessibility and power of the zero-inflated negative binomial mixture model, a flexible heterogeneous negative binomial model offered a superior fit. Incorporation of a random stand effect further improved model performance. A parametric bootstrap analysis was conducted to examine seedling distributions and stand stocking. Mean simulated seedling densities had an expansive range (272–29,257 ha^{-1}). Stocking analyses suggest a high probability of deficient conifer coverage in the majority of lower-elevation high-severity burn stands. In addition, models were fit to fir and pine seedling counts. Only a minority of postfire stands were likely to be stocked in the pine-only analysis. These models will help land managers prioritize limited resources for artificial reforestation in mixed-severity burned landscapes.

Keywords: burn severity, natural regeneration, ponderosa pine, white fir, zero-inflated negative binomial, Storrie Fire, stocking analysis

Many forests in the western United States experience mixed- or moderate-severity fire (Agee 1993, p. 19–24, 305). The immediate effect of mixed-severity fire is often a patchy mosaic of diverse stand structures (Lentile et al. 2005, Halofsky et al. 2011). Natural regeneration or the development of a new cohort is an integral stage in postdisturbance single-cohort or multicohort stand development (Oliver and Larson 1996). In addition to a number of environmental factors that affect conifer regeneration (e.g., Bonnet et al. 2005, Gray et al. 2005, Moghaddas et al. 2008), variable remnant overstory densities that directly result from mixed-severity fire contribute to high spatial and compositional variability in seedling establishment across a landscape (similarly, McDonald 1976, Turner et al. 1997, Jayen et al. 2006).

Managers must decide whether postfire natural regeneration will meet management objectives or whether additional planting is required to meet stocking objectives in a timely manner. Planting is a conventional postfire alternative to the natural development of a new stand. Artificial regeneration can expedite establishment of desirable species at suitable densities (Smith et al. 1997, p. 5), resulting in ecosystems more quickly restored to a productive state for a number of management goals, from timber production to habitat restoration (e.g., Zhang et al. 2008). Despite the potential ecological and future monetary benefits of planting efforts, this avenue of restoration can be costly. To maximize management efficiency after mixed-severity fires, it is important to concurrently determine where natural regeneration is dependable and where artificial regeneration may be preferred for landscape restoration.

In an era of large wildfires in the western United States (Stephens 2005, Westerling et al. 2006, Miller et al. 2009b), land managers may be unable to quickly plant seedlings across a landscape because of constraints of time, resources, and accessibility. When highly variable regeneration is convoluted by a mixed-severity fire event (Turner et al. 1997, Crotteau et al. 2013), a landscape-level regeneration model can inform managers whether supplemental planting to meet silvicultural goals is needed. Although regeneration dynamics may vary substantially by species and ecoregion, modeling of postfire natural regeneration patterns has utility for predicting recovery from future wildfires.

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Natural regeneration is often modeled as discrete count data, for which a collection of linear and nonlinear modeling tools is available (Cameron and Trivedi 2008, p. 15–16, Zeileis et al. 2008). Count data may be assumed to follow a Poisson distribution; however, this distribution has limited applicability because a single parameter quantifies both the mean and variance. In situations in which observed count data exhibit overdispersion, i.e., observed variance exceeds the mean (Cameron and Trivedi 2008, p. 4), distributions such as the discrete Weibull or negative binomial may be favored. The negative binomial distribution is more flexible and well suited for applications where Poisson overdispersion is present. This two-parameter distribution can be parameterized so that a dispersion parameter, θ, relates the mean and variance: $V(y) = \mu + (\mu^2/\theta)$; $\theta > 0$.

Modified Poisson and negative binomial applications have been developed in response to observed phenomena in which mixtures of distributions most aptly describe the underlying process. Two such mixture models include the zero-inflated Poisson (ZIP) and the zero-inflated negative binomial (ZINB), both of which incorporate binary proportions to account for a surplus of zeroes (Lambert 1992, Welsh et al. 1996).

Mixture models are becoming more commonly applied to observational studies in forest sciences, with varying model complexity (e.g., Affleck 2006, Eerikäinen et al. 2007, Eskelson et al. 2009, Flores et al. 2009, Li et al. 2011). Mixtures incorporating flexible (two-parameter negative binomial or Weibull) distributions are often superior to Poisson mixtures (e.g., Fortin and DeBlois 2007, Zhang et al. 2012). Yet, in popular statistical packages (e.g., R, S-PLUS, and SAS software) application of the negative binomial is often restricted by the assumption of a single dispersion parameter. That is, although the mean response may vary conditionally on some explanatory variable(s), the dispersion parameter (θ) remains fixed for all observations. If the data exhibit heterogeneity, as is common in natural regeneration subpopulation distributions, restrictions on the estimation of θ may produce unsatisfactory results (Hilbe 2011, p. 157, 323).

Finally, many contemporary observational studies are designed in a hierarchical fashion (e.g., Booth et al. 2003, Li et al. 2011). Nested studies are often designed for the sake of logistics (resource-saving) or because of a lack of other options (opportunistic empiricism). Observed variances must be calculated and handled with regard to the nesting inherent in these designs, resulting in a tiered model analysis with random and fixed effects. The resultant statistical mixed-effects model, although more complicated in formulation and interpretation than a fixed-effects model, accounts for observed error and may offer a truer description of the potentially autocorrelative error structure and conditional mean (e.g., Garber and Maguire 2005). Furthermore, inclusion of random effects expands the potential for model inference by describing the probability distribution of nested structures.

Our study examined conifer seedling regeneration in the Lassen National Forest approximately 10 years after the 2000 Storrie Fire, a 23,000-ha wildfire that burned with mixed severity. This study was designed to aid future postfire management decisions in the bioregion by identifying remotely sensed postfire landscape characteristics attributable to insufficient conifer seedling densities. We used the Composite Burn Index (CBI) (Key and Benson 2006), as a metric to evaluate the effects of burn severity on postfire regeneration, with regard to forest type. We defined three coniferous species classes to address this objective: all observed species; *Abies* spp.; and select *Pinus* spp. We compared a series of pure and mixed distribution models and, in the interest of model flexibility, restricted and heterogeneous negative binomial models. We finalized our selected model with the inclusion of random effects. Bootstrapped model predicted values were subsequently used in seedling stocking analyses to further gauge regeneration trends on the landscape. The results have utility for predicting regeneration dynamics after wildfire and aiding managers in the prioritization of restoration expenditures.

Methods

Study Site

The study site was a 9,371-ha portion of the Lassen National Forest (hereafter "Lassen") burned by the 2000 Storrie Fire in northeastern California (40°0′0″ N, 121°15′0″ W). The elevation within the study area varies from approximately 900 to 2,100 m above mean sea level. Regional climate is characterized as montane Mediterranean, having warm summers (mean monthly maximum temperature, June to September: 21–26° C) and cool winters (mean monthly maximum temperature, November to March: 6–9° C). Less than 5% of the annual precipitation falls during the summer, with the bulk of the 1,894 mm annual precipitation falling during the winter as snow (30-year prefire average) (PRISM Climate Group 2011).

Vegetation and topography were variable across the study area, as is typical of the montane westside southern Cascades bioregion (see Skinner and Taylor 2006). The most dominant regenerating coniferous species observed after the Storrie Fire were white fir (*Abies concolor* [Gordon & Glend.] Lindley), California red fir (*Abies magnifica* var. *magnifica* Andr. Murray), incense-cedar (*Calocedrus decurrens* [Torrey] Florin), sugar pine (*Pinus lambertiana* Douglas), ponderosa pine (*Pinus ponderosa* Laws.), and Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) (Crotteau et al. 2013). Although less common, Sierra lodgepole pine (*Pinus contorta* Louden var. *murrayana* [Grev. & Balf.] Critchf.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and western white pine (*Pinus monticola* Douglas) were also found. In addition to these conifers, California black oak (*Quercus kelloggii* Newb.) and a suite of shrubs (including pinemat manzanita [*Arctostaphylos nevadensis* A. Gray], greenleaf manzanita [*Arctostaphylos patula* E. Greene], mountain whitethorn [*Ceanothus cordulatus* Kellogg], deer brush [*Ceanothus integerrimus* Hook. & Arn.], snowbrush [*Ceanothus velutinus* Dougl.], bush chinquapin [*Chrysolepis sempervirens* (Kellogg) Hjelmq.], and huckleberry oak [*Quercus vaccinifolia* Kellogg]) were present across the postfire landscape.

