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Forest resilience measured: Using a multi-timescale approach to quantify forest resilience in a changing world.

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By

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Professor Wayne P. Sousa
Professor Robert A. York

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Abstract

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Maintaining the resilience of ecological systems in an era of global change is a priority for management and conservation. In California, forests are currently threatened by a suite of disturbances that include altered fire regimes, legacy effects from timber harvesting, a warming and drying climate, chronic air pollution, and uncharacteristically severe attacks by insects and pathogens. Managing to preserve the characteristic structure and function of California forests under novel disturbance regimes requires a clear understanding of these forests' historical conditions as well as an understanding of the drivers of change in these forests. A major challenge of managing for resilience is the lack of quantifiable metrics to assess changes in a system's resilience over time. This dissertation uses a multi-timescale approach that quantifies changes in the structure and composition of California mixed-conifer forests since European settlement and suggests a framework for measuring and monitoring forest resilience. This work can be used to guide conservation and restoration activities with the goal of maintaining the characteristic structure and function of forests under changing disturbance regimes.

In Chapter 1, I explore the demographic responses that have led to a reordering of species dominance in Sierra Nevada mixed-conifer forests. California mixed-conifer forests have been subjected to a century of fire suppression, resulting in a shift in the structure and composition of these forests over time. Historically, a high-frequency, low-severity fire regime maintained structurally heterogeneous forests where dominance was shared among several conifer species. With the removal of fire from this system, forest density increased, as did the prevalence of shade-tolerant fir species at the expense of pines. Previous work suggests that species-specific differences in demography have contributed to a shift away from a heterogeneous, resilient forest to a monodominant forest that is more susceptible to catastrophic loss from fire, drought, or invasive pests or pathogens. However, these conclusions are typically derived from extrapolations from short-term data. I use a 57-year inventory record from an old-growth mixed-conifer stand in the Plumas National Forest, CA, where fires have been excluded since the early 20th century. Using a Bayesian hierarchical modeling approach, I measure species-specific rates of mortality, recruitment, and growth over this 57-year period. I also correlated climate trends with demographic data to determine whether climate may be a driver of shifts in species composition. I found that basal area, density, and aboveground carbon have increased linearly over the 57-year period in spite of increasing temperatures, which I expected might have

negatively affected growth. The recruitment and growth rates of *Pseudotsuga menziesii* (Douglas-fir) and *Abies concolor* (white fir) were significantly higher than the community-level means, while the recruitment and growth rates of *Pinus lambertiana* (sugar pine) and *Pinus ponderosa* (ponderosa pine) were significantly lower than the community-level means. Mortality rates were similar among species. These results indicate that differences in species-specific growth and recruitment rates are the main drivers of a shift towards a low-diversity forest system and may potentially lead to the loss of pines from mixed-conifer forests. These results also quantify the strong effect that fire has on the regulation of forest biomass and density in this system.

In Chapter 2, I address the need for accurate understandings of historical forest conditions to be used as guides when implementing management and restoration plans. Because historical Sierra-Nevada mixed conifer forests were considered to be resilient to disturbance due to their heterogeneous structure and function, historical conditions are often considered to be the target state for restoration. However, multiple methods for estimating historical forest conditions are available and these methods sometimes give conflicting results regarding the density of forests prior to European settlement. The General Land Office (GLO) surveys of the late 19th and early 20th centuries provide data on forest structure across a broad geographic range of the western US. Distance-based plotless density estimators (PDE) have been used previously to estimate density from the GLO data but this approach is limited due to errors that arise when trees are not randomly distributed. Recently, an area-based method was developed in order overcome this limitation of distance-based PDEs. The area-based method relies on estimating the species-specific Voronoi area of individual trees based on regression equations derived in contemporary stands. This method predicts historical densities that are 2-5 times higher than previous estimates, and the method has not been independently vetted. I applied three distance-based PDEs (Cottam, Pollard, and Morisita) and two area-based PDEs (Delincé and mean harmonic Voronoi density (MHVD)) in six mixed-conifer and pine-dominated stands in California, US and Baja California Norte, Mexico. These stands ranged in density from 784-159 trees ha^{-1}. I found that the least biased estimate of tree density in every stand was obtained with the Morisita estimator and the most biased was obtained with the MHVD estimator. Estimates of tree density derived from the MHVD estimator were 1-4 times larger than the true densities. While the concept of area-based estimators is theoretically sound, as demonstrated by the accuracy of the Delincé estimates, the Delincé approach cannot be used with GLO data and the extension of the approach to the MHVD estimator is flawed. The inaccuracy of the MHVD method was attributed to two causes: (1) the use of a crown scaling factor that does not correct for the number of trees sampled and (2) the persistent underestimate of the true VA due to a weak relationship between tree size and VA. The results of this study suggest that estimates of historical conditions derived from applying the MHVD method to GLO data are likely to overestimate density and that tree size is not an accurate predictor of tree area in these open-canopy forests. I suggest caution in using density estimates derived from the MHVD method to inform restoration and management in Sierra Nevada mixed-conifer forests, and recommend the Morisita estimator as the least biased of the distance-based estimators.

In Chapter 3, I address the concept of resilience as it relates to forest ecology and management and outline a framework that can be used to determine quantifiable metrics of resilience. Resilience is an aggregate property of ecological systems that maintains the structure, function, and composition of the system when faced with a disturbance. The main challenge inherent in

using resilience to inform management and conservation is the multitude of definitions and concepts that have been developed to describe the resilience of ecological systems. The framework I develop for operationalizing resilience builds on the theoretical concept of resilience but provides explicit metrics for measurement. In this framework, resilience is composed of two properties: resistance to disturbance and recovery from disturbance. I outline four dimensions of resistance and recovery that can be used to measure and monitor resilience, including heterogeneity, complexity, quality, and reserves. I dispense with the concept of strictly-defined alternate stable states and instead focus resilience goals on target states, which are determined by ecological, economic, recreational, or aesthetic considerations. I also conduct a literature review of papers which measure forest resilience to assess measurements and analyses that can be used to quantify the four dimensions of resilience in the context of resistance and recovery. The results of this review indicate that studies of resilience can effectively make use of simple methods for quantification and analysis and that the most compelling studies address both components of resilience (resistance to and recovery from disturbance) and multiple dimensions of resilience. I then apply metrics to quantify the dimensions of resilience in three case study systems: the Sierra Nevada mixed-conifer forest of California, the eastern hemlock forest of the northeastern US, and the northern hardwood forest of the northeastern US. I found that this resilience framework is limited by the fact that no single, absolute measure of resilience can be derived. However, the framework is useful for defining baseline resilience measures and establishing protocols for measuring relative changes in forest resilience over time.

For my biological family and my logical family.

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CHAPTER 1

Long-term demographic trends in a fire-suppressed mixed-conifer forest

ABSTRACT

In the western US, forests are experiencing novel environmental conditions related to changing climate and a suppression of the historical fire regime. Mixed-conifer forests, considered resilient to disturbance due to their heterogeneity in structure and composition, appear to be shifting to a more homogeneous state, but the timescale of these shifts is not well understood. Our objective was to assess the effects of climate and fire suppression on stand dynamics and demographic rates of an old-growth mixed-conifer forest in the Sierra Nevada. We used a Bayesian hierarchical analysis to quantify species and community rates of recruitment, growth, and mortality. Despite a warming climate, we found that stand density, basal area, and carbon have increased over 56 years. Fir recruitment and growth significantly exceeded the community-level median rates, while pine recruitment and growth was significantly lower than the community-level median. Shifts in species composition from a well-mixed stand to a more dense fir-dominated stand appear to be driven by low growth and recruitment rates of pines relative to firs. In forests such as these with consistent and relatively low mortality rates, we recommend that restoration and management activities be focused on promoting pine recruitment and growth.

INTRODUCTION

Novel environmental conditions created by human enterprise (e.g., management decisions and climate change) are contributing to shifts in the structure and function of forests worldwide (Allen et al. 2010). In California, a century of fire suppression has resulted in forest conditions that diverge greatly from pre-settlement forest structure and composition (Dolanc et al. 2014). Historically, frequent, low-intensity fires in the vast California mixed-conifer forest (approximately 3.7 million ha, LANDFIRE 2010) helped to maintain a structurally heterogeneous landscape with dominance shared among several conifer species (van Mantgem et al. 2011). Fire exclusion has resulted in a sharp decrease in the species richness of recruits in the forest understory and changes in the structure of the forest due to the loss of large trees (McIntyre et al. 2015). Abundances of relatively shade-tolerant, fire-sensitive species *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), and *Calocedrus decurren*s (incense-cedar) have increased at the expense of the relatively shade-intolerant, fire-resistant species *Pinus ponderosa* (ponderosa pine) and *Pinus lambertiana* (sugar pine; Scholl and Taylor 2010, Knapp et al. 2013). These compositional changes have been accompanied by increased fuel loads and an increase in the density of small diameter shade-tolerant trees. The resulting increased fuel loads exacerbate fire hazard (Agee and Skinner 2005) and have contributed to an altered fire regime characterized by low frequency but high intensity mega-fires (Stephens et al. 2014).

Climate-induced physiological stress due to increased temperature and drought has also contributed to forest change as a result of recent mortality events (Allen et al. 2010). Increased tree density resulting from fire suppression may interact with changing climate variables and contribute to greater water stress and potentially increased mortality due to competition for resources in these dry forests (Das et al. 2011). In some areas of the Sierra Nevada, rising water deficits resulting from increased annual temperatures have been linked to increased tree mortality (van Mantgem and Stephenson 2007). The possible compounding effects of interacting disturbances (sensu Paine et al. 1998) may be substantial but are not well understood.

The differential responses by species to fire exclusion and climate change appear to be contributing to a species reordering of fire-adapted California forests. This reordering potentially represents the first phase of a transition from a well-mixed, resilient forest to a less diverse community that is more susceptible to catastrophic loss due to fire, pests, or pathogens. However most of the evidence for this trend is based on extrapolations from short-term observations (e.g. van Mantgem et al 2004), reconstructions of historical data (e.g., Scholl and Taylor 2010), or space-for-time substitutions (Minnich et al. 2000). These indirect approaches introduce considerable uncertainty compared to the direct alternative -- long-term observations on repeatedly measured plots (Harmon and Pabst 2015).

In this study, we use a 56-year record of tree mortality, growth, and recruitment to test the hypothesis that the era of fire suppression and climate warming coincides with the "homogenization" of an old-growth, Californian mixed-conifer forest. Specifically we ask: 1) What are the trends in forest composition and structure in this old-growth stand? 2) Are differences in demographic rates among species contributing to a shift in forest composition? 3) What are the relative contributions of fire suppression and climate trends as potential drivers of species reordering at this site over the last six decades?

METHODS

Study Area

The study site is located on an east-facing slope of Little Schneider Ridge in the Plumas National Forest, CA. The elevation of this gently sloping stand (14%) ranges from 1158 to 1219 m (Ansley and Battles 1998). Soils are classified as Ultic Haploxeralf formed from basic igneous bedrock and have been weathered to a relatively fine loam with depths from 1-2 m (Ansley and Battles 1998). Mean annual temperature was 9.8º C and mean annual precipitation was 1144 mm for the period 1956-2010 (PRISM Climate Group 2015).

The stand is an old-growth, all-aged mixed-conifer stand with five major constituent tree species (white fir, Douglas-fir, ponderosa pine, sugar pine, and incense-cedar) and two minor species (California black oak (*Quercus kelloggii*), and Pacific dogwood (*Cornus nuttallii*)). Policies of fire exclusion were implemented in this region in the late 19th and early 20th centuries. Prior to the implementation of these policies, the mean fire interval was estimated to be 12 years (Moody et al. 2006). Since 1900, only two fires have been recorded in the vicinity of the study area (Moody et al. 2006), and there is no record of fire in this stand for the duration of the inventory record (1954-2013).

Data Collection

The measured area of the stand consists of 4.7 ha that were originally surveyed in 1954 by UC Berkeley Professor Frederick S. Baker (the Baker Stand). In this first inventory, all trees >24 cm DBH (diameter at breast height; 1.37m) were measured. Baker conducted the original inventory over a seven year period, from 1954-1961. For simplicity, we refer to the timing of initial measurement by the median of the interval, 1957 (Ansley and Battles 1998). The inventory was repeated in summer 1995, and all trees >9.5 cm DBH were tagged and added to the inventory. All tagged, live trees were remeasured in the summers of 2001, 2008, and 2013. New recruits into the >9.5 cm DBH size class were tagged and added to the inventory at each sampling period. All tagged trees that had died since the previous inventory were recorded. The boundaries of the original Baker Stand were trimmed to a 3.9 ha area for analysis to minimize errors associated with the inclusion or exclusion of trees near the edge of the stand (Ansley and Battles 1998).

