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Relating Stocking and Density for Natural Regeneration of Conifers in Northern California

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Natural regeneration cannot be effectively evaluated by tree density because of spatial heterogeneity typically observed. A proper interpretation of natural regeneration will consider some evaluation of area stocked. However, stocking estimates for natural regeneration are plot-size-dependent. Stocking at the 1-milacre scale is not generally comparable to that on a 4-milacre scale unless a generalized relation with stand density can be established. A generalized relation was first suggested to hold in a paper by Lynch and Schumacher (1941), but this has not been confirmed in subsequent studies. The Lynch and Schumacher hypothesis of a generalized regeneration density-stocking relation across plot size was tested using observations on 60 stands. Results were consistent with Lynch and Schumacher (1941). With evidence of a well-defined relation for plots ranging from 1 to 10 milacres, it appears possible to approximate, for ponderosa pine and associated species, the natural regeneration stocking percentage for a range of stocking standards based solely on observations of regeneration density. Confidence intervals were derived for a range of stocking standards in English units from 1 to 10 milacre and for metric units from 0.0005 hectares to 0.0040 hectares.

Keywords: natural regeneration, probit model, stocked quadrat, ponderosa pine, mixed-conifer

Early studies of natural regeneration in the forests of North America consistently demonstrated the problem of aggregated spatial distribution of natural regeneration. This spatial aggregation results in high variability and skewness associated with observations of seedling density per unit area (e.g., Lowdermilk 1927, Cowlin 1932, Isaac and Meagher 1938). When trees exhibit a highly aggregated spatial pattern, it is quite possible to have a large mean number of seedlings on a unit area but still find much of the area bereft of trees. This led to the work of Haig (1929, 1931) and acceptance of stocking instead of, or in addition to, density as an informative metric, where stocking is determined by the proportion (or percent) of stocked plots of a given fixed reference size, and density is the number of stems per acre. The condition that defines successful stocking on an individual plot is often the presence of at least one tree on a plot of a fixed size. The reference size for plots can vary but has often been determined by an estimate of spacing related to a stand at maturity, such that if one assumed that 250 trees ac^{-1} defines a fully stocked mature stand, the appropriate reference plot size for a stocking standard would be 1/250 = 0.004 ac or 174 ft^2.

The probability of observing a tree on the plot is influenced by plot size. If plot size is reduced, the probability of detecting a tree also decreases; this leads to an inevitable reduction in stocking expressed as a percentage. Because this probability changes with plot size, stocking evaluation requires a defined plot size.

A problem with the stocked-plot (also referred to as the stocked-quadrat) method is the difficulty in determining a widely accepted standard plot size. This prompted some debate among researchers (Wellner 1940, Lynch and Schumacher 1941). Common practice for many years called for either a 1-milacre (Lowdermilk 1927, Gordon 1970), or 4-milacre plot standard (Cowlin 1932, Isaac and Meagher 1938, Bever 1949). Although both tree density and stocked-plot methods may be used to evaluate regeneration (Stein 1978), it is sometimes useful to derive stocking from density, particularly where density metrics are derived from a sampling scheme that may not conform to a desired or mandated stocking standard, or in instances where density has been estimated but stocking has not.

While density may be estimated using any plot size, stocking can only be estimated using a defined standard plot size, unless a generalized relation can be established that allows one to choose a stocking standard at will. If such a relation can be found, then any estimate of density, regardless of plot configuration may be used to estimate stocking. Furthermore, if an organization or regulatory body changes stocking standards, one may then be able to respond without having to change sampling methods.

The previously mentioned work of Lynch and Schumacher (1941) is of particular interest in this regard, as they first suggested an empirical approach to resolve issues with stocking and variation in plot size. Using the data of Wellner (1940), they developed a model effectively relating tree density to stocking and statistically

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tested their assumptions of model form, the effect of species mix, and the effects of changing plot reference size. Using a linear probit transformation model using stand-level observations, they found a single fitted equation sufficed for western white pine and associated species in Idaho, allowing a generalization across reference size. Thus, they suggested that the choice of plot size might be relegated to "a matter of convenience rather than an outcome of pedantic debate" (Lynch and Schumacher (1941 p. 51). They also speculated that their results might be robust across other timber types, but this was not tested.