Sampling Methods

To evaluate the effect of burn severity (Keeley 2009) on conifer regeneration after accounting for prefire overstory species variability, we divided the postfire landscape into 12 condition classes: 4 levels of severity × 3 levels of forest type. The CBI was used to determine burn severity category for the postfire stands. Because CBI is a field-based assessment of burn severity, we calculated the relative differenced normalized burn ratio (RdNBR) to remotely obtain CBI estimates (Miller and Thode 2007, Miller et al. 2009a). The RdNBR formulated a continuous index from prefire and 1-year postfire Landsat Thematic Mapper images, which was subsequently transformed into four CBI categories: unchanged (minimal or no visible effect of fire); low-severity; medium-severity; and high-severity (Table 1). Forest types were segregated by three elevation bands: mixed conifer (978–1,463 m); low-elevation fir (1,463–1,774 m);

Table 1. CBI thresholds used to create four burn-severity classes within the Storrie Fire perimeter, Lassen National Forest.

Fire severity level	CBI thresholds	
	Lower	Upper
Unchanged	0.00	0.10
Low-severity	0.10	1.25
Medium-severity	1.25	2.25
High-severity	2.25	3.00

CBI values were approximated via RdNBR (Miller et al. 2009a) using prefire and 1-year postfire Landsat imagery.

Table 2. Society of American Foresters (SAF) cover type and elevation thresholds used to delineate three forest types within the Storrie Fire perimeter, Lassen National Forest.

Forest cover type	SAF type	Elevation	
		Minimum	Maximum
		.....(m).....	
Mixed conifer	Mixed conifer (243)	978	1,463
Low-elevation fir	White fir (207), red fir (211)	1,463	1,774
High-elevation fir	White fir (207), red fir (211)	1,774	2,188

and high-elevation fir (1,774–2,188 m) (Table 2). Abbreviated strata names reflect forest type (MC, mixed conifer; LF, low-elevation fir; and HF, high-elevation fir) modified by burn severity (U, unchanged; LS, low-severity; MS, medium-severity; and HS, high-severity); e.g., MCLS represents mixed conifer low-severity.

Sixty stands were randomly selected (five per stratum) with probability proportional to size from a population of 2,292 stand polygons identified from 1-year postfire GIS data, ranging in area from less than 0.4 to 195 ha. Field data were collected over the course of two summers (half in 2009 and half in 2010), 9 and 10 years after the Storrie Fire. A randomly located and oriented hexagonal cluster of at least 19 0.004-ha (3.59-m radius) circular plots 20 m apart was established in each of the 60 selected stands, resulting in a total of 1,166 plots visited (see Crotteau et al. 2013, Appendix B).

Live mature seedlings were counted on each of the plots. Mature seedlings are here defined as seedlings that were "well-established," i.e., taller than 15.24 cm, up to any stem with dbh <10.16 cm. We did this to avoid counting ephemeral first-year seedlings.

Woody shrub cover (%) was estimated on each plot to assess perennial competing understory competition. Surviving overstory trees were sampled using a concurrent point sample (basal area factor: 4.592 m^2 ha^{-1}). These additional vegetation measurements varied across the strata (stratum-level values incorporated into Figures 2–4). Because of the random sampling of stands across the landscape, topographic attributes within and among strata were also highly variable.

Model Distributions

Models were developed for three separate natural regeneration response variables (counts) to assess three species-preferential factors: "all conifers"; *Abies* spp.; and select *Pinus* spp., in which the *Abies* spp. were *A. concolor* and *A. magnifica* and *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* comprised the *Pinus* class. The count response exhibited a high proportion of zeroes (31% for all species combined; 40 and 65% for *Abies* and *Pinus* classes, respectively), large arithmetic mean (14.1 for all species combined; 12.2 and 1.2 for *Abies* and *Pinus* classes, respectively), and extensive range (0–560 per plot for all species combined; 0–560 and 0–48 for *Abies* and *Pinus* classes, respectively). We considered a number of discrete distributions to find the best model fit for the skew-positive data, as many options were available (e.g., Zeileis et al. 2008).

Count data are inherently discrete and nonnegative. A traditional distribution for count data is the Poisson (P) distribution (Cameron and Trivedi 2008, p. 1–3). The Poisson probability mass function (PMF) is

$$f_P(y, \lambda) = \frac{\lambda^y e^{-\lambda}}{y!} \tag{1}$$

where y is a nonnegative integer value and λ is both the mean and variance. The primary limitation of the Poisson distribution is the assumption that mean and variance are equal. As is common in modeling of ecological data, when the observed variance is greater than the mean, the data are considered to be overdispersed (Cameron and Trivedi 2008, p. 77).

The negative binomial distribution (NB), a mixture between Poisson and gamma distributions, is a bivariate function that permits the shape of the distribution to be more flexible than that of the Poisson distribution (Cameron and Trivedi 2008, p. 71). The negative binomial PMF is

$$f_{NB}(y, \theta, p) = \frac{\Gamma(y + \theta)}{\Gamma(\theta)\Gamma(y + 1)} p^\theta (1 - p)^y \tag{2}$$

where $\theta > 0$ is the dispersion parameter and $0 < p < 1$. The expected value of y in this parameterization is μ, where

$$E(y) = \mu = \frac{\theta}{p} - \theta \tag{3}$$

and the variance of y is

$$V(y) = \mu + \frac{\mu^2}{\theta} \tag{4}$$

The Poisson distribution is a special case of the NB where $\theta \to \infty$. In NB fits, the estimated value of θ is often assumed to be constant across factors ("NB2" in Hilbe 2011, p. 39). If data exhibit heterogeneity, θ may vary ("NB-H" in Hilbe 2011, p. 39, 319). For the purpose of this study, we refer to models with a fixed θ parameter as "restricted" negative binomial (RNB) and models with varying θ parameters as "heterogeneous" negative binomial (HNB).

In observational abundance studies, it is common to encounter an abundance of zeroes, as in measuring abundance of a rare species. "Zero-inflated" modifications of the Poisson and NB distributions have been used to account for observed zeroes that are in excess of those expected from the Poisson or NB distribution (Lambert 1992, Welsh et al. 1996). Recent work suggests that the ZIP and ZINB may also be applicable for modeling natural regeneration (Barry and Welsh 2002, Keefe 2004, Affleck 2006, Rathbun and Fei 2006, Fortin and DeBlois 2007, Flores et al. 2009, Li et al. 2011, Zhang et al. 2012). These two-part mixture models incorporate a binary proportion for excess zeros, which can be expressed as a mixture parameter, ω. The ZIP PMF is

$$f_{ZIP}(y, \omega, \lambda) = \begin{cases} \omega + (1 - \omega) f_P(y, \lambda) & y = 0 \\ (1 - \omega) f_P(y, \lambda) & y > 0 \end{cases} \tag{5}$$

where ω is the probability of observing a zero independent of the Poisson process. Similarly, the ZINB PMF is

$$f_{\text{ZINB}}(y, \omega, \theta, p) = \begin{cases} \omega + (1 - \omega) f_{\text{NB}}(y, \theta, p) & y = 0 \\ (1 - \omega) f_{\text{NB}}(y, \theta, p) & y > 0 \end{cases} \quad (6)$$

where the probability of observing a zero independent of the negative binomial process, ω, adjusts the restricted (RZINB) or heterogeneous (HZINB) model.