Analytical approach

To assess the possible effect of climatic conditions on demographic processes, we tested for trends in average annual temperature (°C), total annual precipitation (mm), and annual climatic water deficit (mm) for the period 1956-2010. Annual climatic water deficit is an index that represents a biologically relevant metric of climate variability by integrating temperature and precipitation (van Mantgem and Stephenson 2007). To calculate deficit, we used the Basin Characterization Model. This physically-based model includes data inputs for topography, soil composition and depth, underlying bedrock geology, and spatially-explicit values of air temperature and precipitation (Flint et al. 2013). Temperature and precipitation values were monthly average values from the empirically-based Parameter-Elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994). We evaluated trends using linear regression.

We calculated basal area (BA), stem density, and aboveground forest C for all trees >9.5 cm DBH for the four modern inventories (1995, 2001, 2008, and 2013). We calculated the same metrics for trees >24 cm DBH for all five inventories (1957, 1995, 2001, 2008, and 2013), because only trees >24 cm DBH were measured in the 1957 inventory. We used species-specific regional volume equations (Waddell and Hiserote 2005) and wood density estimates to calculate the carbon density (Mg C ha^{-1}) of aboveground biomass to maintain consistency with national forest inventory procedures (Zhou and Hemstrom 2009). Since all trees were measured in this complete inventory, there is no sampling error in these estimates. We evaluated trends using linear regression. We also calculated the relative dominance of each of the five major and two minor species present in the stand at each sampling interval. Relative dominance is defined as the proportion of total BA per species. Calculations were carried out in R ver. 3.1.1 (R Development Core Team 2014).

To estimate annual rates of mortality, growth, and recruitment, we used a hierarchical Bayesian approach to quantify community and individual species demography (Condit et al. 2006). This model accounts for variation in two levels, between-species and within-species, by defining a joint probability distribution that incorporates distributions from both the species and community levels. This method is advantageous because scant observations for rare species are informed by the overall community mean. The annual rate constant of mortality (m) was calculated as:

$$m = \frac{\ln(N_0) - \ln(N_1)}{t} \qquad \text{Eq. 1}$$

where N_0 and N_1 are the population size at $time_0$ and $time_1$, respectively, and t is the number of years between inventories. Mortality rates were calculated for each species and for the overall community.

Average annual growth rates were calculated for surviving trees. Because negative growth rates are biologically unrealistic, Condit et al. (2006) recommend that these values be excluded from growth rate calculations. To avoid introducing bias, we also excluded an equal proportion of trees above the upper growth threshold, defined by the interquartile range (IQR). This approach is a nonparametric method that uses the distribution of the data to identify outliers (Sokal and Rohlf 1981). The diameter growth between inventory intervals were ranked from lowest to highest, and the quartiles and the difference between the quartiles (IQR) were determined. Observations below Q1 – (1.5 × IQR) and above Q3 + (1.5 × IQR) were excluded from the growth analysis. This process omitted an average of 3% of surviving trees for the three modern inventory intervals we evaluated: 1995-2001 (54 of 2830 trees), 2001-2008 (83 of 2803 trees), and 2008-2013 (114 of 2950 trees). After the IQR outliers were excluded, remaining negative growth rates were recalculated by adding the overall minimum growth change for each inventory interval (Condit et al. 2006) because the log component of the relative growth rate equation requires non-negative values. The average annual growth rate of survivors (G) was calculated as:

$$G_k = \frac{\ln(dbh_{k,j+1}) - \ln(dbh_{k,j})}{t} \qquad \text{Eq. 2}$$

where dbh is the tree diameter (cm), k refers to individual trees, and j refers to inventories. The time interval t between inventories j and j+1 is calculated for each individual tree. Growth rates were calculated for individual trees, for each species, and for the overall community.

The average annual rate of recruitment was calculated as the number of trees ha^{-1} yr^{-1} that recruited into the >9.5 cm DBH size class between inventories. These three demographic rates were calculated for the three modern inventory intervals (1995-2001, 2001-2008, and 2008-2013). The number of years between inventories varied slightly (6, 7, and 5 years, respectively for the three inventory intervals). The variation in the length of the census interval introduces some census-period dependence bias that we did not account for in the model, but we assume this error to be minimal (Sheil and May 1996).

We used a hierarchical Bayesian model to estimate recruitment, growth, and mortality of the overall community and seven individual tree species (white fir, Douglas-fir, incense-cedar, sugar pine, ponderosa pine, black oak, and Pacific dogwood). Bayes theorem is used to define the joint probability distribution for the overall community as the product of the species-level and the community-level probabilities. For each of the three demographic processes, we selected probability distributions that best fit the observed data. For annual mortality rates, the community level distribution we observed was an exponential distribution among the seven species and at the species level, mortality was distributed as a binomial probability (dead or alive). For growth, both the community-level and species-level distributions followed a log-normal distribution. For recruitment, we observed an exponential distribution at the community-level and a normal distribution at the species level.

The Markov Chain Monte Carlo technique with the Gibbs sampler (10,000 runs with a 1,000 run burn-in) was used to solve the integration and fit the parameters using uninformed priors. We report the median value of the runs as well as the 2.5th and 97.5th percentiles (the Bayesian 95% credible intervals.) We define a significant difference between species or inventory intervals to be non-overlapping 95% Bayesian credible intervals (CI). Calculations were carried out using the software packages R ver. 3.1.1 (R Development Core Team 2014) and OpenBUGS 3.0.2 (Lunn et al. 2009).

RESULTS

Climate trends

Over the period 1957-2010, we detected a significant increasing trend in average annual temperature (mean±standard deviation = 9.8±0.6°C; $p < 0.001$, $r^2=0.19$) but did not detect a significant trend in total annual precipitation (mean±standard deviation = 1144±380 mm; $p = 0.77$; Figure 1). While there appears to be a weak trend of increasing water deficit at this site due to increasing temperatures, we did not find a significant long-term increase in the annual water deficit from 1957-2010, which averaged 504.8 mm (standard deviation = ±80.4; $p = 0.09$).

Stand dynamics (1957-2013)

Basal area increased linearly by 11% for trees >9.5 cm DBH over the 18-year period from 1995-2013 ($p=0.009$, $r^2= 0.98$) and by 81% for trees >24 cm DBH over the 56-year period from 1957-2013 ($p=0.003$, $r^2= 0.99$; Table 1; Figure 2). There was a notable increase in white fir dominance over the 56-year period from 1957-2013 (Figure 2). Stem density increased by 8% for trees >9.5 cm DBH over the 18-year period from 1995-2013 though this trend was not significant ($p=0.13$, $r^2= 0.75$) and by 116% for trees >24 cm DBH over the 56-year period from 1957-2013 ($p=0.0007$, $r^2= 0.99$; Table 1). Forest carbon increased linearly by 8% for trees >9.5 cm DBH over the 18-year period from 1995-2013 ($p=0.005$, $r^2= 0.99$) and by 116% for trees >24 cm DBH over the 56-year period from 1957-2013 ($p=0.0003$, $r^2= 0.99$; Table 1).

When the stand was first measured 1957, Douglas-fir accounted for 43% of the total BA, while the other 4 major species (white fir, incense-cedar, ponderosa pine, and sugar pine) had relative dominance values similar to one another, ranging from 9% (ponderosa pine) to 20% (sugar pine; Figure 2). Between 1957 and 2013, ponderosa pine decreased in relative dominance by 41% (from 9% relative dominance in 1957 to 5% in 2013) and sugar pine relative dominance decreased by 27% (from 20% relative dominance in 1957 to 15% in 2013). White fir increased in relative dominance by 94% (from 15% relative dominance in 1957 to 28% in 2013). The relative dominance of Douglas-fir changed little from 1957-2013, decreasing from 43% in 1957 to 40% in 2013.

Mortality (1995-2013)

Community-wide mortality rates varied among inventory intervals. Mortality was significantly lower (0.14% yr^{-1}, 5% CI = 0.10, 95%CI = 0.34) from 1995-2001 than the later inventories (2001-2008: 1.37% yr^{-1}, 5% CI = 0.67, 95%CI = 3.60; 2008-2013: 0.84% yr^{-1}, 5% CI = 0.38, 95%CI = 2.47; Figure 3). Species mortality rates did not differ systemically from one another throughout the study, but some species differed significantly among individual inventory intervals. Douglas-fir and white fir had significantly lower mortality rates in 1995-2001 as compared to the later inventories. White fir had significantly higher mortality rates in the 2001-2008 inventory period relative to the other periods. There tended to be more variation in mortality rates among inventory intervals than among species within inventory periods. Douglas-fir had significantly lower mortality than the community median for the 2001-2008 inventory period, which was the only instance of a species differing significantly from the community median (Table S1).

Growth (1995-2013)

Growth rates of white fir, Douglas-fir, and incense-cedar significantly outpaced the growth rates of the pines and hardwoods in all inventory periods (Figure 4). The growth rates of white fir, Douglas-fir, and incense-cedar were significantly higher than the community median for all three inventory periods, which ranged from 0.45-0.67% ha^{-1} yr^{-1} (Table S2). The growth rates of ponderosa pine and sugar pine were significantly lower than the community median for those same intervals. The community median did not differ significantly among inventory periods (Table S2).

Recruitment (1995-2013)

Recruitment rates of white fir and Douglas-fir into the potential canopy tree size class (>9.5cm DBH) were significantly higher than the recruitment rates of the pines (Figure 5). There was no recruitment of hardwoods in any of the inventory periods and no recruitment of pine species in the 1995-2001 and 2008-2013 inventory periods. The recruitment rates of white fir and Douglas-fir were significantly higher than the community median for all three inventory periods, while the recruitment rates of ponderosa and sugar pine were significantly lower than the community median for those same intervals. The community median did not differ significantly among inventory periods (Table S3).

DISCUSSION

Long-term trends of forest composition, structure, and demography

Our longitudinal results documenting forest change over the last half-century indicate that a species reordering is underway in this old-growth mixed-conifer forest. White fir relative dominance increased by 94% from 1957-2013. In contrast, the relative dominance of both sugar pine and ponderosa pine declined over the 56-year study period (Figure 2). Throughout the study, Douglas-fir remained the largest contributor to total BA. Forest structure also changed over the 56-year study period. From 1957-2013, we observed a linear increase in BA, stem density, and forest C of trees >24cm DBH (Figure 2). Similar trends were observed for all trees >9.5cm DBH at the shorter timeframe of 1995-2013. It does not appear that increased competition as a result of greater density has resulted in a plateau of forest growth at this site. This forest is an example of the capacity of old-growth forests to act as an important net C sink in the absence of disturbance (Luyssaert et al. 2008). However, forests can easily transition from a net carbon sink to a carbon source when wildfires re-enter the system (Gonzales et al. 2015). Densifying, fire suppressed forests such as the Baker stand are at high risk for such a transition (Stephens et al. 2014).

Evidence from our study suggests that differences in growth and recruitment rather than mortality appear to be responsible for the observed trend towards a species reordering. Mortality did not systematically differ among the major constituent species (Figure 3). The mortality rates we observed in the Baker stand (an average media community mortality rate of 0.78% yr^{-1} for the three inventory period with a 95% Baysian credible interval 0.1%-3.6%) overlap with mortality rates for California forests reported by van Mantgem et al. (2009; plot-level mean mortality rates of 1.2% and 1.6% $year^{-1}$ for two census intervals). However, recruitment and growth of firs has far outpaced that of pines (Figs.4 and 5), leading to an absence of pines in smaller diameter classes (9.5–24 cm DBH) in this stand and a decline in the relative dominance of pine species.

Potential drivers of forest reordering

We were interested not only in quantifying trends over time in an old-growth mixed conifer stand but also assessing the potential role of climate and disturbance regimes as drivers of shifts in composition and structure. Climate stress has been identified as an important factor in increased mortality rates in the Western US (Allen et al. 2010, van Mantgem and Stephenson 2007, Anderegg et al. 2015). While the average annual temperature increased over the study period (1957-2010), neither annual precipitation nor water deficit showed a significant trend. While climatic correlates with tree mortality have been documented extensively in the southern Sierra Nevada (Das et al. 2013), no trend over time in annual water deficit or tree mortality was detectable at our study site in the northern Sierra Nevada. The more mesic conditions relative to more southern sites indicates that there may be areas of the Sierra Nevada that are less susceptible to climate-induced mortality (Dettinger et al. 1998). These sites may serve as refugia for drought-sensitive species under future climate conditions.

The lack of a strong climate signal at this site implies some other force(s) driving trends in vegetation away from the steady-state behavior expected of old-growth forests (senus Bormann and Likens 1979). Our results are consistent with expected consequences of a disturbance regime altered by a century of fire suppression (Collins et al. 2011). Historically, mixed-severity fires would remove relatively fire-intolerant fir saplings and small trees, allowing sufficient gaps for relatively shade-intolerant pines to recruit (York et al. 2012). It is likely that the increasingly crowded Baker Stand has constrained the regeneration of the shade-intolerant pines (Table 1). The lack of pine recruitment as a legacy of fire suppression policies is well-documented throughout the Sierran mixed conifer forest (Dolanc et al. 2014, Knapp et al. 2013, North et al. 2007, Scholl and Taylor 2010, Zald et al. 2008).