It is somewhat remarkable that in the nearly 80 years since their original finding, there has been no published attempt to confirm the results of Lynch and Schumacher (1941). In fact, based on a review of the citation record, the work of Lynch and Schumacher (1941) has been largely ignored. Thus, it remains unknown if their results are repeatable. Just how stable is the relation between density and stocking across a range of plot sizes? And what is the uncertainty associated with this relation?

The problem of evaluating natural regeneration stocking is still relevant today. With the current problems presented by widespread high-severity wildfires throughout the western United States, there has been a resurgence of interest in natural regeneration of conifers after disturbance (Donato et al. 2006, Shatford et al. 2007, Zald et al. 2008, Collins and Roller 2013, Crotteau et al. 2014, Welch et al. 2016, Shive et al. 2018). One finds no commonality among field methods among recent published works on natural regeneration of western conifers. Some recent studies have ignored stocking and focused on density (Welch et al. 2016, Shive et al. 2018). To the extent that stocking is presented, estimates of stocking are often not comparable. Not only do plot sizes vary across published works, but also they vary within (Kemp et al. 2016).

Lynch and Schumacher (1941) hypothesized a solution to this problem using a linear probit transformation model and a clever adjustment of the x-axis to allow testing across a range of plot standards. The first objective of this paper is to validate the model of Lynch and Schumacher (1941), using data with a different species mix from a different region (Crotteau et al. 2014). This will provide insight into the robustness of the original model. The second objective is to develop 95 percent confidence intervals across a range of defined stocking standards for natural regeneration and demonstrate how this relation shifts across a range of stocking standards.

Materials and Methods

The data from this study are observations on conifer natural regeneration after the Storrie Fire in northern California (Crotteau et al. 2014). The Storrie Fire took place in 2000, and observations on natural regeneration were gathered during 2009 and 2010. The burn area was stratified into different elevations and burn severities, and sites within the strata were randomly selected for sampling. In each selected site, a grid of 0.01-acre (10-milacre) circular plots was established, and the number of seedlings was counted on each plot. Note this is a larger plot than those presented by Wellner (1940) and Lynch and Schumacher (1941). A total of 60 sites, with no postfire management, were sampled. The average number of plots per site was 19.4, with a range of 18–23. The composition of species in these stands, prior to the wildfire, varied from pine-dominated mixed-conifer to a more fir-dominated mix at higher elevations.

From these observations, density of naturally regenerated conifer seedlings (stems acre^{-1}) and stocking were observed with stocking defined by the presence of at least one conifer seedling per 10-milacre plot. Thus, for each site (stand) within the Storrie Fire, estimates were derived for both density and percentage stocking, where candidate trees were conifers >0.5 ft in height and <4 in. in diameter at breast height.

The Lynch and Schumacher Model

Wellner's (1940) graphical analysis of stocking percentage and tree density was conducted for the white pine type of Idaho. In these forests, western white pine (*Pinus monticola*) is often found in a mix with other conifers such as Douglas-fir (*Pseudotsuga menziesii*), grand fir (*abies grandis*), western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) (Haig et al. 1941). Weller (1940) did not present information on the particular species mix represented in his data. He found a strong relation between stocking percentage and seedling density expressed as a sigmoidal function over the log of tree density, and it varied by the plot size used to define stocking. Lynch and Schumacher (1941), recognized an opportunity, using the Weller data, to conduct a statistical analysis to test several assumptions. They developed a unifying approach to the problem by fitting the proportion of stocking over density using a probit transformation. Their results were presented as:

$$\Phi^{-1}(p) = 1.0417 + 1.2344\log_{10}(x)$$

where $\Phi^{-1}(p)$ is the inverse of the standard normal (probit) of the proportion (p) of stocked plots, and x is the mean number of trees per plot. The generic probit transformation is the inverse of the standard normal cumulative distribution function. The sample size was 100 sites. The choice of the number of trees per quadrat rather than trees per acre for fitting was made to facilitate the most direct evaluation of the effect of plot size.