Model Selection and Evaluation

We used Akaike's information criterion (AIC) and Pearson's dispersion parameter (φ) for model selection and validation. AIC is calculated as

$$\text{AIC} = -2L + 2k \quad (7)$$

where the model's log-likelihood L is penalized by parameters k. The best models were selected using AIC in an information theoretic approach. With regard to the lowest calculated AIC, models with $\Delta\text{AIC} \leq 2$ were considered to be relatively well supported by the data; models with $\Delta\text{AIC} \geq 10$ were regarded as unsupported (Burnham and Anderson 2002, p. 70). AIC is a relative metric that only considers rankings among models considered in the analysis; the bias-corrected AIC_c was not used because there is no agreement as to the proper calculation of the bias-correction term for discrete dependent variables (Burnham and Anderson 2002, p. 380).

Pearson's dispersion parameter is defined as

$$\varphi = \Sigma \frac{(R_i^P)^2}{n - k} \quad (8)$$

where n is total sample size, k is the number of estimated parameters, and Pearson's residuals (R_i^P) are

$$R_i^P = \frac{y_i - \hat{y}_i}{\sqrt{V(\hat{y}_i)}} \quad (9)$$

where $\hat{y}_i$ is the predicted value and $V(\hat{y}_i)$ is the variance of the ith observation y_i. Values for φ near 1.0 indicate equidispersion of the variance within the data set and thus better model fit (Zuur et al. 2009, p. 224, Hilbe 2011, p.88–89); $\varphi > 1.0$ may indicate model distribution misspecification or improper estimation of the mean and variance (Cameron and Trivedi 2008, p. 151).

Models were fit and analyzed using both R (The R Foundation for Statistical Computing 2012) and SAS software (SAS Institute, Inc. 2012) with strata as a 12-level independent factor, or class, variable in an effort to gauge the effect of burn severity on dependent seedling counts in three forest types. Models were developed in a piecemeal approach using R's pscl (Jackman et al. 2012) and glmmADMB (Skaug et al. 2011) packages and paralleled in SAS software's PROC NLMIXED. We began by modeling the all conifers response with a Poisson generalized linear model (GLM). The presence of overdispersion ($\varphi = 57.89$) led us to consider a RNB GLM; the RNB had a dispersion parameter much lower than that of the Poisson ($\varphi = 1.36$). Yet, the preponderance of zeroes in addition to large values prompted us to also fit a RZINB. After including strata predictors, the RZINB mixture model had lower total AIC ($\Delta\text{AIC} = 39.1$) and Pearson's φ than the corresponding RNB model (25 and 13 predictors, respectively). Despite a better fit, the shape of the RZINB-predicted distribution of seedling counts differed from the empirical distribution in many strata as a result of the common (restricted) θ parameter. In addition, the estimated probability of observing an excess zero (ω) was 0 for 3 of the 12 strata ($\omega < 0.05$ in two other strata), thus providing little or no evidence of a zero-inflated process.

We hypothesized that a HNB model may properly account for variation within our data set, allowing θ to vary by stratum. For comparison purposes, we fit a suite of models with parameters conditioned on forest type and burn severity: (1) Poisson; (2) ZIP; (3) RNB; (4) HNB; (5) RZINB; and (6) HZINB. In the interest of model convergence and simplicity, plots were treated as independent observations. Models were subsequently compared via inspection of AIC, model variance, and Pearson's φ.

After selecting the HNB from the candidate distributions, we amended the model error structure to include the random effect of sampled stands from the study area, thereby more appropriately addressing the hierarchical nature of the study design. We did not pursue altering the P, ZIP, RNB, RZINB, and HZINB error structures because of their inferior AIC values. A random stand-level error term $\varepsilon_{ij} \sim N(0, \sigma_i^2)$, i = stratum, $j = [1, 5]$ was included within the log-link, thereby creating a HNB model with mixed effects (HNBmixed). In so doing, we shift the interpretation of the data's count response from being unconditionally negative binomial to negative binomial conditioned on any given stand's random normal variate. To generate biologically meaningful values, as per the data, the unconditional means were calculated using a parametric bootstrapping technique (Efron and Tibshirani 1994). We simulated conifer counts using the data-derived HNBmixed model, creating a data set that mimicked the hierarchical structure of its parent [12 strata, each composed of 5 stands with $\varepsilon_{ij} \sim N(0, \sigma_i^2)$, which in turn house 19 plots]. This process was executed 10,000 times after we set a random start seed, whereby we attained the unconditional simulated count means by stratum.

Although biotic and abiotic variables commonly assumed to influence seedling growth were measured on plots, they are not here presented as model covariates because of convergence failure or only marginal significance in some of the more complex models. Furthermore, the core predictors in the HNBmixed model used up 36 *df* and was already approaching overparameterization, given the sample size. We therefore refrained from further complicating the model form in the spirit of parsimony.

Stocking Analysis

A conventional method for assessing regeneration densities, natural or artificial, is a stocking analysis. The goal of stocking analyses is to determine whether the spatial distribution of regeneration is sufficiently balanced within a stand. Within the USDA Forest Service (US Department of Agriculture 1987), plots are evaluated as "stocked" or "not stocked" based on regional density thresholds: at least 50% of plots visited must be stocked for adequate restocking certification (US Department of Agriculture 1987). In California, the recommended standard for reforestation is 741 trees ha^{-1} (3.7-m spacing) in red and white fir cover types, whereas the recommended density threshold for the mixed conifer type (having a significant *Pinus* spp. component) is 494 seedlings ha^{-1} (4.5-m spacing) on 0.004-ha plots or larger (US Department of Agriculture 1987). Actual stocking certification further requires that sample plots be systematically located at a sample intensity of 1%; our study does not fully accomplish the recommended sample intensity but

Table 3. ΔAIC values for six conifer seedling regeneration models across 12 strata 9–10 years after the 2000 Storrie Fire, Lassen National Forest.

Model	Parameters	Stratum											
		MCU	MCLS	MCMS	MCHS	LFU	LFLS	LFMS	LFHS	HFU	HFLS	HFMS	HFHS
Poisson	1	636.2	1,571.5	5,689.4	633.8	934.9	5,140.7	2,148.9	123.9	527.0	9,151.9	3,514.6	634.5
ZIP	2	553.9	1,176.5	4,217.4	228.5	699.2	3,904.3	1,364.5	56.2	368.6	6,450.5	2,632.1	283.1
RNB	2	64.8	20.5	61.6	44.3	19.2	34.6	19.7	26.2	28.1	42.4	75.4	71.2
HNB	2	16.8	20.2	58.7	31.1	14.2	21.7	19.7	25.5	9.1	22.7	71.6	71.2
RZINB	3	—	24.1	67.5	31.5	—	41.1	20.5	28.3	—	34.0	73.4	71.0
HZINB	3	—	—	—	31.5	—	—	20.5	—	—	—	73.3	69.6
HNBmixed	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

These values are only comparable within columns, where the number of parameters used to calculate AIC is given and ΔAIC is obtained by subtracting best model AIC per stratum. Parameters given indicate the number of estimated parameters necessary to calculate likelihood values for each individual stratum. —, convergence collapsed to a non-zero-inflated RNB and HNB, respectively.