Our study included only one stand, which we acknowledge limits the scope of inference of our results. Though the spatial extent of the Baker Stand is small, the insights provided by this 56-year record are valuable because in addition to being one of the few long-term inventories in the Sierra Nevada, old-growth forests in the northern reaches of the Sierra Nevada are particularly rare (Barbour et al. 2002). Thus our work complements observations from the more extensive old-growth forests in the Central (Yosemite NP) and Southern (Sequoia-Kings Canyon NP) Sierra Nevada.

CONCLUSION

Old-growth forests have many important ecological functions. Their heterogeneous structure and composition can confer resilience in the face of drought, pests, pathogens, and fire (Stevens et al. 2014). Additionally, they serve as an important carbon sink, with a large amount of atmospheric carbon removed annually by large trees (Stephenson et al. 2014). It is important to understand the demographic drivers of forest change in order to maintain resilient old-growth forests as mortality risks from climate change and catastrophic fire continue to accelerate. Long-term, in-depth studies of forest dynamics are a crucial source of information regarding best practices for sustaining these forests in the future.

Our results indicate that creating opportunities for pine recruitment and growth is essential to maintain the shared-dominance characteristic of the mixed conifer forest. Research suggests that pine species in pre-settlement Sierra Nevada forests regenerated in canopy gaps created by hotspots in otherwise low-intensity fires (White 1985). Ponderosa pine requires disturbances for regeneration that reduce competition, increase light availability, and create a charred seedbed (White 1985, York et al. 2012). Sugar pine regeneration has not been as closely linked to disturbance as ponderosa pine, but sugar pine’s shade-intolerance leads it to regenerate where larger gaps have formed in fires (North et al. 2005). A gap-based approach to harvesting, followed by a post-harvest burning treatment within gaps has been suggested as one method to encourage pine recruitment in mixed-conifer forests (York et al. 2012). However, Zald et al. (2008) found that high seed rain of white fir and incense cedar relative to pines after experimental fire and thinning treatments negated efforts to increase pine abundance. Control of competitors as well as planting may also be required for successful pine recruitment in fire-suppressed forests.

TABLES

Table 1. Stem density (stems ha^{-1}), basal area (m^2 ha^{-1}), and forest carbon (Mg ha^{-1}) in the Baker stand from 1957-2013. Only trees >24cm DBH were measured in the 1957 inventory. Because this is a complete inventory, there is no error around the estimate.

		1957	1995	2001	2008	2013
Density (stems ha^{-1})	>9.5 cm		727	774	773	789
	>24 cm	119	230	240	249	257
Basal Area (m^2 ha^{-1})	>9.5 cm		77.7	81.2	83.7	86.1
	>24 cm	42.1	68.8	71.7	74.3	76.4
Forest Carbon (Mg ha^{-1})	>9.5 cm		231	241	251	256
	>24 cm	137	220	228	238	243

FIGURES

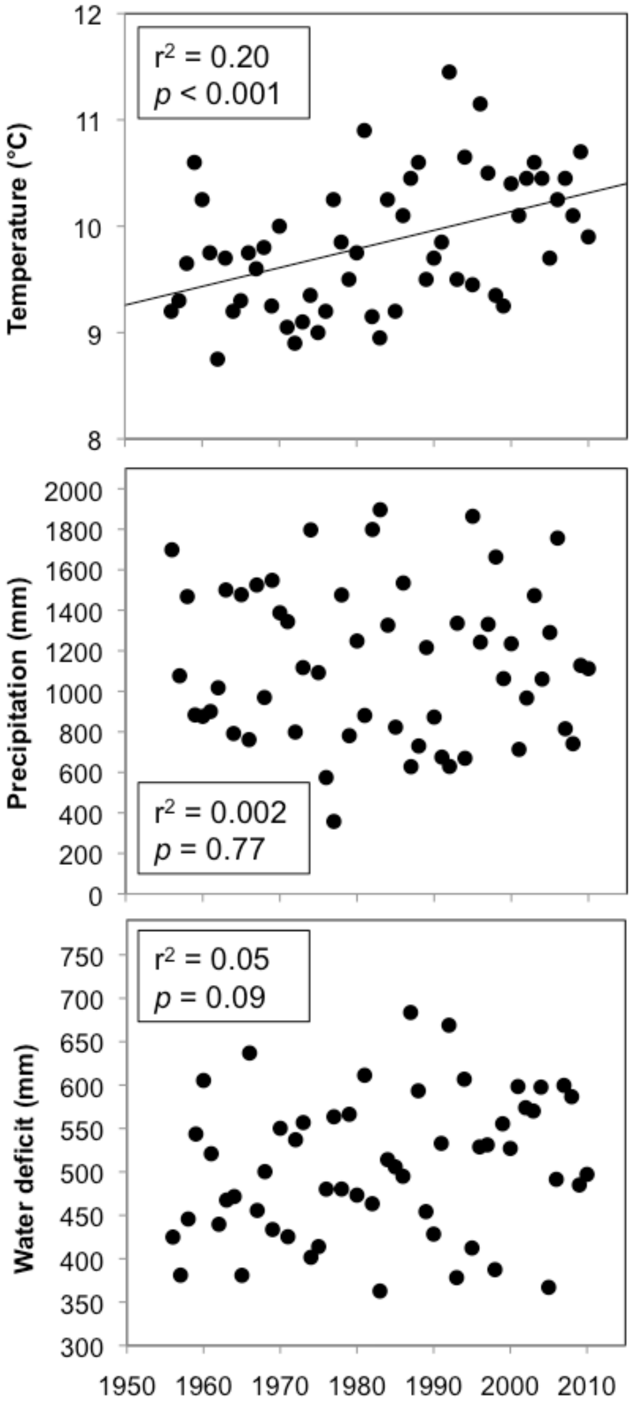

Figure 1. Average annual temperature increased significantly from 1956-2010 ($p < 0.001$, $r^2 = 0.20$). Average annual precipitation and annual water deficit did not have significant long-term trends over the same period.

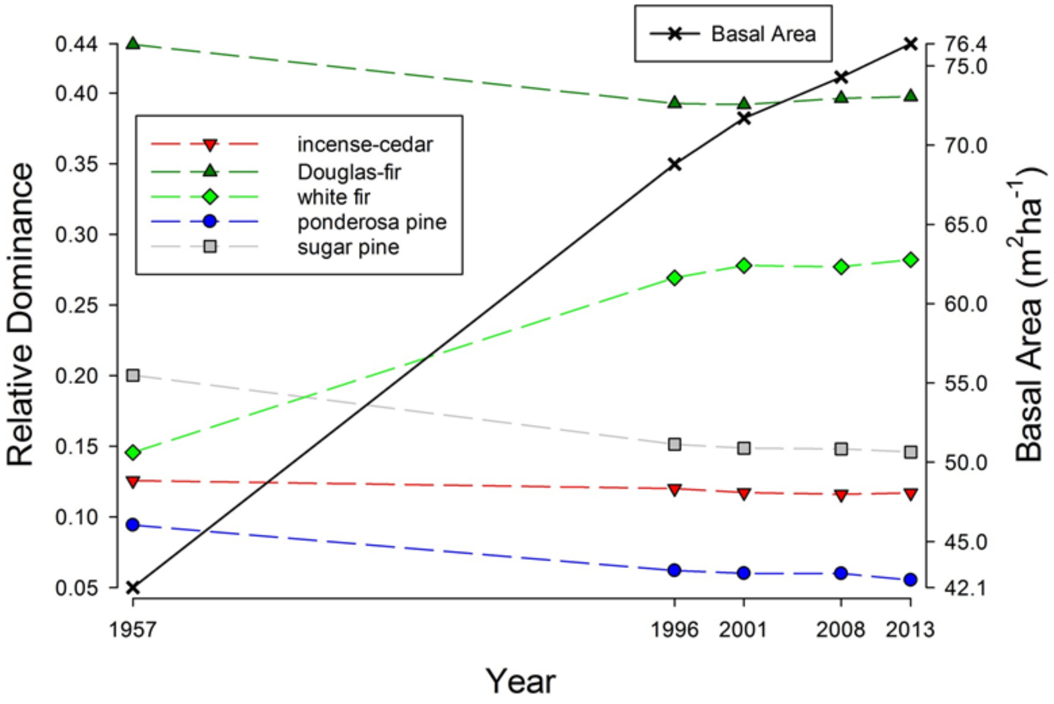

Figure 2. Changes in relative dominance of trees >24 cm DBH by species (1957-2013) and the total basal area increase over the 56-year study period. Relative dominance is defined as the proportion of total basal area for that species.

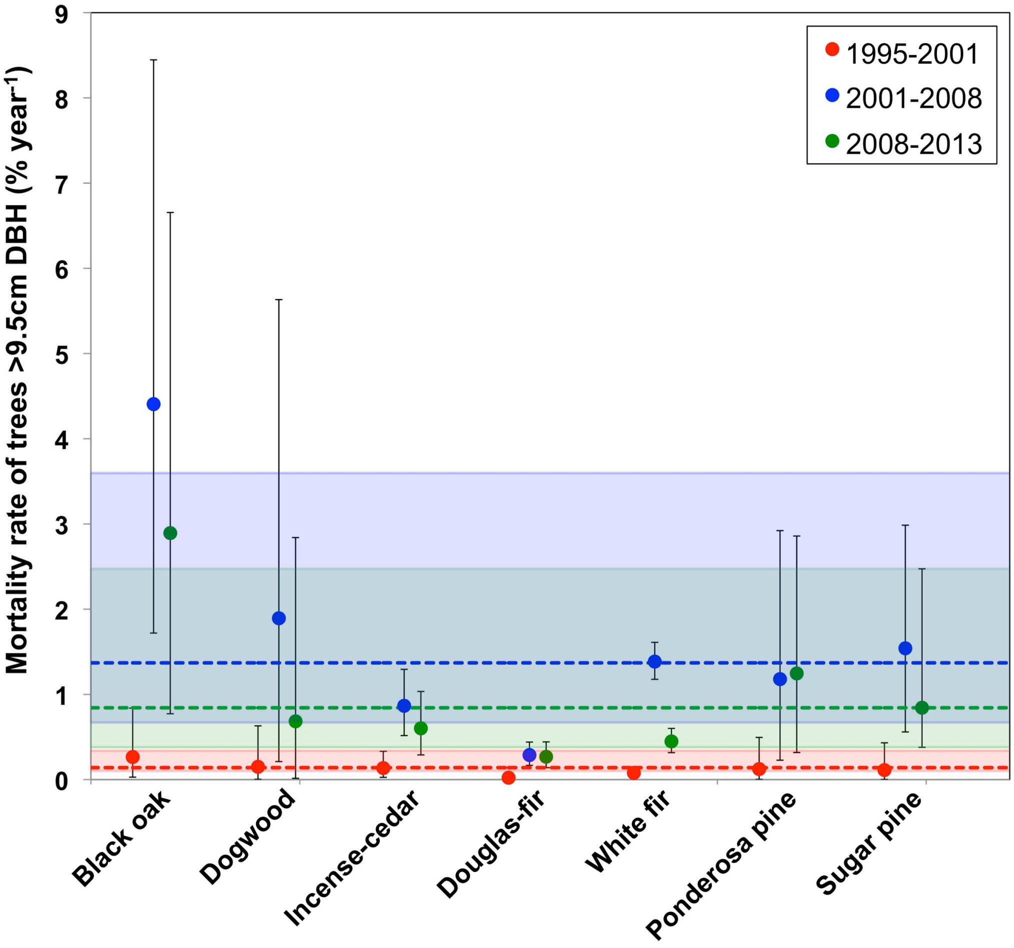

Figure 3. Mortality rate (% yr^{-1}; median and 95% CI) from 1995-2013 of the community and of individual species. The mortality rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Baysian credible interval. The species rates are shown as points with error bars indicating the 95% Baysian credible interval.