A close inspection of the relation of Figure 1 in Lynch and Schumacher (1941) revealed an inconsistency with the generic definition of probit and their own results. An adjustment of +5 was applied to avoid negative values (Lynch and Schumacher 1941, p. 49), as was common practice at the time (Bliss 1934, Finney and Stevens 1948). They also appear to have divided the mean plot count by 20, although this second adjustment is not mentioned anywhere in the manuscript. The resulting correction to the intercept

Management and Policy Implications

Application of stocking standards for natural regeneration is constrained because of the dependence on a reference plot size. This validation of a method first proposed by Lynch and Schumacher (1941) presents a means for translating natural regeneration seedling density metrics for mixed-conifer stands into stocking estimates across a range of stocking reference plot sizes, enabling one to evaluate conifer natural regeneration stocking from studies using various field methods and plot sizes for data collection as long as an unbiased estimate of tree density is available. The results also suggest that the original work of Lynch and Schumacher (1941) may be robust to changes in stocking standards and perhaps even forest type.

is $\log_{10}(20^{-1}) = -1.30103$. These modifications likely were made to ease the cumbersome calculations required for the analysis and development of the ANOVA table. When the fitted model is then corrected for this discrepancy, the result is:

$$\Phi^{-1}(p) = -0.25933 + 1.2344\log_{10}(x)$$

This corrected response surface is consistent with the previously mentioned figure and the sample calculations provided by Lynch and Schumacher (1941). Standard errors of the parameter estimates were not presented in Lynch and Schumacher (1941), so there is no way of evaluating uncertainty associated with their model.

To validate this relation, the observed density and stocked-plot observations from Crotteau et al. (2014) were fit with a generalized linear model using the *glm()* function, specifying: family = binomial or quasibinomial (link = "probit"), in R version 3.5.3 (R Core Team 2013). The quasibinomial family option adds an overdispersion correction parameter. It is important to note that this is not the same parameter-estimation method as that used by Lynch and Schumacher (1941) who approximated the relation with a linear fit of transformed stand-level observations. However, the use of a generalized linear model on plot-level success:failure observations is a more modern, and arguably more correct, model specification. This level of analytical sophistication was not available to Lynch and Schumacher.

Confidence intervals were calculated using the R function *add_ci()* from the package ciTools (Haman and Avery 2019) with a specification of type = "boot" for bootstrap analysis with 1,000 replications on a range of densities from 2 to 10,000 trees acre^{-1}. The 95 percent confidence intervals were calculated for 10-, 4- and 1-milacre standards. For display purposes, the stand-level observations for the 10-milacre plots were then estimated for 4- and 1-milacre by simulation. Pseudodata were created by resampling from the original data such that the probability of selection was consistent with plot size. To do this, each observed tree was compared with a random variable on the interval 0–1. Trees were kept if the random variable was below 0.4 and 0.1 for the 4-milacre and 1-milacre reference. This simulation was repeated 10,000 times and the results plotted over the fit. The mean value of these 10,000 simulations was reported as the observed value for that stand and plot size.

Results and Discussion

The result of the probit-linked quasibinomial general linear model fit to the Crotteau et al. (2014) data produced an estimated response surface of:

$$\Phi^{-1}(p) = -0.21307 + 1.22876\log_{10}(x)$$

with standard error estimates of 0.06200 and 0.07728, respectively, and a covariance of –0.0104. The probit-linked model is by no means the only solution for this particular problem of relating stocking and density. A logit model could be a consideration. However, the probit analysis allows for a very desirable comparison with the Lynch and Schumacher. Initially, it appeared that the confidence intervals were conservative because of overdispersion. In evaluating both binomial and quasibinomial models, a modest quasibinomial dispersion of 3.1 was found, indicating moderate overdispersion. Although differences between the two fits in parameter estimates and in confidence intervals were negligible, results from the quasibinomial are presented here, as this produces a slightly wider (more conservative) confidence interval.