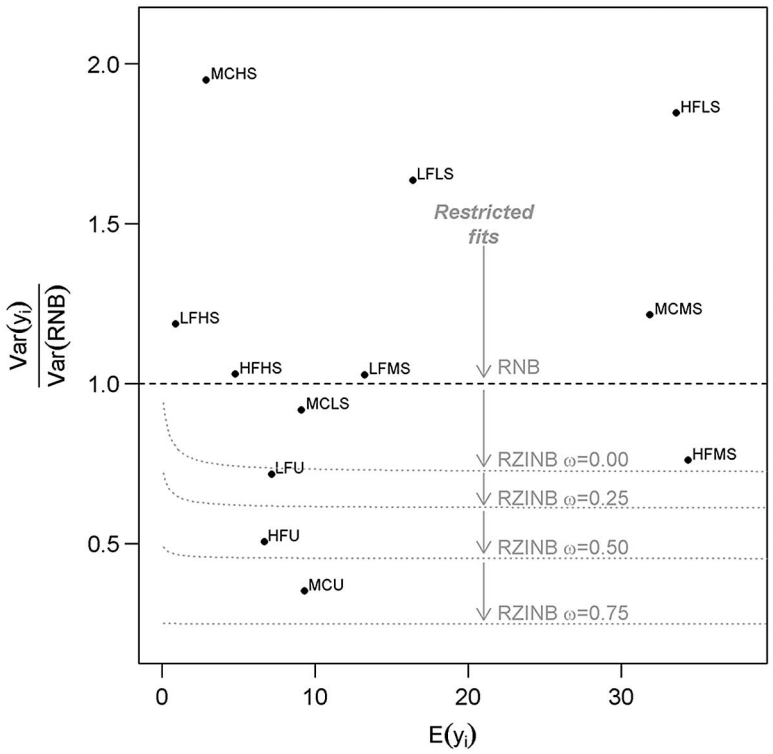

Figure 1. HNB conifer seedling count relative variance as modeled by the RNB and RZINB alternatives after the 2000 Storrie Fire, Lassen National Forest.

assumes that within-stand variability is captured within the model distributions. We calculated the probability of stocked stands, based on the aforementioned specific density thresholds, via the parametric bootstrap procedure to evaluate stocking by stratum.

Results

Model Distribution Selection

The HNB produced the most favorable fit statistics. ΔAIC values subdivided by the 12 factors are presented in Table 3, using the lowest model AIC within each stratum to calculate ΔAIC. The HNB AIC was the lowest of the model structures for 11 of the 12 strata. The Poisson and ZIP models consistently had the largest AIC values across strata, suggesting they are not supported by the data. ΔAIC suggested that the RNB was no different from the HNB in three strata. RZINB and HZINB zero-inflated mixture parameters, ω, reached the bound at 0 in three and eight instances, respectively, although when convergence was successful, ΔAIC was relatively low.

Stratum-by-stratum AIC values indicated that the HNB was clearly a better fit than the Poisson and ZIP, and the HZINB collapsed to the HNB more often than not. Therefore, we proceeded to examine this model in comparison with the more typical alternatives, i.e., the RNB and RZINB. Whereas the stratum-by-stratum approach taken to examine the inner workings of the models was useful, we proceeded in the typical full model approach to inspect the overall AIC. The 13-parameter RNB model had the largest total AIC of the three models, whereas the 24-parameter HNB had the lowest despite the penalty for additional parameters.

Calculated model variances (Equation 4) from the HNB expressed as a proportion of the RNB estimate demonstrate that the restricted model imprecisely estimated strata variance, which we defined as the free-to-vary HNB variance (Figure 1). It also appeared

that the RZINB underpredicted variance for 8 of the 12 strata; underprediction was exacerbated as estimated binary proportion ω increased. These differences are a direct consequence of estimating a single common model θ parameter.

Pearson's dispersion parameters (φ) incorporate model variance in the calculation of Pearson's residuals. RZINB Pearson's residuals produced the largest φ value; φ was lowest for HNB (Table 4). With a value nearest 1.0, the HNB φ (1.2153) indicated that the model best accounted for dispersion relative to the mean; this value was 15% smaller than that of the RZINB.

Overall, model comparison techniques supported the HNB. Although the RZINB appeared to be considerably better than the RNB, the HNB more properly addressed variance than the more accessible RZINB. Furthermore, the HNB estimated one less parameter than the RZINB; thus, it was chosen as the most appropriate discrete distribution. Finalization of the HNB by including random effects to formulate the HNBmixed yielded a model that was both more statistically sound and more supported by the data than any of the fixed-effects models (Table 4). The HNBmixed model addressed the hierarchical nature of the data and affirmed that some level of spatial autocorrelation was present, i.e., that plots within a stand are more similar than plots from another stand within a given stratum. To verify that the model had altogether marginalized the effects of spatial autocorrelation, we further inspected within-stand variability in a georeferenced nearest neighbor approach using Moran's *I* (Moran 1950). We calculated a grand *I* statistic of 0.05 (range of potential values [−1, 1]) and associated *P* value of 0.37 in a four nearest neighbor analysis, indicating that the within-stand seedling spatial autocorrelation was negligible.

Table 4. Select model fit statistics under heterogeneous and restricted approaches, modeling seedling regeneration 9–10 years after the 2000 Storrie Fire, Lassen National Forest.

Response	Model	*k*	AIC	φ
All conifers	RNB	13	7,173.30	1.3592
	RZINB	25	7,134.20	1.4014
	HNB	24	7,070.79	1.2153
	HNBmixed	36	6,767.00	1.1042
Abies spp.	HNB	24	6,302.18	1.0853
	HNBmixed	36	5,742.76	1.0771
Pinus spp.	HNB	16	1,993.47	1.0616
	HNBmixed	24	1,727.00	0.9258

AIC values are only comparable within similar response variables.

Natural Regeneration

The above approach was performed with the all conifers count as the dependent variable; *Abies* and *Pinus* models were subsequently fit with the HNBmixed distribution as well, similarly using the strata as independent variables and incorporating the random effect of forest stands in which the plots were located.

The HNBmixed all conifers response model φ was 1.1042 (Table 4). Simulated model means ranged from 1.1 to 118.4 counts/plot (Table 5). The two lowest simulated means were for counts in MCHS and LFHS, both high-severity strata. HFMS, HFLS, and MCMS had the greatest simulated means. Within each forest type, the largest simulated mean was at least 13 times greater than the smallest. The greatest deviation of the simulated means from the sample mean was in the high-elevation fir forest type (HFLS and HFHS; 3.5 and 3.8 times greater, respectively). Overall, model θ coefficients varied from 0.305 in HFLS to 1.589 in HFHS.

The *Abies* spp. HNBmixed model had a φ of 1.0771 (Table 4). Simulated model means ranged from 0.6 to 143.9 seedlings plot^{-1} (Table 6). The model's simulated means were just below the all conifers response means in the majority of strata. Means positively deviated from the all conifers response, however, in the MCU, MCMS, HFLS, and HFMS. Model θ coefficients were generally similar to those for the all conifers model.

We only observed a total of seven *Pinus* seedlings in the high-elevation fir forest type. Because this was, as expected, such a rare event, we omitted the high-elevation fir forest type in formulating the *Pinus* model. The *Pinus* model φ was 0.9258 (Table 4). Simulated means were low, ranging from 0.1 to 4.6 seedlings plot^{-1} (Table 7). The greatest means within each forest type were in medium- and low-severity burns, whereas coefficients for unchanged and high-severity burns were the lowest. Although simulated means for the *Pinus* model had a much smaller range than the means for the first two models, model θ values ranged from 0.209 in the LFU to 2.408 in the LFLS. In addition, the ratio of the SD of the random error term to the model μ coefficients was much larger than the all conifers and the *Abies* models, indicating high interstand variability.

The mean portion of simulated stands stocked ranged from 5.7 to 97.8% across strata (Figure 2). The bootstrap simulation using the all conifers model predicts that there are four strata that have more unstocked/understocked stands than stocked: the LFLS,

Table 5. HNBmixed model coefficients and parametric bootstrap simulated mean "all conifers" seedling counts 9–10 years after the 2000 Storrie Fire, Lassen National Forest.