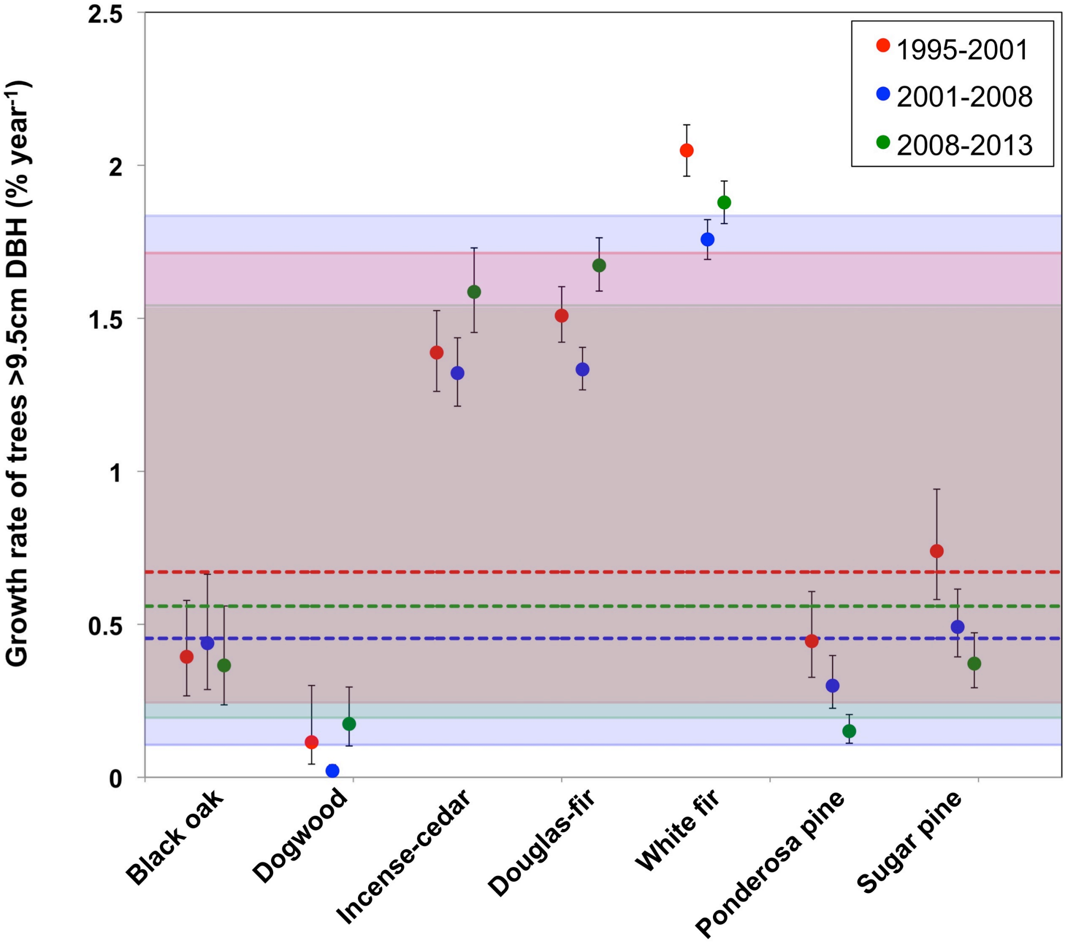

Figure 4. Growth rate (% yr^{-1}; median and 95% CI) from 1995-2013 of the community and of individual species. The growth rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Baysian credible interval. The species rates are shown as points with error bars indicating the 95% Baysian credible interval.

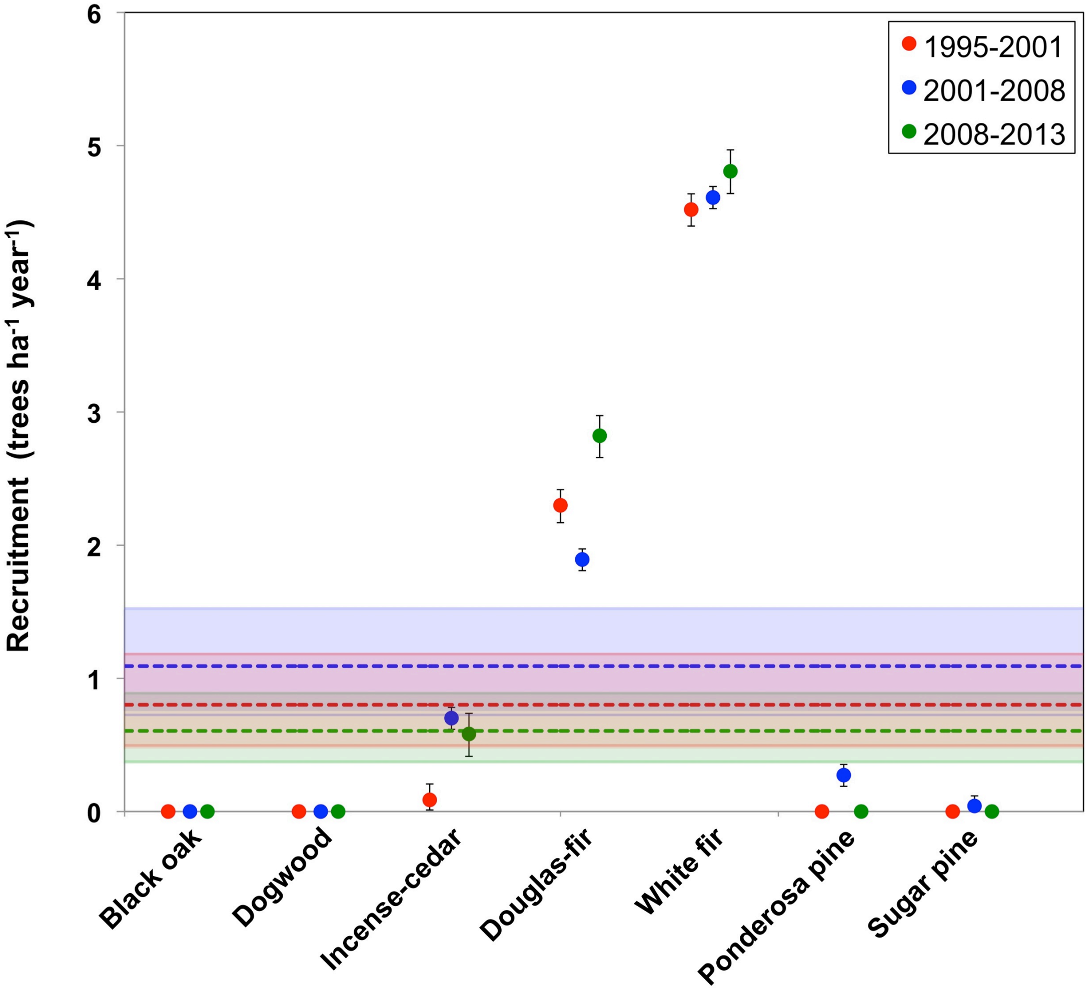

Figure 5. Recruitment rate to the >9.5 cm DBH class (trees ha^{-1} yr^{-1}; median and 95% CI) from 1995-2013 of the community and of individual species. The recruitment rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Baysian credible interval. The species rates are shown as points with error bars indicating the 95% Baysian credible interval. There was no recruitment of black oak or dogwood in any inventory. There was no recruitment of ponderosa pine or sugar pine in the 1995-2001 or 2008-2013 intervals.

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CHAPTER 2

Evaluating a new method for reconstructing forest conditions from General Land Office survey records

ABSTRACT

Historical forest conditions are often used to inform contemporary management goals because historical forests are considered to be resilient to ecological disturbances. The General Land Office (GLO) surveys of the late nineteenth and early twentieth centuries provide regionally quasi-contiguous datasets of historical forests across much of the Western United States. Multiple methods exist for estimating tree density from point-based sampling such as the GLO surveys, including distance-based and area-based approaches. Area-based approaches have been applied in California mixed-conifer forests but their estimates have not been validated. To assess the accuracy and precision of plotless density estimators with potential for application to GLO data in this region, we imposed a GLO sampling scheme on six mapped forest stands of known densities (159-784 trees ha^{-1}) in the Sierra Nevada in California, US, and Baja California Norte, Mexico. We compared three distance-based plotless density estimators (Cottam, Pollard, and Morisita) as well as two Voronoi area (VA) estimators – the Delincé and mean harmonic Voronoi density (MHVD) – to the true densities. We simulated sampling schemes of increasing intensity to assess sampling error. The relative error (RE) of density estimates for the GLO sampling scheme ranged from 0.36 to 4.78. The least biased estimate of tree density in every stand was obtained with the Morisita estimator and the most biased was obtained with the MHVD estimator. The MHVD estimates of tree density were 1.2-to-3.8 times larger than the true densities and performed best in stands subject to fire exclusion for 100 years. The Delincé approach obtained accurate estimates of density, implying that the Voronoi approach is theoretically sound but that its application in the MHVD was flawed. The misapplication was attributed to two causes: 1) the use of a crown scaling factor that does not correct for the number of trees sampled; and 2) the persistent underestimate of the true VA due to a weak relationship between tree size and VA. The magnitude of differences between true densities and MHVD estimates suggest caution in using results based on the MHVD to inform management and restoration practices in the conifer forests of the American West.

INTRODUCTION

Forests in the western United States are threatened by a suite of stressors that include altered fire regimes, legacy effects from timber harvesting, a warming climate, chronic air pollution, and uncharacteristically severe attacks by insects and pathogens (Bytnerowicz et al. 2013, Perry et al. 2011, Hessburg et al. 2016). In response, management seeks to restore diverse landscapes that maintain native species and characteristic processes (North et al. 2009, Hessburg et al. 2016, Stephens et al. 2016). These management goals are informed by the structure and composition of the forest prior to European settlement (Churchill et al. 2013), a time when western forests are thought to have sustained form and function despite fire, drought, and insect attack (Mast et al. 1999, Stephens et al. 2015). Given the current emphasis on forest restoration and resilience in public lands (USFS 2011, USFS 2013) accurate characterizations of historical forests are particularly important.

Estimates of pre-settlement forest conditions are derived from data with inherent limitations. Historical inventories are a primary source of information (Stephens 2000, Hagmann et al. 2013) but even the most geographically extensive records (e.g., > 10,000 ha, Stephens et al. 2015) may not necessarily represent regional forest characteristics. Forest reconstructions using fire scars, stumps, and tree-rings also provide useful references (Taylor 2004, North et al. 2007) but physical evidence of the pre-settlement forest degrades with time and the effort involved constrains the spatial extent of the reconstruction. In contrast, the public land survey system conducted by the General Land Office (GLO) is a systematic, historical sample of trees over a broad domain from Ohio to the West Coast of the US (Schulte and Mladenoff 2001).

The purpose of the GLO survey was to delineate boundaries of federal lands for sale. The survey consisted of 9.7 x 9.7 km (6 x 6 mile) townships containing thirty-six 1.6 x 1.6 km (1 x 1 mile) sections. Section corners marked with permanent monuments demarcated the end of 1.6-km section lines and quarter corners were located equidistant to two section corners. In order to provide reference points to the corners, nearby bearing trees (also called witness trees) were selected. Section corners were referenced with four bearing trees; quarter corners were referenced with two bearing trees. For each bearing tree, the distance and direction from the point along with species identification and stem diameter were recorded. In effect, these bearing tree records represent a systematic sample of forest conditions (Schulte and Mladenoff 2001).

While the GLO bearing tree data overcome the restricted geographic extent shared by historical inventories and forest reconstructions, it is a sparse sample (i.e., 1 point per 0.8 km) beset by questions regarding data quality and analysis (Bourdo 1956, Bouldin 2008, Hanberry et al. 2011, Liu et al. 2011). Cottam (1949) was one of the first to use the pre-settlement survey to estimate past forest characteristics. As he noted, the key challenge is an accurate estimate of tree density from the information contained in the bearing trees. Although surveyor bias and error in the selection of bearing trees are concerns (Bourdo 1956, Grimm 1984, Bouldin 2008, Williams and Baker 2011, Liu et al. 2011), this paper focuses on the fundamental task of calculating tree density from distance data (e.g., Cottam and Curtis 1956, Morisita 1957, Pollard 1971, Williams and Baker 2011). Specifically, we evaluated the performance of a new plotless density estimator (PDE) developed to maximize the utility of GLO data to reconstruct pre-settlement forests in the arid western US by using area-based metrics (*sensu* Williams and Baker 2011, Baker 2014) as opposed to traditional distance-based estimators.

Background

Plotless density estimators (PDEs) are a frequent alternative to plot-based sampling for forest inventory (Kronenfeld 2009). They rely on point-to-tree and/or tree-to-tree distances to efficiently sample heterogeneous landscapes. Of the many possible PDEs (e.g., Engeman et al. 1994), we tested the bias and precision of three PDEs that have been applied by previous studies to GLO data. These PDEs are appropriate to GLO data because they rely only on the distance data recorded by surveyors when documenting bearing trees. We refer to these PDEs by the name of their most often-cited source: Cottam, Pollard, and Morisita (Table 1). The equations share a similar format to estimate tree density from a sample of points where the distance to the nearest tree is measured in each sector (four 90° sectors for corner points; two 180° sectors for quarter corners). This common format for tree density (λ) includes: a unit scalar (K), an expression of design parameters (Ω), and an estimate of either the squared mean or the mean squared point-to-tree distance (*ptd*):

$$\lambda \propto K * \Omega * \frac{1}{\overline{ptd^2} \ or \ (\overline{ptd})^2} \qquad \textit{Eq. 1}$$

Applications of the Cottam estimator to GLO survey data include Rhemtulla et al. (2009) and Maxwell et al. (2014); the Pollard — Kronenfeld and Wang (2007); the Morisita — Hanberry et al. (2012).