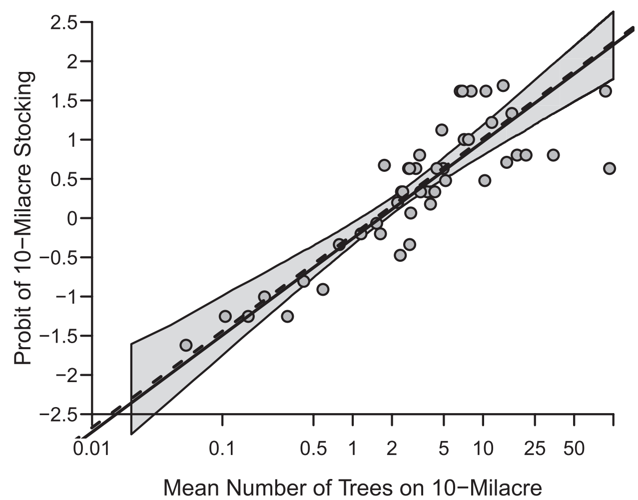

Figure 1. Fitted probit model (dashed line) and stand-level observations (plotted points) of 10-milacre stocking on mean number of trees per 10-milacre plot with bootstrapped 95 percent confidence interval (gray); the original fitted model of Lynch and Schumacher (1941) is shown by the solid line.

A comparison with Lynch and Schumacher (1941) is presented graphically in Figure 1. This figure is of some interest in that it shows that the fit from the data of Crotteau et al. (2014) using 10-milacre plots is quite close to that of Lynch and Schumacher (1941). This lends support to the contention of Lynch and Schumacher that their model was robust to changes in stocking standard. This consistency is also somewhat surprising given the change in species under consideration, as one might expect a different species mix to behave differently.

The relation between stocking and density is influenced by numerous factors that impact dispersal and viability of seed. For example, cone crop periodicity varies among species, so that differing species mixes of parent trees could contribute to some variation in the relation between stocking and density. Variability in the spatial distribution of parent trees following disturbance can contribute as well. Successful germination and survival to the point of being observed in a sampling effort are also affected by seed predation and numerous insects and diseases. This complex set of factors leads to a fairly high degree of variability, particularly at high seedling densities.

The relation between seedling density and stocking has been shown to be related to degree of spatial aggregation (Gill 1950, Feng et al. 2006). To the degree that our fitted equation is applicable elsewhere is dependent to a large degree on the degree of aggregation being similar to that we observed.

It is quite possible to find high seedling counts in an area with relatively low stocking. This might occur in an area where fire has removed all but a few clumps of sparse and widely spaced survivors. With this naturally occurring variability, testing for differences among different forest types, or other factors such as slope and aspect, will likely require a much larger between-site sample size than that presented by either the Lynch and Schumacher (1941) or the Crotteau et al. (2014) data. Such comparisons would also be aided by increasing the within-site sample size.