	Sample statistics		HNBmixed coefficients			Bootstrap simulation		
Stratum	Mean	Median	$\hat{\mu}$	$\hat{\theta}$	$\hat{\sigma}$	Mean	Median	90th percentile
MCU	9.3	6.5	7.9	1.552	0.57	9.3	8.9	13.0
MCLS	9.1	3.0	6.2	0.598	0.89	9.2	8.1	15.1
MCMS	31.9	6.0	11.9	0.724	1.60	41.6	25.2	85.3
MCHS	2.9	0.0	1.1	0.580	1.30	2.6	1.9	5.0
LFU	7.2	3.0	5.5	0.706	0.67	6.9	6.4	10.1
LFLS	16.4	1.0	8.3	0.327	1.04	14.2	11.7	25.2
LFMS	13.2	4.5	9.1	0.525	0.90	13.6	11.9	22.7
LFHS	0.9	0.0	0.4	0.841	1.48	1.1	0.7	2.2
HFU	6.7	4.0	6.0	0.984	0.53	6.8	6.5	9.3
HFLS	33.6	3.0	12.9	0.305	2.12	118.4	42.8	247.4
HFMS	34.3	19.0	17.3	1.394	1.41	46.7	32.8	91.0
HFHS	4.8	2.0	1.3	1.589	2.29	18.2	5.5	35.3

HNBmixed μ represents a negative binomial mean count conditional on the normally distributed random effect of stands within a stratum. Statistics derived using the parametric bootstrap algorithm are unconditional, less biased, and not of a strictly negative binomial distribution.

Table 6. HNBmixed model coefficients and parametric bootstrap simulated mean *Abies* spp. seedling counts 9–10 years after the 2000 Storrie Fire, Lassen National Forest.

	Sample statistics		HNBmixed coefficients			Bootstrap simulation		
Stratum	Mean	Median	$\hat{\mu}$	$\hat{\theta}$	$\hat{\sigma}$	Mean	Median	90th percentile
MCU	4.6	2.0	1.5	1.251	2.25	19.5	6.0	36.2
MCLS	3.6	1.0	3.0	0.399	0.63	3.7	3.4	5.4
MCMS	26.5	1.0	5.5	0.590	2.05	44.1	17.6	88.5
MCHS	2.0	0.0	0.6	0.567	1.57	2.1	1.3	4.2
LFU	5.9	2.0	4.0	0.649	0.78	5.4	4.9	8.4
LFLS	15.3	1.0	7.5	0.252	1.06	13.3	10.8	23.6
LFMS	11.4	2.0	5.9	0.472	1.26	13.1	9.8	25.1
LFHS	0.5	0.0	0.3	0.397	1.25	0.6	0.4	1.1
HFU	6.5	4.0	5.8	0.910	0.52	6.6	6.4	9.0
HFLS	33.4	3.0	11.9	0.296	2.26	143.9	45.0	289.3
HFMS	34.0	19.0	14.9	1.316	1.60	52.6	32.4	107.8
HFHS	4.6	1.0	1.2	1.730	2.29	16.6	5.0	32.7

HNBmixed μ represents a negative binomial mean count conditional upon the normally distributed random effect of stands within a stratum. Statistics derived using the parametric bootstrap algorithm are unconditional, less biased, and not of a strictly negative binomial distribution.

Table 7. HNBmixed model coefficients and parametric bootstrap simulated mean *Pinus* spp. seedling counts 9–10 years after the 2000 Storrie Fire, Lassen National Forest.

	Sample statistics		HNBmixed coefficients			Bootstrap simulation		
Stratum	Mean	Median	$\hat{\mu}$	$\hat{\theta}$	$\hat{\sigma}$	Mean	Median	90th percentile
MCU	0.8	0.0	0.3	0.867	1.24	0.7	0.6	1.4
MCLS	1.8	0.0	1.1	0.752	0.90	1.7	1.5	2.8
MCMS	3.8	2.0	2.2	0.944	1.25	4.6	3.6	8.7
MCHS	0.7	0.0	0.2	0.825	1.84	1.3	0.6	2.6
LFU	0.1	0.0	0.1	0.209	1.07	0.1	0.1	0.3
LFLS	0.9	0.0	0.3	2.408	1.88	1.5	0.8	3.1
LFMS	1.2	1.0	1.1	1.075	0.47	1.2	1.2	1.6
LFHS	0.3	0.0	0.1	0.482	1.98	0.5	0.2	1.1

HNBmixed μ represents a negative binomial mean count conditional upon the normally distributed random effect of stands within a stratum. Statistics derived using the parametric bootstrap algorithm are unconditional, less biased, and not of a strictly negative binomial distribution.

MCHS, LFHS, and HFHS. The probability that no more than 20% of postfire stands are naturally stocked is highest in the LFLS (0.97) and MCHS (0.69). *Abies* spp. stocking probabilities similarly mirror the all conifers response (Figure 3). The MCMS is the only stratum in the *Pinus* model in which nearly half of simulated stands are stocked (mean = 0.46) (Figure 4). Simulations in the remaining strata suggest a high probability of poor stand stocking across the landscape despite evaluation of *Pinus* spp. at the 494 seedlings ha^{-1} density level in both the mixed conifer and low-elevation fir forests.

Discussion

Model Selection

Our data strongly suggest that the Poisson distribution is a poor choice for modeling natural regeneration after the Storrie Fire (as in, e.g., Affleck 2006, Zhang et al. 2012). Even the more flexible ZIP model was not supported by the data in the stratum-by-stratum model analysis ($\Delta AIC > 30$) (Table 3). The variance-mean equivalency restriction that defines the Poisson process does not adequately describe the shape of the response even if one entertains a zero-inflated process. Although the maximum likelihood estimation (MLE) of the classic Poisson distribution provides the proper framework for estimating our sample means (Cameron and Trivedi 2008, p. 59–60), the seedling variability inherent to this study suggests the NB is a more appropriate distribution for proper variance calculation.

We observed that the HZINB mixture was capable of closely matching the empirical distribution of seedling counts in various strata. Strata in which the HZINB model excelled were not necessarily bimodal; where the HNB distributions were simultaneously driven by a multitude of zeroes and large response values, resulting in underestimated third quartiles, the mixture model was able to account for slight deviations from an otherwise HNB distribution. Yet, the AIC penalization of additional parameters estimated by the HZINB was not sufficiently counterbalanced by the reduction in log likelihood (Affleck 2006), and the cases for which ω reached the zero-bound and reverted to the HNB further suggests that the HZINB mixture overfit the data. Overall, the more parsimonious HNB appeared adequate for most observed conditions. Negative binomial models were similarly selected over more complex options via parsimony in stand mortality (Affleck 2006) and snag abundance (Eskelson et al. 2009) applications, although expressly "restricted" model forms were reported.

Modeling strata subsets of our data naturally created heterogeneous NB components, yet the HNB is not necessarily the standard alternative to the RNB. In discrete ecological applications with multiple factors, the common modeling pathway begins with fitting the Poisson distribution followed by the RNB, depending on dispersion; the RZINB is then the recommended tool if the RNB is still an imperfect fit for a data set with abundant zeroes, whereas the HNB is scarcely mentioned (e.g., missing in Zeileis et al. 2008, Zuur et al.