The theoretical basis for these three PDEs rests on the assumption that the distribution of the point-to-tree distances indicates the average surface area occupied by the average tree (Cottam and Curtis 1956, Morisita 1957). Cottam and Curtis (1956) consider this sample space as the exclusive surface area occupied by the nearest trees. Thus the reciprocal of the average area occupied (area per tree) is the density (trees per area). However point-to-tree distances are unbiased variables only when the spatial distribution of trees follows a random pattern and the density of trees remains constant (Kleinn and Vilčko 2006). The PDEs vary in their performance, but in general accuracy and precision decrease as the trees diverge from random spacing and/or tree density varies across the landscape (Cottam and Curtis 1956, Engeman et al. 1994, Kronenfeld 2009). The challenge posed by a non-random distribution of trees is particularly important in dry forests of western North America, where clumped tree spacing is typical (Larson and Churchill 2012).

The new PDE recommended by Williams and Baker (2011) uses the predicted Voronoi area (VA) of individual trees to overcome the limitations of distance-based estimators. VAs are applied in a variety of disciplines to describe spatial positions of points on a plane (Okabe et al. 2000). Mark and Esler (1970) were among the first to suggest a design-based, point-to-tree PDE that relied on the exclusion zone of individual trees to avoid potential biases introduced by the point pattern of the trees. This zone delineates a polygon where the tree defining the polygon will be the closest to any sample point in the polygon. Delincé (1986) subsequently provided the theoretical justification for this approach and the application to calculate tree density from point samples (Table 1). In Delincé's (1986) method, the exclusion zone is the VA with the vertices of the VA defined by half the distance to each neighboring tree. The obvious constraint with the Delincé PDE with regard to the GLO data is that only the distance to the nearest tree in each sector is recorded at the corner points. There is no information on the location of the neighboring trees in GLO data.

The innovation in Williams and Baker (2011) was the adaptation of Delincé's (1986) approach to the GLO data. Since there was no way to measure the VA of bearing trees in historical data sets such as the GLO data, they developed region-specific regression equations from contemporary data that predict VA as a function of tree diameter and local tree density, which can then be applied to historical data (Table 1). The accuracy of the VA prediction is crucial. The expectation that tree size is a good indicator of VA assumes that competition is a major factor driving the spatial arrangement of trees. In short, bigger trees are expected to have larger exclusion zones. A host of distance-dependent tree competition indices incorporate tree size to account for this size-dependency (Biging and Dobbertin 1992, Aakala et al. 2013) but competition is not only distance-dependent (Lorimer 1983). For mixed-conifer forests in the Sierra Nevada, Biging and Dobbertin (1995) reported that distance-independent competition indices performed slightly better than the best distance-dependent measures. The assumption inherent in Williams and Baker's (2011) methodology that the size of a tree is the most important determinant of its spatial configuration relative to neighboring trees must be investigated in order to determine whether the density estimates derived from this approach are accurate.

Research objectives

The application of this new area-based PDE to GLO data from dry conifer forests across the western US has often produced drastically higher estimates of pre-settlement tree density than expected (Williams and Baker 2012, Baker 2012, Baker 2014). For example, in the Californian mixed-conifer forests on the western slopes of the Sierra Nevada, pre-settlement tree density estimates based on Baker's (2014) analysis of GLO data exceeded estimates based on historic forest inventories by 200 to 500% (Stephens et al. 2015). Hagmann et al. (2013, 2014) found similar discrepancies between the historical forest inventories they analyzed in mixed-conifer forests of central and northern Oregon and density estimates for the same areas reported by Baker (2012) using the new area-based PDE. These results challenge our understanding of the natural dynamics of the Sierra Nevada and eastern Oregon mixed-conifer forests where frequent low- and moderate-severity fires were thought to maintain relatively open forests (Hessburg et al. 2015, Safford and Stevens, in press). Moreover, Baker's (2014) reconstructions raised important questions regarding the appropriate strategy to restore contemporary Sierra Nevada forests (Odion et al. 2014, Hanson and Odion 2016).

This new perspective on the historical western forest has engendered criticism (e.g., Fulé et al. 2014, Hagmann et al. 2013, Williams and Baker 2014, Baker 2014) but the performance of the novel density estimator that underpins these controversial findings has not been independently tested. Therefore, we simulated a GLO sampling scheme in six 4 ha mapped stands that span much of the latitudinal range of mixed-conifer forest in the California Floristic Province, some of which had experienced fire exclusion whereas others had relatively intact fire regimes. Mapped stands, where the location of all trees is known, are required to verify the true VA of trees. We compared the accuracy of traditional PDEs to the method used by Baker (2014) and assessed whether VA regression equations are able to accurately predict true VA. Given the potential of the GLO bearing tree data to characterize pre-settlement forest conditions of the United States, it is essential to review the theoretical basis of any new PDE and to test its application.

METHODS

Study sites

We identified six old-growth mixed-conifer and pine-dominated stands across the latitudinal gradient of the Sierra Nevada and Sierra de San Pedro Mártir of California, United States and

Baja California, Mexico (Table 2). Sites included three stands on the western slope of the Sierra Nevada: one stand in the Plumas National Forest (PLUM), one stand in the Teakettle Experimental Forest (TEAK), and one stand in Yosemite National Park (YOSE). A fourth site (BRID) was located on the eastern slope of the Sierra Nevada in the Humboldt-Toiyabe National Forest. All of the California stands had not been harvested but experienced approximately 100 years of fire exclusion. The remaining two stands were in the Sierra de San Pedro Mártir National Park on the western slope of the Sierra de San Pedro Mártir, where fire suppression did not begin until the 1970s (Stephens et al. 2010). The two sites in Baja differ in their underlying geology, with one site on soil derived from metamorphic parent material (META) and the other site on soil derived from granitic parent material (GRAN; Stephens and Gill 2005, Fry et al. 2014). In addition to covering a latitudinal gradient of the mixed-conifer and pine forests, these stands also encompass a density gradient ranging from 159-784 trees ha^{-1} (Table 2). Each stand included in this study was 4 ha in area and included the mapped locations of all stems ≥ 9.5cm diameter at breast height (DBH; 1.37 m; Figure 1). Five of the stands were 200 × 200 m in configuration and the PLUM stand was 100 × 400 m. To illustrate the range of results, we included figures from two sites: YOSE, a site that is representative of contemporary density in the Sierra Nevada (FIA 2015), and GRAN, a site that is representative of pre-settlement density (Stephens et al. 2015). Figures for the other four sites can be found in Appendix S1.

Site-specific spatial patterns

We applied an inhomogeneous Ripley's *L* function (*L*) to determine the spatial patterning of the trees at each of the six stands. The inhomogeneous function avoids assuming a null model characterized by a homogeneous Poisson process, which may result in the misinterpretation of the point structure when point density varies within a mapped study area (Wiegand and Moloney 2004). We used a radius of 25 m at the PLUM stand (the maximum allowable radius due to the stand configuration) and a radius of 30 m at the other five stands. Thirty meters was chosen as the cutoff because this radius was larger than the maximum distance required to locate a nearest neighbor to a random sampling point in the least dense stand (GRAN, 28 m maximum distance to nearest neighbor). Thus, a 30-m radius captures all potential tree-to-tree competitive interactions relevant to PDE calculations. For each stand, we simulated 1,000 runs of a random distribution of trees to determine the 95% confidence interval (CI). The empirical *L* value from the mapped trees was compared to the simulated 95% CI to determine at what scales the distribution of trees significantly differed from a random distribution (Cressie 2015). The criterion for significance was the non-overlap of observed *L* with the 95% CI of the random simulations.

GLO density estimators

We compared density estimates from the six mapped stands based on the three traditional PDEs (i.e., the Cottam, Pollard, and Morisita) as well as the mean-based harmonic Voronoi density (MHVD, Table 1). Williams and Baker (2011) found the MHVD to be one of the most accurate Voronoi-based estimators they tested, and Baker (2014) applied the MHVD to sites in the Sierra Nevada of California. The calculation of the traditional PDEs relies on the information contained in the GLO survey, namely the number of corners (n), the number of sectors (m), and the point-to-tree distances (r) in each sector (Table 1). In contrast, the MHVD requires predicting the mean Voronoi area (MVA) via a three-step process: 1) predict a tree's crown radius (CR) from the allometric relationship between crown size and stem diameter; 2) calculate the mean neighborhood density (MND) correction factor; and 3) estimate a tree's MVA from its CR scaled by the MND (Williams and Baker 2011). The CR for tree$_i$ was predicted from the diameter at breast height (DBH, breast height = 1.37 m) of tree$_i$ according to the equation:

$$\ln(CR) = a + b \times \ln(DBH) \qquad \textit{Eq. 2}$$

where *a* and *b* are species-specific regression parameters for CR (Table D1 in Baker 2014). At each corner, the MND was calculated as:

$$MND_j = \frac{1}{\left(\sum_{i=1}^{m} \frac{r_{ij}}{m}\right)^2} \qquad \textit{Eq. 3}$$

where *r* is the distance from the sampling point$_j$ to the nearest neighbor tree$_i$ in *m* sectors (Williams and Baker 2011). The MVA of tree$_i$ at sampling point$_j$ was then estimated as:

$$MVA(tree_i) = \exp\left(a + b * \left(\frac{\ln[CR(tree_i)]}{MND_j}\right)\right) \qquad \textit{Eq. 4}$$

where *a* and *b* are species-specific regression parameters for MVA (Table D1 in Baker 2014), MND$_j$ from Equation 3, and CR(tree$_i$) from Equation 2. Note: we used DBH to estimate CR in accord with the equation in Baker (2014). However, an unpublished erratum (W. Baker, *personal communication*) corrected the CR predictor to diameter at stump height (DSH; 0.30 m). Thus we also calculated MHVD with DSH. See Appendix S2 for details.

Bias and precision assessment

We applied simulations to quantify the performance of the PDEs. Each test included 1,000 realizations of randomly placed sampling corners in each of the six mapped stands. Sample corner intensity spanned the range of GLO point pools considered by Williams and Baker (2011) — three, six, nine, and 21 — as well as the recommended minimum intensity of 50 points (Kronenfeld 2009, Hanberry et al. 2011) and a saturation intensity of 1,000 points. To minimize edge effects, the location of the random points was excluded from a buffer zone along the stand boundaries with the buffer width ranging from 10-20 m depending on tree density. Less dense stands required a larger buffer to ensure the presence of a bearing tree in each sector for every simulated point.

The GLO sampling regime includes section corners with four bearing trees (one tree in each 90º quadrant) and quarter corners with two bearing trees (one tree in each 180º semicircle). Bearing trees are referred to as nearest neighbors (nn) for the purposes of density calculation. When calculating the PDEs, we treated all corners as either sections corners with four bearing trees (4nn) or quarter corners with two bearing trees (2nn). We did not apply the correction factors developed in Williams and Baker (2011) to allow the mixing of results from section corners and quarter corners. While the correction factors increase the number of trees available from the GLO data because both 4nn and 2nn corners can be included, the use of the weights has not to our knowledge only been vetted for the Cottam (Cottam and Curtis 1956). Moreover, it is clear from both theory and practice that the number of neighbors measured greatly affects the estimate

(Morisita 1957, Engeman et al. 1994, Kronenfeld 2009). For example, Kronenfeld (2009) demonstrated for the Pollard that the bias in the estimated density diminishes as nn increases, ultimately approaching an asymptote near the true density as nn approaches 50. By excluding correction factors, our comparisons avoided a potential confounding factor.

Although not appropriate for GLO data because it requires measuring the VA, we included the Delincé PDE in the simulation because it constitutes the theoretical underpinning of the MHVD approach. Its inclusion can help to deduce the source of any bias observed. To compute the Delincé (Table 1), the nearest bearing tree to each point (1nn) was selected and its true VA was calculated from the mapped trees.

Results from the 1,000 realizations were summarized by the median as the measure of central tendency and the 95% CI as the measure of variation. Bias was defined by the relative error (RE):

$$\mathrm{RE} = \frac{\lambda_{\mathrm{sim}}}{\lambda_{\mathrm{true}}} \qquad \textit{Eq. 5}$$

where λ_{sim} is the median density from the 1,000 realizations and λ_{true} is the true density of the mapped stand. RE < 1 implies underestimates; RE > 1 implies overestimates. Precision was defined by the relative root mean square error (rRMSE):

$$\mathrm{rRMSE} = \frac{RMSE_{\mathrm{sim}}}{\lambda_{true}} \qquad \textit{Eq. 6}$$

where $\mathrm{RMSE}_{\mathrm{sim}}$ is the root mean square error of the 1,000 realizations in each simulation and λ_{true} is the true density of the mapped stand. Larger values of rRMSE imply less precision.