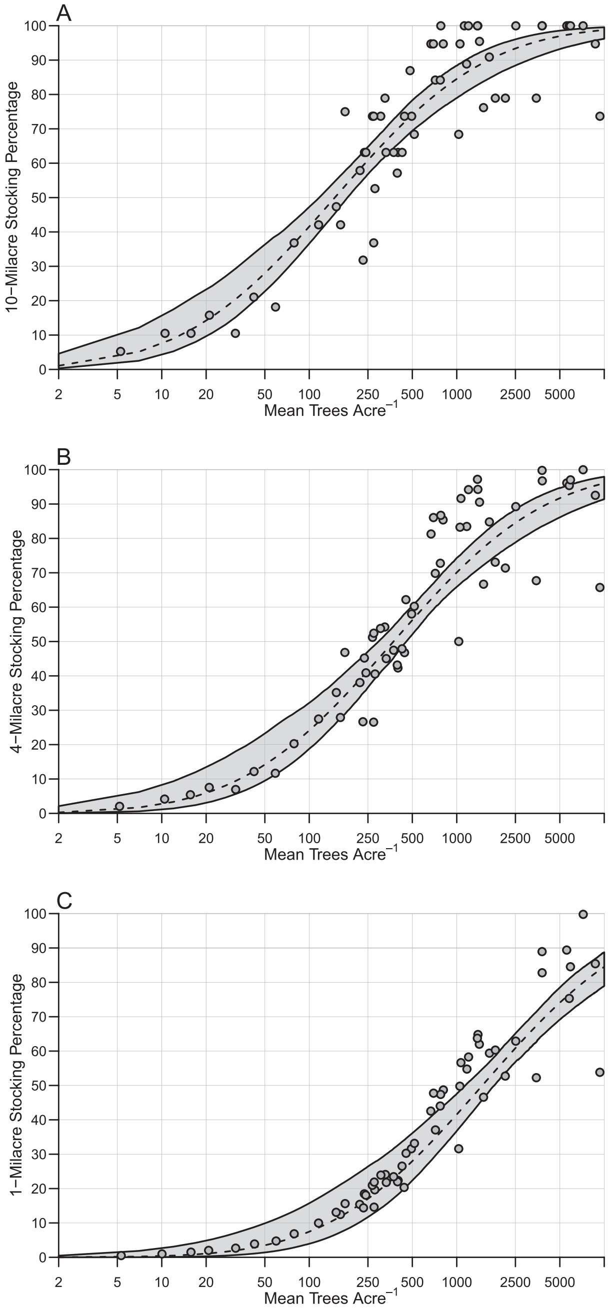

Figure 2. Back-transformed probit fit of 10-, 4-, and 1-milacre stocking (A, B, and C, respectively) and density of natural regeneration (dashed line) with a bootstrapped 95 percent confidence interval (gray). The plotted observed stocking is derived by the simulation for 4- and 1-milacre stocking.

If one assumes a robust model across plot reference size, various references can be considered. For example, in the back-transformed fit that relates trees acre^{-1} to stocking at a 10-milacre standard, it can be seen that the estimate at 1,000 trees acre^{-1} is approximately 85 percent with a 95 percent confidence interval of 80–90 percent (Figure 2A), whereas at 100 trees acre^{-1} the 10-milacre stocking is approximately 43 percent with a confidence interval of 38–48 percent. By the same method, one can also then derive estimates for other standards. In Figure 2B the estimate for 1,000 trees acre^{-1} at 4-milacre stocking standard is 70 percent with a 95 percent confidence interval of 65–76 percent. Results for 1-milacre stocking are shown in Figure 2C.

In comparing the results here with the model of Lynch and Schumacher, it is worth noting the potential for a confounding effect, as both size of the plot and species differ. Thus, it is possible, although perhaps unlikely, that an undetected difference from these two factors is due to some offsetting impacts.

A range of standards for both English and metric units have been prepared and are presented in supplemental information. Predictions and 95 percent confidence intervals were exported (.csv format) for trees acre^{-1} ranging from 2 to 10,000 for stocking standards between 1- and 10-milacre by 1-milacre increments (Data File S1). A table for metric units, for densities in the range ~5–24,700 trees ha^{-1}, was also generated using standards from 0.0005 hectares to 0.0040 hectares by 0.0005 hectares increments (Data Table S2).

It would seem reasonable to apply these results to mixed-conifer forests of in northern California, allowing for estimates of stocking of natural regeneration across a range of stocking standards. Although these results from a mix of pine-dominated and fir-dominated mixed-conifer stands compared favorably with stands of a different species mix from the Rocky Mountains, the cautionary note of Lynch and Schumacher (1941, p. 51) still seems valid: "… generalization to other timber types approaches too close to the speculative to be warranted." It would be beneficial to fit this model in other forest types and other plot sizes to see if there is indeed consistency across a range of conditions.

It is important to acknowledge that the within-site sample size limitation (~20 plots per site) means that stocking can only be estimated to a tolerance of about 5 percent with the data used in this analysis. Future studies evaluating this relation would do well to employ a sample size >50 to reduce error in estimation and produce a more well-defined relation across a range of densities. An increased sample size would also provide the potential to evaluate and address potential lack of fit issues with the probit model.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

Supplement 1. Comma-separated values file (.csv) of 95 percent confidence intervals for stocking percent as a function of trees acre-1 and English unit stocking standards from 1-milacre to 10-milacre by 1-milacre.

Supplement 2. Comma-separated values file (.csv) of 95 percent confidence intervals for stocking percent as a function of trees ha^{-1} and metric unit stocking standards from 0.0005 hectares to 0.0040 hectares by 0.0005 hectares.

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