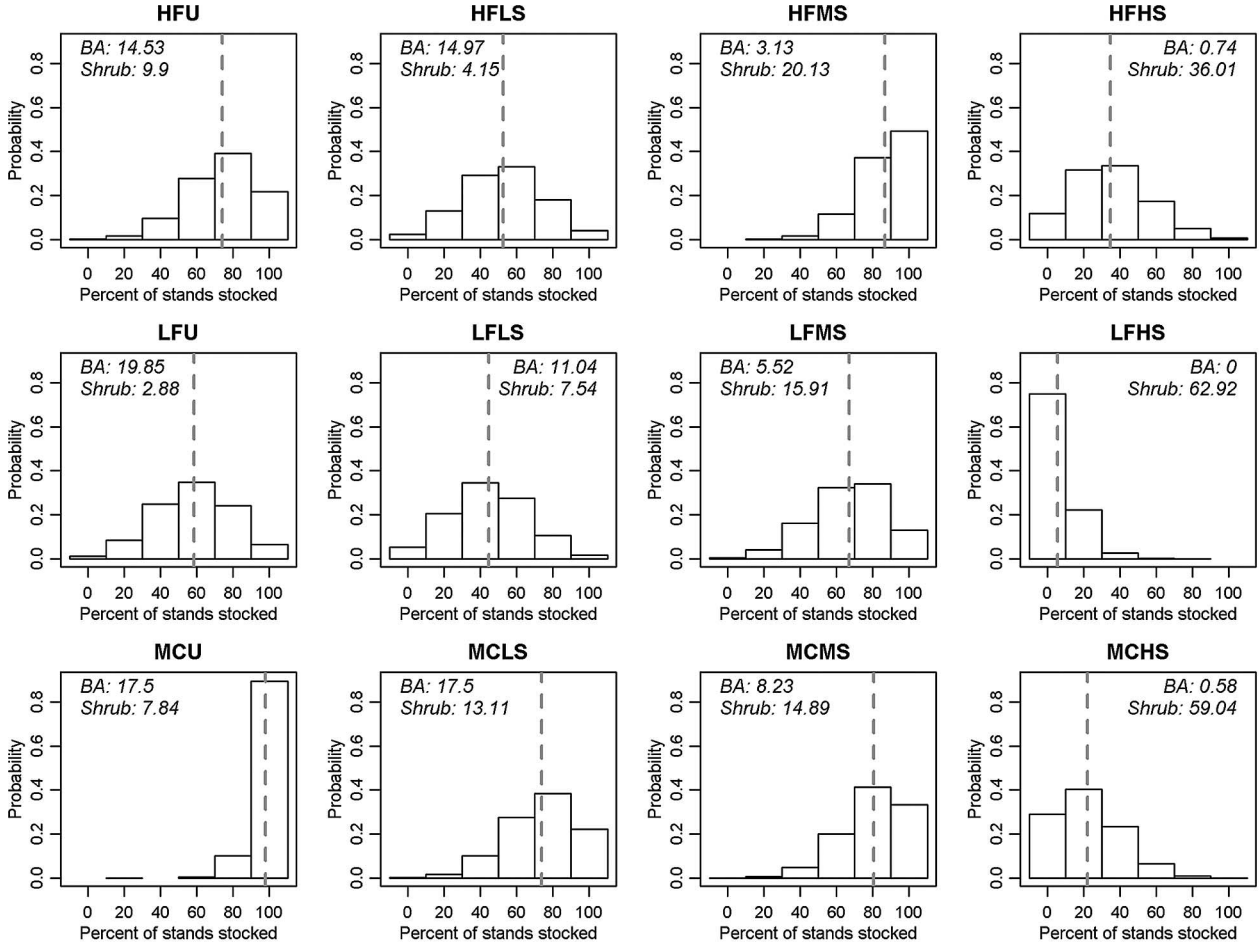

Figure 2. Probability of stocked simulated stands across strata 9–10 years after the 2000 Storrie Fire, Lassen National Forest, using the all conifers response. Parametric bootstrap simulations (N = 10,000) recreated five stands with each stratum, as per the structure of the observed data. Stocking density thresholds are 494 seedlings ha^{-1} in the mixed conifer forest type and 741 seedlings ha^{-1} in the low- and high-elevation fir forest types; sites below 50% stocking do not meet recommended reforestation thresholds (US Department of Agriculture 1987). Dashed vertical lines represent the mean percentages of stands stocked. BA, mean observed remnant "all conifers" stand basal area (m^2 ha^{-1}); Shrub, mean observed woody shrub cover (%).

2009). Common statistical analysis programs, such as R and SAS software, have widely used methods for the RNB and RZINB, yet the heterogeneous alternative is absent from most currently available packages and published procedures for this software (Hilbe 2011, p. 319), requiring that the user develop a specific likelihood function for optimization. The easily accessible zero-inflated packages have the potential to be misapplied when HNB is called for and may in fact improve on the RNB due to unfounded inclusion of the zero-inflated mixture parameters, resulting in erroneous variance calculations (Figure 1) and muddled model interpretation due to imprecise predictor significance tests (Cameron and Trivedi 2008, p. 27, 105). Furthermore, we found that in an improper application, zero-inflated modeling leads to the misdiagnosis of a zero-inflated process in the presence of data heterogeneity. In our data, six of the nonzero ($>$0.001) RZINB ω coefficients assumed zero values when remodeled as a HZINB, suggesting that the RZINB estimate of ω was not influenced by excess zeroes as much as by response heterogeneity. We concluded that the zero-inflated models tended to overfit the data. In addition, we did not have a clear biological justification for this model-fitting approach. Zero-inflated models were not formed for the *Abies* and *Pinus* models because the problems with insufficient sample size for the negative binomial are accentuated when the response was filtered by species. Although our study provides an empirical example of the HNB in application to natural regeneration, further research and the development of such a package in R and SAS software would aid future modeling of heterogeneous trends and may preclude instances of inappropriate ZINB application.

We believe that the inclusion of multiple heterogeneity terms in the HNB was appropriate because the goal was to model the effect of forest type and burn severity on the mean and variability of seedling response. The value of this method is in its assessment of the data's variability, or rather, the shape of seedling distributions within each stratum. Whereas the less sophisticated RNB or even the Poisson distribution may just as adequately estimate strata means, the HNB can additionally be used to estimate seedling count probability densities that more precisely fit empirical distributions. In our application, this capability was valuable in the parametric bootstrapping procedure for both addressing unconditional means and stand stocking. We noticed that slight variations in the estimated θ parameter were highly influenced by the proportion of both zeroes and very large counts within each stratum. Allowing for heterogeneous θ values enabled more specialized and precise estimates of zero and