MHVD deconstruction

We evaluated the three steps needed to calculate the MHVD. For crown radius (CR, Equation 2), we compared the regression fits described in Baker (2014) to equations estimated from Forest Health Monitoring (FHM) data collected as part of the Forest Inventory and Analysis Program. This database included measured crown radii from monitoring plots in the mixed-conifer forest of the Sierra Nevada in California (http://www.fia.fs.fed.us/tools-data/other_data/index.php). Predictions of CR were fit from the FHM data for all species present in the six stands (ten species total; *n* per species ranging from 59-746).

Williams and Baker (2011) used the mean neighborhood density (MND, Equation 3) to adjust the MVA prediction by the local density, with the assumption that a tree of a given diameter will have a larger MVA in a less dense stand and a smaller MVA in a more crowded stand. To isolate the effect of the MND correction, we simulated a 6-point section corner (4nn) and a 6-point quarter corner (2nn) sampling scheme in each of the six mapped stands and reported the median MND and 95% CI (from 1,000 realizations) for the 2nn and 4nn sampling schemes. This 6-point scheme is recommended by Williams and Baker (2011) as being sufficient for estimating density with a 22% relative mean absolute error (RMSE). We used the 1,000 simulated MND values to estimate the median and 95% CI of the MVA for a representative tree (Equation 4). For each stand, the representative tree was defined by the dominant species and the median DBH; MVA was fit using the equation parameters in Baker (2014).

We tested the strength of the relationship between CR/MND and true VA by least-squares regression. We calculated the MVA regression parameters in Equation 4 for the common species (>5% dominance) in each stand and compared them to the species-specific fits in Baker (2014). Only section corners (4nn) were considered for the MND values in this analysis to avoid potential confounding errors from calculating MND with two or four bearing trees. CR was estimated using parameters derived from the FHM data set (as above); MND was calculated for 21 regularly spaced section corners (4nn). True VAs were calculated from mapped tree locations. Thus in this analysis we had large, well-distributed samples for both the CR and MVA regressions.

We assessed the accuracy of the MVA regression equation by comparing the predicted VA of individual trees to the true VA. We used the tree maps to calculate the true VA of each tree. For each stand, a buffer ranging from 5-18 m from the stand boundaries was applied with the width set to ensure that trees included in the analysis had a neighbor on all sides. MND was derived from 21 regularly spaced section corners (4nn, as above). Only section corners were considered in this analysis to avoid potential confounding errors from calculating MND with two or four bearing trees. The MVA for trees was computed using the CR and MVA coefficients in Baker (2014); the recorded tree species and DBH; and the MND for the point nearest to each tree (Equation 4). We also estimated the mean difference ($\overline{VA}_{difference}$) between MVA and true VA, calculated as:

$$\overline{VA}_{difference} = \sum_{i=1}^{n} \frac{MVA_i - VA_{true_i}}{n} \qquad Eq.\ 7$$

where *i* refers to the individual tree and n is the total number of trees. We calculated the comparison for each stand with three different size classes of trees: trees ≥9.5cm DBH, trees >20 cm DBH, and trees >60 cm DBH. All data processing and analyses were conducted in R ver. 3.2.4 (R Development Core Team 2014); spatial metrics relied on functions in the spatstat package (Baddeley et al. 2015).

Results

Tree spatial distribution in each stand

Despite differences in geography, density, and composition, the overall spatial pattern was consistent among all six stands. Trees were significantly clumped at spatial scales relevant to the PDE calculation and showed inhibition at larger scales due to the presence of gaps throughout the stand (Appendix S1: Figure S1). The inhomogeneous Ripley's *L* values exceeded the 95% CI for randomly spaced trees from 0-1 m at the minimum and 13-29 m at the maximum – an indication of an aggregated distribution (Appendix S1: Figure S1).

Bias and precision assessment

Considering only the GLO appropriate PDEs for a 50-point sampling intensity, the least biased estimate of tree density in every stand was obtained with the Morisita and the most biased was obtained with the MHVD (Table 3). The direction of the bias in the Morisita varied with some underestimates and some overestimates. In contrast, the Cottam and Pollard consistently underestimated true density and the MHVD always overestimated true density. In general, the 4nn sampling had less bias than the 2nn sampling. This difference was particularly pronounced in the MHVD. For the 2nn MHVD, the median REs ranged from 2.04 to 3.58 whereas for the 4nn MHVD, it ranged from 1.16 to 1.59 (Table 3). The performance of the Delincé PDE was exceptional (Table 3). The biases were small and non-directional with median REs ranging from 0.92 to 1.14. The performance in regard to the bias of individual estimators documented for the 50-point sampling intensity was consistent at other sampling intensities (Appendix S1: Tables S1-S9).

The precision of the tree density estimates systematically increased with sampling intensity for all PDEs. Not only did the width of confidence interval shrink with increasing point density (Figure 2, Appendix S1: Figure S2 for the Delincé) but the rRMSE also declined systematically with increasing point density in every case (Appendix S1: Tables S1-S9). Moreover, the 4nn sampling scheme consistently produced more precise estimates (i.e., lower rRMSE) than the 2nn.

Among the PDEs, the MHVD was the least precise for a given sampling scheme and intensity (Figure 2, Table 3). The Morisita tended to produce less precise density estimates at sample intensities <50. The improvement in precision with increasing sample intensity was steepest for the MHVD and Delincé. For both PDEs, the rRMSE was an order of magnitude lower for the 1,000-point sample compared to the 3-point sample (Appendix S1: Tables S1-S9). In the 50-point sampling simulations, the Delincé obtained not only the least biased estimates of density but also the most precise (Table 3). The Morisita 4nn estimator was the next best in terms of minimizing bias and maximizing precision.

MHVD deconstruction

Tree diameter proved to be a robust predictor of crown radius. Based on the coefficient of determination (r^2), the fits of ln(CR) to ln(DBH) for conifer trees in the FHM data ranged from 0.43 for *Pseudotsuga menziesii* (PSME, n=196) to 0.83 for *Pinus monticola* (PIMO, n=59). The r^2 values for the hardwoods were lower, ranging from 0.22 for *Populus tremuloides* (POTR, n=65) to 0.44 for *Quercus kelloggii* (QUKE, n=254). All fits showed a significantly increasing relationship of ln(CR) to ln(DBH) ($p<0.05$; Appendix S1: Figure S3). The slope and intercepts of the relationship of ln(CR) to ln(DBH) were generally similar to those listed in Baker (2014) for the same species.

The 4nn sampling scheme resulted in a significantly higher mean distance to nearest trees compared to the 2nn sampling (Figure 3A, C). This difference translated into a lower MND. When we applied the MND to the estimation of the MVA of a representative tree, the 4nn MND correction resulted in significantly higher estimations of MVA for the same tree relative to the 2nn MND (Figure 3B, D). The results were replicated at every site — the 2nn sampling resulted in a higher MVA estimate (Appendix S1: Figure S4).

For the mapped trees in the six stands we tested, CR was a very weak predictor of VA (Figure 4). Although the slope of the regression line was positive and often significant (i.e., $p < 0.05$), the fits were very poor. The coefficient of determination (r^2) ranged from a minimum of 0.003 for *Abies concolor* (ABCO) at the GRAN site (n=73) to a maximum 0.29 for *Pinus jeffreyi* (PIJE) at the META site (n=773; Appendix S1: Table S10).

The MVA calculated with the parameters provided in Baker (2014) consistently underestimated the true VA of the trees at all sites (Figure 5 and Appendix S1: Figure S5). The difference increased with increasing tree size (Table 4). For example, the median $VA_{difference}$ for all mapped trees (DBH ≥ 9.5 cm) in the six stands was -21.2 m^2; for large trees (DBH > 60 cm) the median difference was -36.7 m^2. The underestimate of MVA relative to the true VA increased as tree density decreased (Table 4).

Calculating MVA using DSH as opposed to DBH reduced the bias of the MHVD 4nn estimator. However, both the MHVD 2nn and 4nn estimators overestimated stand density in all cases. Additionally, MVA consistently underestimated true VA, regardless of whether MVA was calculated with DSH or DBH. Results for relevant analyses using DSH in place of DBH are presented in Appendix S2.

DISCUSSION

The mean harmonic Voronoi area (MHVD) as specified in Baker (2014) consistently provided the least accurate estimate of tree density among the plotless density estimators (PDE) tested. In every scenario, the MHVD was biased toward overestimating tree density with lower precision than alternative metrics. Two factors contributed to this bias: 1) the difference in mean neighborhood distance (MND) between 2nn and 4nn sampling; and 2) the persistent underestimate of the true Voronoi area (VA).

Williams and Baker (2011) recognized that local tree density influences the allometric relationship between tree diameter and crown radius, specifically that for a given species and DBH, the crown width decreases with increasing tree density (Bragg 2001). They evaluated three different crown scaling factors and found that the MND was ultimately the best. Baker (2014) subsequently applied this MND to scale CR in the Sierra Nevada based on the recommendation of Williams and Baker (2011) and supported by local validation (Appendix D in Baker 2014). The well-known influence of the number of sectors in the CR scaling factor (e.g., Cottam and Curtis 1956) was clearly a concern — one of the alternative neighborhood density equations Williams and Baker (2011) tested explicitly included a correction for mean distances obtained with 2nn vs 4nn sampling (the correction factor neighborhood density, CFND, Table 2 in Williams and Baker 2011). However, the PDE that included the CFND (the correction factor geometric Voronoi estimator, CFGVD) was generally not as accurate as the MHVD in their evaluation (Table 3 in Williams and Baker 2011). In contrast, in our simulations the lack of a correction factor for the number of bearing trees included in the calculation of MHVD almost doubled (1.85x), on average, the estimate of tree density in the 2nn sampling compared to the 4nn (Table A7, A8). Why this flaw was not noted earlier may be due to two facts. Baker (2014) developed local MVA regressions as functions of CR and MND (Baker 2014, Appendix D) but only used points with four bearing trees. In addition, the performance of the MHVD in the Sierra

Nevada was not compared to plot estimates of tree density as done in previous applications (e.g., Williams and Baker 2012, Baker 2012).

Independent of the MND, the MVA equations in Baker (2014) systematically underestimated true VA (Figure 5, Table 4). In particular, the MVA (calculated using a MND based on 4nn) reached a maximum area much lower than the true VA. For example, at YOSE, the median true VA was 18 m^2 while the median MVA was only 8 m^2, and 18% of the mapped trees had a true VA that exceeded the maximum MVA (Figure 4). Similar results were obtained at the five other stands and the effect appeared to increase as density decreased (Appendix S1: Figure S5). One explanation for the mismatch could be that samples included in Baker's (2014) MVA regressions did not capture the full range of variation.

We found a weak predictive ability of CR in our stands, with the r^2 of true VA~CR/MND for conifers ranging from 0.003-0.29 (Table A10). In contrast, Baker (2014) found strong relationships between MVA and CR with r^2 values ranging from 0.52-0.95 for these same conifer species. The weak predictive ability of CR in these mixed-conifer forests may be due to the fact that tree spacing can sometimes be more dependent on edaphic factors (Meyer et al. 2007) or disturbance legacies than on competitive interactions. On drier microsites or nutrient-poor soils or in old canopy gaps, some trees grow in relative isolation due to factors unrelated to competition or tree size. These circumstances occur across the semi-arid Western US forests in general (Larson and Churchill 2012) and specifically in the stands included in our analysis (e.g., Figure 1, North et al. 2002, Fry et al. 2014). Only at our most dense site (PLUM, Table 2) where canopy approaches closure (canopy cover = 90%, Kayler et al. 2005) from the effects of 100 years of fire suppression might spacing be influenced by crown area. Interestingly the least bias in the MHVD density estimate was observed at PLUM (RE = 1.16 for MHVD, 4nn, 50 points, Table 3). Thus, it seems likely that the MHVD approach will overestimate tree density in the Sierra Nevada and in other forests of the arid Western US with similar stand structure.

Our critique of the MHVD does not extend to its underlying theory. Using the Voronoi area to measure the inclusion probability of the nearest tree in a PDE (Delincé 1986) proved to be the best predictor of tree density in all simulations (Table 3, Table S9). However, at the lower sampling intensities (i.e., < 50 sampling points), the precision of the Delincé PDE was low resulting in large confidence intervals. This imprecision is not surprising given that the Delincé PDE only considers the nearest tree to each point (1nn) in its calculation (Table 1). The Delincé PDE also had a tendency to underestimate the true tree density at the lower sampling intervals (Appendix S1: Figure S2). Klein and Vilčko (2006) extend the VA-based PDE to include more than the nearest tree to each point in an effort to improve precision. Advances in tree mapping technology (e.g., laser hypsometers) make measuring the VA of trees in the field more efficient. Thus the VA-based PDEs are viable plotless methods for forest inventory. However, for GLO applications, the challenge of predicting VA with the available data severely limits its utility.