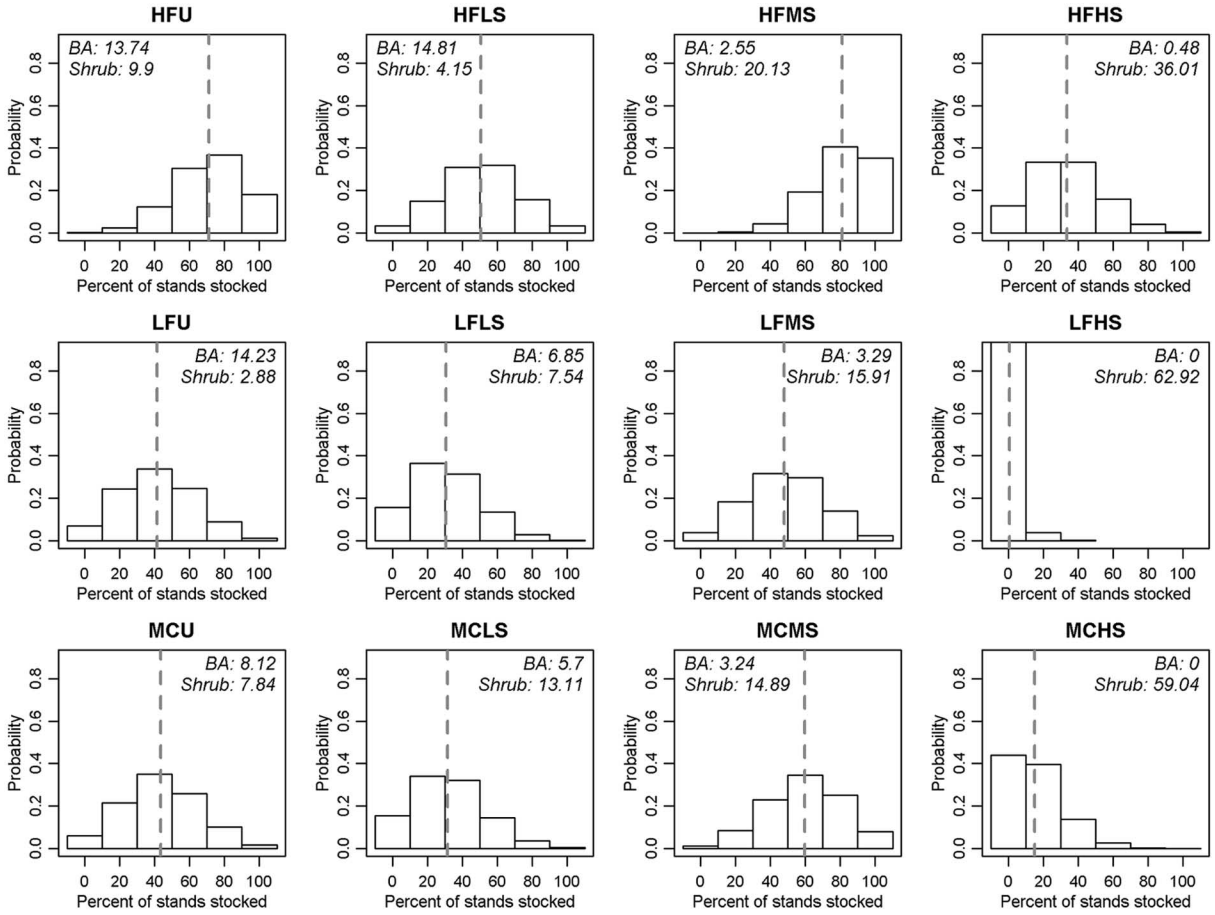

Figure 3. Probability of stocked simulated stands across strata 9–10 years after the 2000 Storrie Fire, Lassen National Forest, using the *Abies* spp. response. Parametric bootstrap simulations (N = 10,000) recreated five stands with each stratum, as per the structure of the observed data. Stocking density thresholds are 494 seedlings ha^{-1} in the mixed conifer forest type and 741 seedlings ha^{-1} in the low- and high-elevation fir forest types; sites below 50% stocking do not meet recommended reforestation thresholds (US Department of Agriculture 1987). Dashed vertical lines represent the mean percentage of stands stocked. BA, mean observed *Abies* spp. stand basal area (m^2 ha^{-1}); Shrub, mean observed woody shrub cover (%).

near-zero count probabilities, which happen to be the most influential probabilities in our stocking analysis and thus the most valuable asset to the manager.

Incorporation of stand-level random effects in the mixed-effects models was supported by our data, as indicated by a substantial reduction in AIC. When the stand-level error term was included, model means appeared to have a sizeable log-bias. We know of no established log-bias correction for this application. The bootstrapping algorithm, however, is a widely accepted means of obtaining statistics from non-Gaussian distributions, including unconditional means. Most of the simulated means appropriately corresponded with the empirical arithmetic mean, yet there were a few discrepancies in which the simulated mean far exceeded the latter. We attribute this to the influence of large magnitude random stand effects (e.g., $\sigma > 2.0$) (Tables 5–7) on model μ coefficients, which are exponentially susceptible to changes in the Gaussian random effects once back-transformed from within the log-link of the negative binomial model. These discrepancies do not reduce our confidence in the simulated means (parametric bootstrap procedures were executed with 10,000 iterations); rather it is clear that when one is dealing with highly skewed and discrete non-Gaussian distributions, the mean is a less stable and iconic statistic than might be expected. The data in this study, therefore, emphasize the importance of characterizing the response distribution rather than leaning solely on a model mean. In light of the high variability even within strata, future researchers examining negative binomial processes should increase sample size to both better characterize model error and provide the opportunity to include ancillary environmental predictors within the model form.

Natural Regeneration

Simulated all conifers count means across the Storrie Fire translate to mean densities between 272 and 29,257 conifer seedlings ha^{-1}; correspondingly, *Abies* spp. densities were between 148 and 35,558 seedlings ha^{-1}, and *Pinus* densities ranged from 25 to 1,137 seedlings ha^{-1} (less than densities observed by van Mantgem et al. 2006 and Moghaddas et al. 2008). Median simulated counts were more stable than means in highly variable strata (e.g., LFLS and LFHS) (Tables 5–7), suggesting that 50th percentile simulated seedling densities may be roughly one-third of the mean. Although we observed abundant seedling densities in many strata, examination of simulated stocking suggests that postfire regeneration after the Storrie Fire was not uniformly distributed within or among stands in a stratum. The USDA Forest Service Region 5 mixed conifer forest stocking density threshold is lower than that of the low- and high-elevation fir forests; a lower threshold paired with the

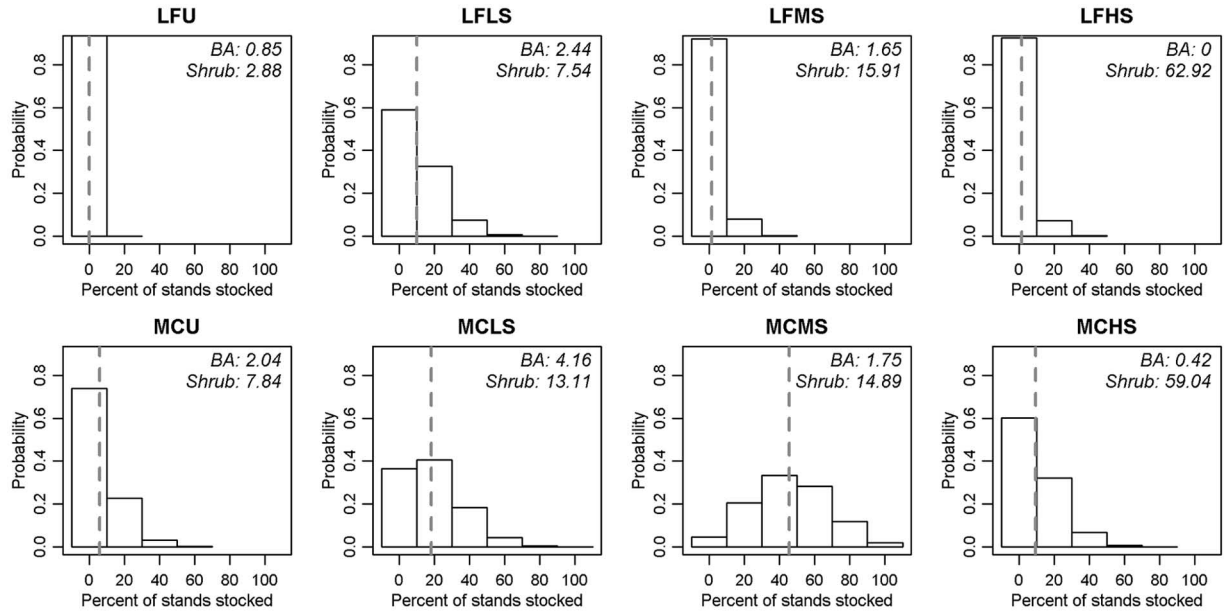

Figure 4. Probability of stocked simulated stands across strata 9–10 years after the 2000 Storrie Fire, Lassen National Forest, using the *Pinus* spp. response. Parametric bootstrap simulations (N = 10,000) recreated five stands with each stratum, as per the structure of the observed data. Stocking density thresholds are 494 seedlings ha^{-1} in the mixed conifer forest type and 741 seedlings ha^{-1} in the low- and high-elevation fir forest types; sites below 50% stocking do not meet recommended reforestation thresholds (US Department of Agriculture 1987). Dashed vertical lines represent the mean percentage of stands stocked. BA, mean observed *Abies* spp. stand basal area (m^2 ha^{-1}); Shrub, mean observed woody shrub cover (%).

inclusion of *C. decurrens* and *P. menziesii* suggests that all conifers stocking in the MCU, MCLS, and MCMS was acceptable for the majority of stands (Figure 2). In addition, the stands in the HFU and HFMS were predominantly stocked because of heavy *A. magnifica* establishment. Although roughly 50% of the simulated stands in the remaining non-high-severity strata were stocked, the presence of remnant overstory in these strata (Figure 2) may eliminate the need for further concern in two regards: the assumption that overstory adjacency promotes some degree of regeneration on available sites means that further regeneration of shade-tolerant species is likely (Laacke 1990a, 1990b, Oliver and Larson 1996); and these strata are now in the process of developing multicohort stands, which the current stocking analysis procedure does not adequately address, because no weight is assigned to mature trees (US Department of Agriculture 1987). These strata are different, however, from high-severity strata, which have few or no nearby seed sources. Our models indicate that fewer high-severity sites (stands in the MCHS, LFHS, and HFHS) are likely to be stocked by Region 5 standards 10 years after the fire event. The sparse regeneration observed in high-severity strata reflects the scarcity of surviving, seed-producing overstory trees and the highly competitive woody shrub colonization (Figures 3 and 4) (Bonnet et al. 2005, Crotteau et al. 2013). Without intervention, the resulting landscape would consist of a patchy conifer overstory intermingled with resprouting California black oak (Cocking et al. 2011) and shrubby expanses.

Model θ coefficients were similar between the all conifers and *Abies* spp. models, underscoring the distributional similarity between the two. Low θ values were driven by frequent zeroes in conjunction with the occasional large observed count (e.g., >200 seedlings plot^{-1}). This variability is similar to the natural regeneration trends observed by McDonald (1983), Chappell and Agee (1996), and Larson and Franklin (2005).

The all conifers and the *Abies* models are more similar than the *Pinus* spp. model, which emphasizes the abundance and density dominance of *A. concolor* and *A. magnifica* across the burned landscape (as in van Mantgem et al. 2006). Although pine is just one component in the mixed conifer forest type, there is widespread concern that pine abundance may have declined relative to that of *Abies* spp. (Oliver and Ryker 1990, Ansley and Battles 1998, van Mantgem et al. 2006). Fire-resilient and shade-intolerant *P. ponderosa* is generally maintained via frequent low- and mixed-intensity fire (Graham and Jain 2005, Taylor 2010), a feature no longer characteristic of many of the montane ecosystems in the southern Cascades since the era of fire suppression (Beaty and Taylor 2001). In the absence of frequent low-intensity fire, a combination of intensive forest management (i.e., prescribed fire, supplemental planting, and stand maintenance) coupled with extensive forest and fuels management (including managed wildfires) may improve the prospects of maintaining pine on western landscapes (Moghaddas et al. 2008) while promoting landscape diversity and mosaics of fire-resilient stands.

Model Application to Management

This study's models confirm that natural seedling densities vary spatially and compositionally across elevation and burn severity in this region, 9–10 years postfire (similar to Turner et al. 1997). Total dependence on natural processes to yield timely, fully stocked stands as dictated by management goals may be insufficient. Although planting has the advantage of more rapidly reestablishing trees after fire (Zhang et al. 2008), the need for planting may not be uniform throughout the landscape, as we observe in the Storrie Fire.

Our models suggest that postfire natural regeneration was generally abundant after the Storrie Fire, except when a nearby seed source was absent (i.e., high-severity burns; similarly, Donato et al. 2009). Approximately one decade after fire, residual conifer cover

within the unchanged, low-severity, and medium-severity burns remains; managers may consider the majority of these now multicohort stands intact and focus planting efforts elsewhere. The lowest overall seedling densities and poorest conifer stocking were observed in the high-severity burns within each of the three forest types; these strata were also typified by high levels of woody shrub cover (predominantly *Ceanothus* spp. and *Arctostaphylos* spp.) and resprouting hardwood cover (*Q. kelloggii*) (Cocking et al. 2013, Crotteau et al. 2013), exacerbating competitive stress and shading out young shade-intolerant trees. The sparse natural conifer cohort present after high-severity burns, therefore, would most likely benefit from supplemental artificial regeneration paired with vegetation management methods such as mechanical mastication and herbicide application (McDonald and Fiddler 2010).

Overstory and regeneration in the high-elevation fir forest type was predominantly *A. magnifica* (Crotteau et al. 2013). Due to the effect of elevation on other woody species in the region, *A. magnifica* has limited competition in reforesting the HFHS. In fact, simulated seedling stocking in the HFHS indicated the best odds of stand stocking of all the high-severity strata; the probability of no stands meeting stocking standards was only 0.12. If conifers are desired, postfire planting would be most beneficial in the MCHS and LFHS; these forest types are more compositionally complex than their upper-elevation counterpart and previously contained many mature, legacy pines (J.S. Crotteau, USDA Forest Service, pers. observ., 2010). Our model suggests that there is a 60% chance that none of the stands in the 449-ha MCHS and a 93% chance that none of the stands in the 472-ha LFHS are sufficiently stocked with pine seedlings to meet the regional pine stocking standard. In the case of the Lassen portion of the Storrie Fire, this equates to just 10% of the total burned area for which means of artificial regeneration may be of the highest priority, given management objectives. If managers wish to encourage pine-prominent (as opposed to the currently more abundant *A. concolor*) forests in the lower-elevation sites, planting pine to supplement natural *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* regeneration may restore valuable timber while supporting the development of plant communities better adapted to endure future fires and promote lower-severity burns (Agee 1993, p. 305–306). It is likely, however, that site preparation (e.g., herbicides or mechanical mastication) and intermediate treatments (e.g., thinning or prescribed fire) would be required to maximize tree growth while limiting the vertical and horizontal continuity of these developing stands.

Although we initially suspected that the high-severity burns would have the least conifer regeneration and that lower-severity burns would support greater numbers, the magnitudes of these densities were unknown. There are several reasons for this uncertainty in this region's potential regeneration. First, the species commonly found in this region express periodicity in regeneration. Sometimes this is severe: it is feasible that 7 or 8 years may pass without a good ponderosa pine crop (Oliver and Ryker 1990). Fir in this region tends to be less variable (1–4 years between good crops) but exhibits periodicity as well (Laacke 1990a, 1990b). Over a 10-year period, therefore, it is possible to find scant natural ponderosa pine regeneration even in the presence of mature seed trees. A second reason for uncertainty in postfire regeneration is that even high-severity classified burns may host some degree of sparse overstory survival, manifested either as individuals or small islands of trees (a confounding factor expressed in Donato et al. 2009). Survivors of high-severity fire sometimes produce stress crops, which can lead to patchy areas of high seedling densities, as observed after the 1992 Fountain Fire in northern California (DiTomaso et al. 1997). Third, additional uncertainty regarding postfire regeneration densities may stem from the fact that our measure of burn severity was indirect, not field-based. We used the CBI modeled by RdNBR, which was derived from prefire and 1-year postfire Landsat imagery (30-m resolution) to estimate fire severity across the landscape, a technique that is powerful because it is inexpensive and can be calculated for any fire. It was not known how well this readily available metric would relate to observed regeneration 9–10 years after fire, or if the nominal classes would highlight differences in conifer regeneration between neighboring classes on the scale. Although more detailed specifics require further research, we believe that linking the remotely sensed CBI to postfire conifer regeneration can be informative to help managers make key restoration decisions and focus limited resources.

In the future, large-scale mixed-severity burns are likely to influence western landscapes (Westerling et al. 2006, Miller et al. 2009b). This study emphasizes that properly specified model distributions can more precisely address the high variability of postfire natural regeneration, useful for guiding a number of forest restoration objectives. Our models are site-specific and any extrapolation should be made cautiously, yet we believe the overarching trends observed may be applicable to similar western forest types burned with mixed-severity wildfire. Where time and resources are limiting factors under timber growth or site reclamation objectives, managers may consider prioritizing postfire revegetation efforts with areas less likely to quickly recover to stocking standards.

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