Our assessment of the MHVD as a theoretically sound but technically flawed means to reconstruct historical forest density from GLO data was constrained by the availability of data and the specificity of our question. The spatial scale of our analysis was on the order of hectares whereas the GLO data span km^2. As often noted (e.g., Engeman et al. 1994, Kronenfeld and Wang 2007, Bouldin 2008, Hanberry et al. 2011), the non-random dispersion of trees at the local level and differences in tree density at the regional level affects PDE performance. Thus the stand-level tests presented here probably do not capture the full range of variation in forest structure present in the landscape sampled by GLO survey points, although we attempted to account for this by testing six stands of widely varying densities across >8° of latitude. We also restricted our focus to PDE performance under ideal conditions without complications from sampling inconsistencies or surveyor biases (sensu Bourdo 1956). Ongoing research in the Sierra Nevada and Sierra de San Pedro Mártir (unpublished data, C. Restaino and H. Safford) seeks to address these constraints by testing PDEs at the landscape scale while also quantifying the influence of survey data quality.

The Morisita was consistently the least biased estimator of tree density from GLO data across a gradient of forest conditions (Tables A1-A8). This result supports previous research that found the Morisita to be the best choice when bearing trees have an aggregated distribution. The Cottam (Bouldin 2008) and Pollard (Hanberry et al. 2011) tended to underestimate true density in these situations while the Morisita provided more accurate estimates. Note that we relied on the median as the measure of central tendency instead of the more commonly reported mean (e.g., Engemen et al. 1994, Hanberry et al. 2011). Given the right skew in the distribution of the simulations due to the fact that the minimum density was constrained at 0 while the maximum was unconstrained (i.e., zero-truncation), the median was less than or equal to the mean. Thus our conclusions regarding overestimates are based on a more conservative measure of central tendency. However, we also report the mean density from the simulations to allow comparison with previous efforts (Appendix S1: Tables S1-S9).

In our simulations, both the Morisita 4nn and Morisita 2nn predictors were unbiased in estimating density at a range of sampling intensities. Although the Morisita 4nn was less biased and more precise than the 2nn (e.g., Table 3), the Morisita 2nn has the advantage of a larger potential sample intensity because both section and quarter corners can be included in the density estimate. Moreover, the Morisita 4nn appears to be sensitive to local non-random dispersion (C. Cogbill, personal observation). The well-vetted performance of the Morisita 2nn suggests it should be considered the current standard for GLO applications.

Pre-settlement forest conditions derived from the GLO records for the Sierra Nevada (Baker 2014) differ substantially from results based on inventories conducted before EuroAmerican influence and on reconstructions from live and dead plant material (Taylor 2004, North et al. 2007, Scholl and Taylor 2010, Collins et al. 2011, Barth et al. 2015, Collins et al. 2015, Stephens et al. 2015, Safford and Stevens, in press). Specifically, Baker (2014) rejected the prevailing hypothesis that the pre-settlement Sierra Nevada mixed-conifer forests were mostly open, park-like landscapes with low tree densities maintained by low to moderate severity fires. For example, in the vicinity of Yosemite National Park in the central Sierra Nevada, Collins et al. (2011) reported an average tree density of 52 trees ha^{-1} for trees ≥15.2 cm DBH in a 1911 timber inventory. Working in the same area, Scholl and Taylor's (2010) reconstruction of the 1899 forest put tree density at 86 trees ha^{-1} for trees ≥10 cm DBH. In the Yosemite Forest Dynamics Plot, a more mesic forest than Scholl and Taylor (2010), Barth et al. (2015) reconstructed forest density in 1900 to be between 62 – 122 trees ha^{-1} for trees ≥10 cm DBH. In contrast, the GLO estimate for the area including all of these direct density estimates (Table G1 in Baker 2014) was 212 trees ha^{-1}. The much greater tree densities obtained from the MHVD analysis of GLO data (Baker 2012, Baker 2014) have been noted for forests in Oregon (Hagmann et al. 2013, Hagmann et al. 2014) and California (Stephens et al. 2015, Collins et al. 2015). Notably the magnitude of the differences — namely GLO densities 2 to 5 times larger than ones based on inventories or reconstructions — match the methodological bias detected in our analysis.

The management implications of these contrasting perspectives of the pre-settlement forest are significant. Baker (2014) used GLO-derived tree densities to infer that extensive stand-replacing fire was a major component in the natural disturbance regime of the Sierra Nevada mixed-conifer forests. This conclusion implies that ongoing efforts by forest managers to mitigate wildfire behavior (e.g., North et al. 2009, USFS 2011, USFS 2013) are misguided. Subsequent papers have attempted to add support for this alternate interpretation about historical forest and fire interactions (Odion et al. 2014, Baker 2015), which collectively promote management practices that foster denser forests susceptible to high-severity fire. Although these authors posit other lines of evidence supporting this alternative perspective, the much higher estimates of tree density are the quantitative linchpin of the thesis (Baker 2014). The propensity of the MHVD to significantly overestimate tree density challenges the validity of the argument.

In this era of global change, historical conditions play an increasingly important role as we seek to inform the future by understanding the past (Safford et al. 2012). As forest conditions and disturbance impacts deviate from the range of natural variation (Safford and Stevens, in press), effective intervention depends on our knowledge of forest dynamics and our ability to explain the processes involved (Stephens et al. 2010). The GLO survey represents a spatially extensive window into the pre-settlement forest of the American West that complements the detailed site-specific information obtained from historical inventories and forest reconstructions. Given the paucity of data, there is a premium on methods that extract as much insight as possible. Innovation must be encouraged. At the same time, new methods must be independently validated, especially when they directly impact management and policy. It is in this spirit of sound scientific practice that we present our findings.

TABLES

Table 1. Equations used to estimate tree density (trees ha^{-1}) in this study. Term definitions: m = number of sectors; n = number of points, r_{ij} = is the distance from point j to tree i; K is the scaling coefficient to return density in trees ha^{-1}; λ is tree density; VA is the measured Voronoi area; and *MVA* is the mean Voronoi area (estimated). In this paper, r_{ij} is measured in meters, thus K = 10,000. Also note in all cases only the nearest tree in each sector is measured. Thus the total number of trees is $m*n$ (mn).

Name	Equation	Ref
Cottam (C)	$\lambda_C = K * \frac{m}{4} * \frac{1}{\left(\sum_{j=1}^{n}\sum_{i=1}^{m}\frac{r_{ij}}{nm}\right)^2}$	1
Pollard (P)	$\lambda_P = K * \frac{(mn-1)m}{\pi} * \frac{1}{\sum_{j=1}^{n}\sum_{i=1}^{m}{r_{ij}}^2}$	2
Morisita (M)	$\lambda_M = K * \frac{(m-1)m}{\pi n} * \sum_{j=1}^{n}\frac{1}{\sum_{i=1}^{m}{r_{ij}}^2}$	3
Delincé (D)	$\lambda_D = K * \frac{1}{mn/\sum_{i=1}^{mn}\left(\frac{1}{VA(tree_i)}\right)}$	4
Mean Harmonic Voronoi Density (MHVD)	$\lambda_{MHVD} = K * \frac{1}{mn/\sum_{i=1}^{mn}\left(\frac{1}{MVA(tree_i)}\right)}$	5

References: 1 from Cottam and Curtis (1956); 2 from equation #16 in Pollard (1971); 3 from equation #31 in Morisita (1957); 4 from equation #7 in Delincé (1986); 5 from Table 2 in Williams and Baker (2011).

Table 2. Site description for the six stands included in this study. Density and basal area are for trees ≥9.5 cm DBH.

Site	Latitude	Longitude	Elevation (m)	Density (trees ha^{-1})	Basal area (m^2 ha^{-1})	% Fir	% Pine	Ref
PLUM	W 121º 02'	N 39º 55'	1158-1219	784	87	87%	3%	1
YOSE	W 119º 49’	N 37º 46’	1774-1911	562	56	79%	13%	2
TEAK	W 119º 02’	N 36 º 58’	1880-2485	313	56	64%	27%	3
META	W 115° 59’	N 31 º 37’	2400-2500	254	23	0%	100%	4
BRID	W 119º 28’	N 38 º 24’	2500-2600	236	36	38%	50%	4
GRAN	W 115° 59’	N 31 º 37’	2400-2500	159	25	13%	87%	4

Site code: PLUM refers to Plumas National Forest; YOSE refers to Yosemite National Park; TEAK refers to Teakettle Experimental Forest; META refers the site in the Sierra de San Pedro Mártir with soil derived from metamorphic parent material; BRID refers to the site in the Humboldt-Toiyabe National Forest near Bridgeport, CA; GRAN refers to the site in the Sierra de San Pedro Mártir with soil derived from granitic parent material. % Fir and % Pine refer to the percentage of the number of trees in either category in each 4 ha stand. References: 1 from Levine et al. (2016), 2 from Lutz et al. (2012), 3 from North et al. (2007), 4 from Fry et al. (2014).

Table 3. Relative performance of the density estimates for the 50-point simulations. Results are reported as relative values with the results from the 1,000 realizations divided by the true density. rRMSE refers to the relative root mean square error. Bold text indicates site estimates where the 95% CI of the simulation overlaps the true density.

	Site	PLUM	YOSE	TEAK	META	BRID	GRAN
Measure (nn trees)	True density (trees ha^{-1})	784	562	313	254	236	159
Cottam (4 trees)	2.5% CI	**0.79**	0.66	0.49	0.52	0.63	0.68
	Median	**0.93**	0.79	0.62	0.66	0.75	0.80
	97.5% CI	**1.09**	0.96	0.82	0.85	0.91	0.97
	rRMSE	**0.10**	0.22	0.38	0.36	0.26	0.22
Cottam (2 trees)	2.5% CI	**0.74**	**0.62**	0.47	0.49	0.57	**0.66**
	Median	**0.92**	**0.80**	0.63	0.66	0.73	**0.83**
	97.5% CI	**1.16**	**1.05**	0.87	0.89	0.94	**1.08**
	rRMSE	**0.13**	**0.22**	0.37	0.36	0.29	**0.20**
Pollard (4 trees)	2.5% CI	**0.79**	0.64	0.43	0.46	0.62	0.66
	Median	**0.92**	0.75	0.54	0.58	0.73	0.77
	97.5% CI	**1.07**	0.90	0.69	0.74	0.87	0.92
	rRMSE	**0.11**	0.26	0.46	0.43	0.29	0.25
Pollard (2 trees)	2.5% CI	**0.72**	0.59	0.41	0.43	0.55	**0.64**
	Median	**0.90**	0.76	0.54	0.58	0.68	**0.80**
	97.5% CI	**1.11**	0.98	0.73	0.79	0.88	**1.04**
	rRMSE	**0.15**	0.25	0.46	0.44	0.33	**0.22**
Morisita (4 trees)	2.5% CI	**0.80**	**0.72**	**0.71**	**0.67**	**0.69**	**0.69**
	Median	**0.96**	**0.94**	**1.15**	**1.06**	**0.89**	**0.87**
	97.5% CI	**1.21**	**1.24**	**2.08**	**1.76**	**1.23**	**1.29**
	rRMSE	**0.11**	**0.14**	**0.40**	**0.30**	**0.17**	**0.20**
Morisita (2 trees)	2.5% CI	**0.66**	**0.61**	**0.65**	**0.67**	**0.57**	**0.62**
	Median	**0.92**	**0.90**	**1.24**	**1.19**	**0.85**	**0.94**
	97.5% CI	**1.57**	**1.62**	**2.85**	**2.78**	**1.70**	**1.98**
	rRMSE	**0.25**	**0.31**	**0.78**	**0.67**	**0.38**	**0.37**
MHVD (4 trees)	2.5% CI	1.02	1.16	1.15	**0.94**	1.09	**0.99**
	Median	1.16	1.40	1.59	**1.30**	1.34	**1.21**
	97.5% CI	1.32	1.72	2.31	**1.80**	1.69	**1.50**
	rRMSE	0.18	0.16	0.14	**0.38**	0.37	**0.25**
MHVD (2 trees)	2.5% CI	1.72	2.17	2.30	2.08	2.13	2.03
	Median	2.04	2.89	3.58	3.09	2.83	2.68
	97.5% CI	2.47	4.17	6.13	4.70	3.84	3.72
	rRMSE	1.06	1.07	1.02	2.25	1.89	1.75
Delincé (1 tree)	2.5% CI	**0.83**	**0.79**	**0.77**	**0.72**	**0.71**	**0.73**
	Median	**0.99**	**0.99**	**1.14**	**1.02**	**0.92**	**0.96**
	97.5% CI	**1.21**	**1.27**	**1.85**	**1.59**	**1.21**	**1.41**
	rRMSE	**0.10**	**0.12**	**0.34**	**0.24**	**0.14**	**0.18**

Table 4. The mean difference between the true VA and MVA (m^2; Equation 7) for all trees ≥9.5 cm DBH, trees >20 cm DBH, and trees > 60 cm DBH at each site. Negative values indicate the extent to which the MVA underestimated the true VA. Sites are listed in order of decreasing stand density with PLUM being the most dense and GRAN the least dense.

Site	Trees ≥ 9.5 cm DBH	Trees >20 cm DBH	Trees > 60 cm DBH
PLUM	-6.82	-6.02	-6.87
YOSE	-10.1	-9.61	-14.4
TEAK	-15.6	-16.4	-28.3
META	-26.7	-39.2	-83.7
BRID	-33.8	-33.7	-45.1
GRAN	-43.6	-45.7	-71.2

FIGURES

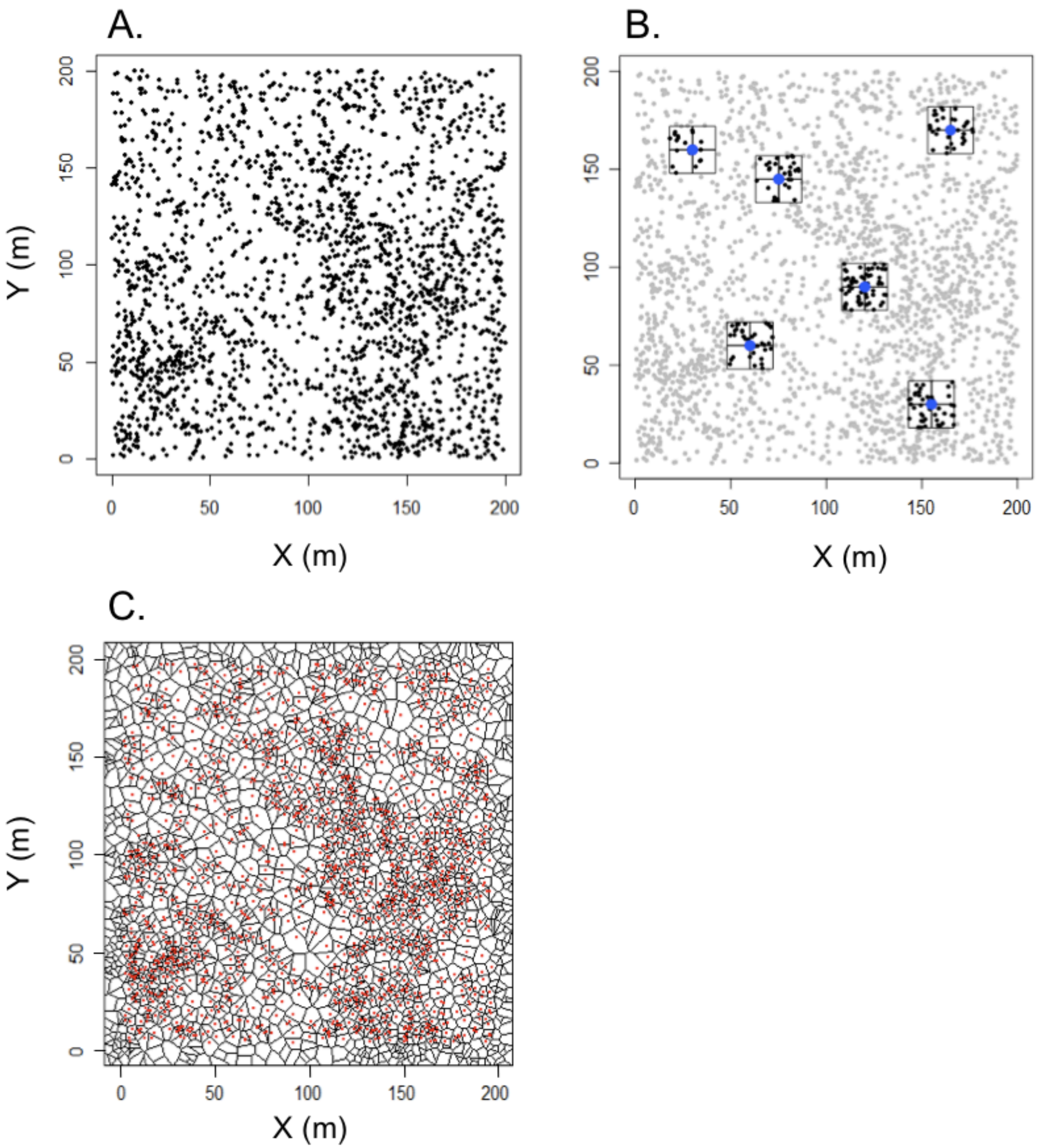


Figure 1. An example (YOSE) of the mapped tree plots used in the analysis. (A) The spatial distribution of trees in the mapped plot; (B) section corner sampling points (blue) and neighboring trees for a six-point sampling scheme; (C) and true Voronoi areas.

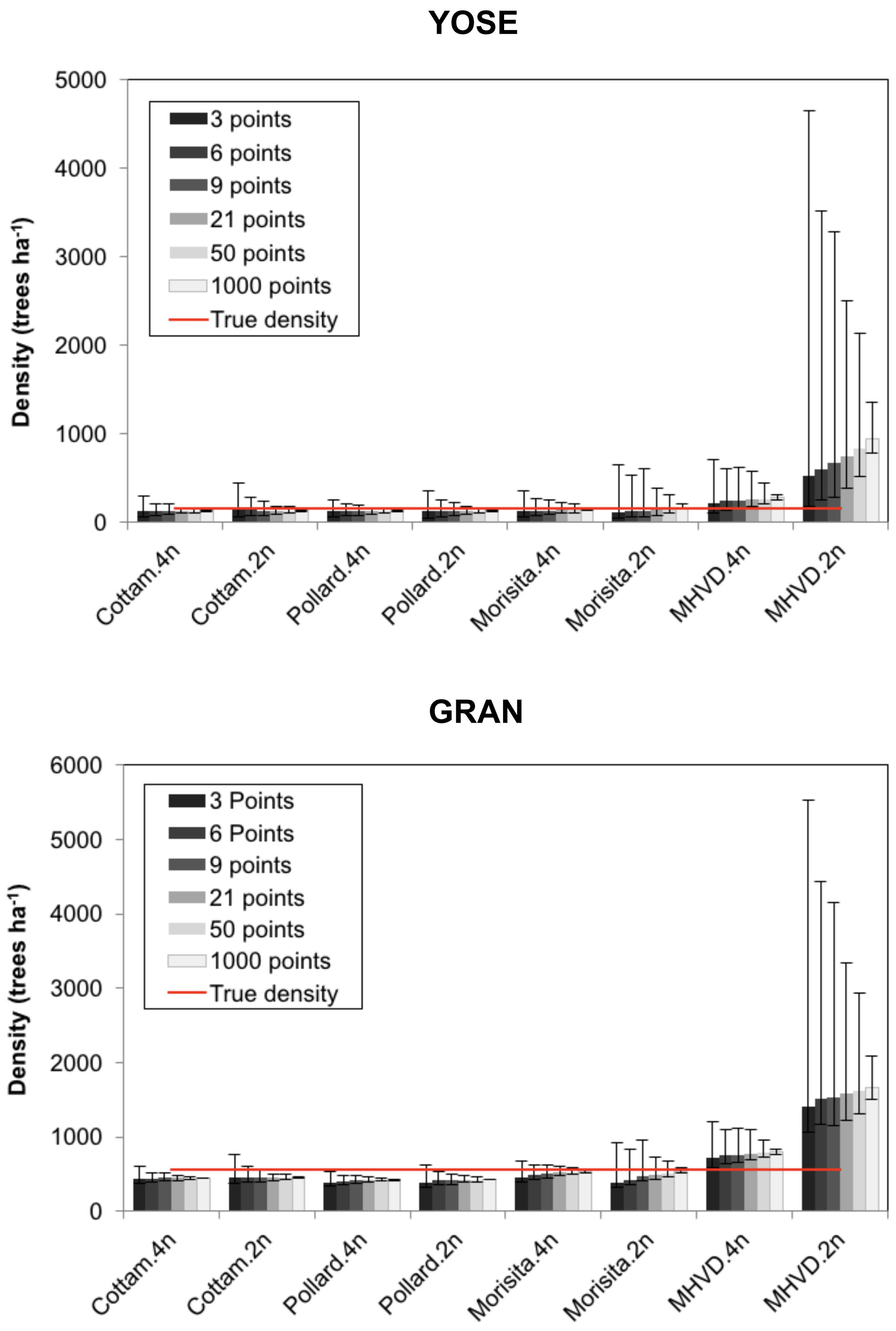
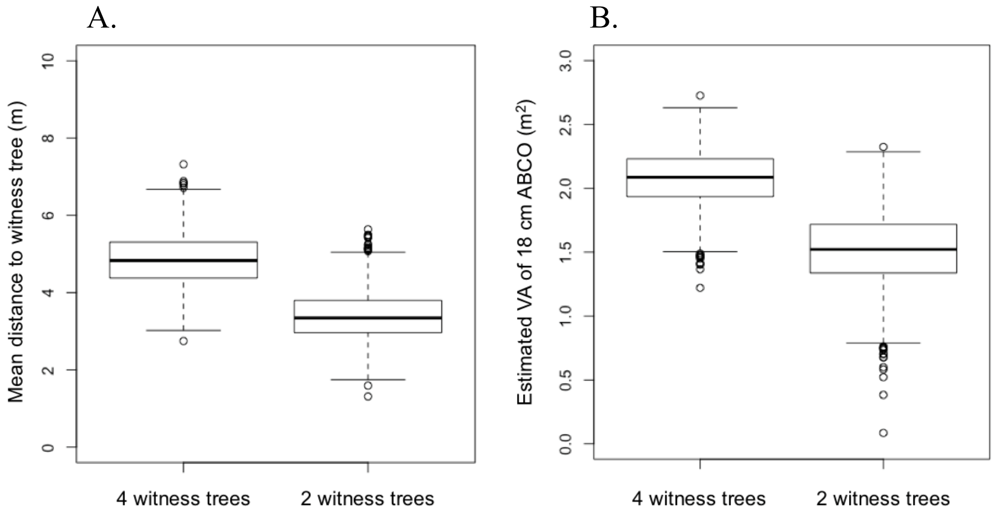


Figure 2. Results of simulations testing the effect of sampling intensity (number of sampled points) on the Cottam, Pollard, Morisita, and MHVD estimators at the YOSE and GRAN sites. Bars show the median value of 1,000 realizations and error bars show the 95% confidence intervals. Simulation summaries can be found in tables A1-A9.

YOSE



GRAN

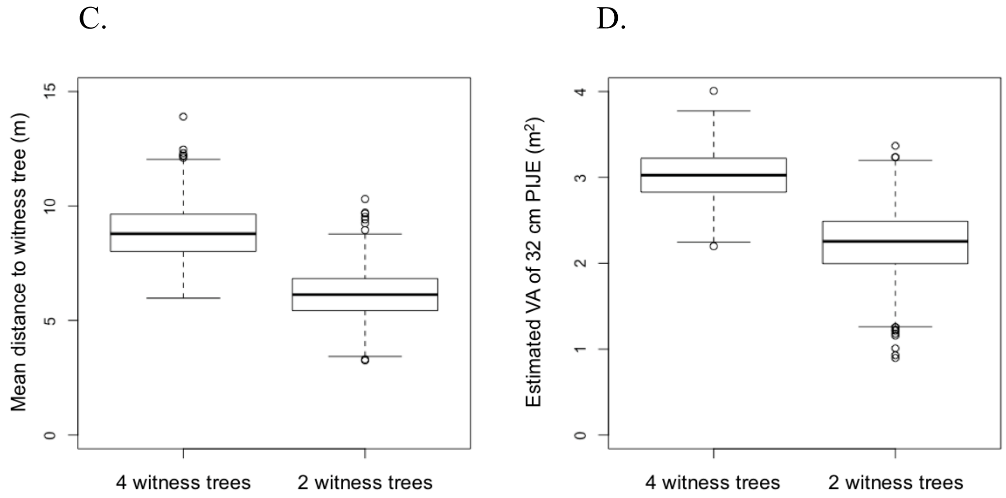


Figure 3. Simulation results (1000 runs) of the mean neighborhood distance (A, C) when two nearest neighbors (2nn) or 4 nearest neighbors (4nn) are used for a 6-point sampling scheme for the YOSE and GRAN sites, respectively. The discrepancy in mean neighborhood distance is reflected in the estimate of the Voronoi area of a single tree of the dominant species (B, D) of the median DBH in that plot using the method and equation parameters in Baker (2014). Results for other sites are shown in Figure A4. ABCO refers to *Abies concolor* (white fir); PIJE refers to *Pinus jeffreyi* (Jeffrey pine).

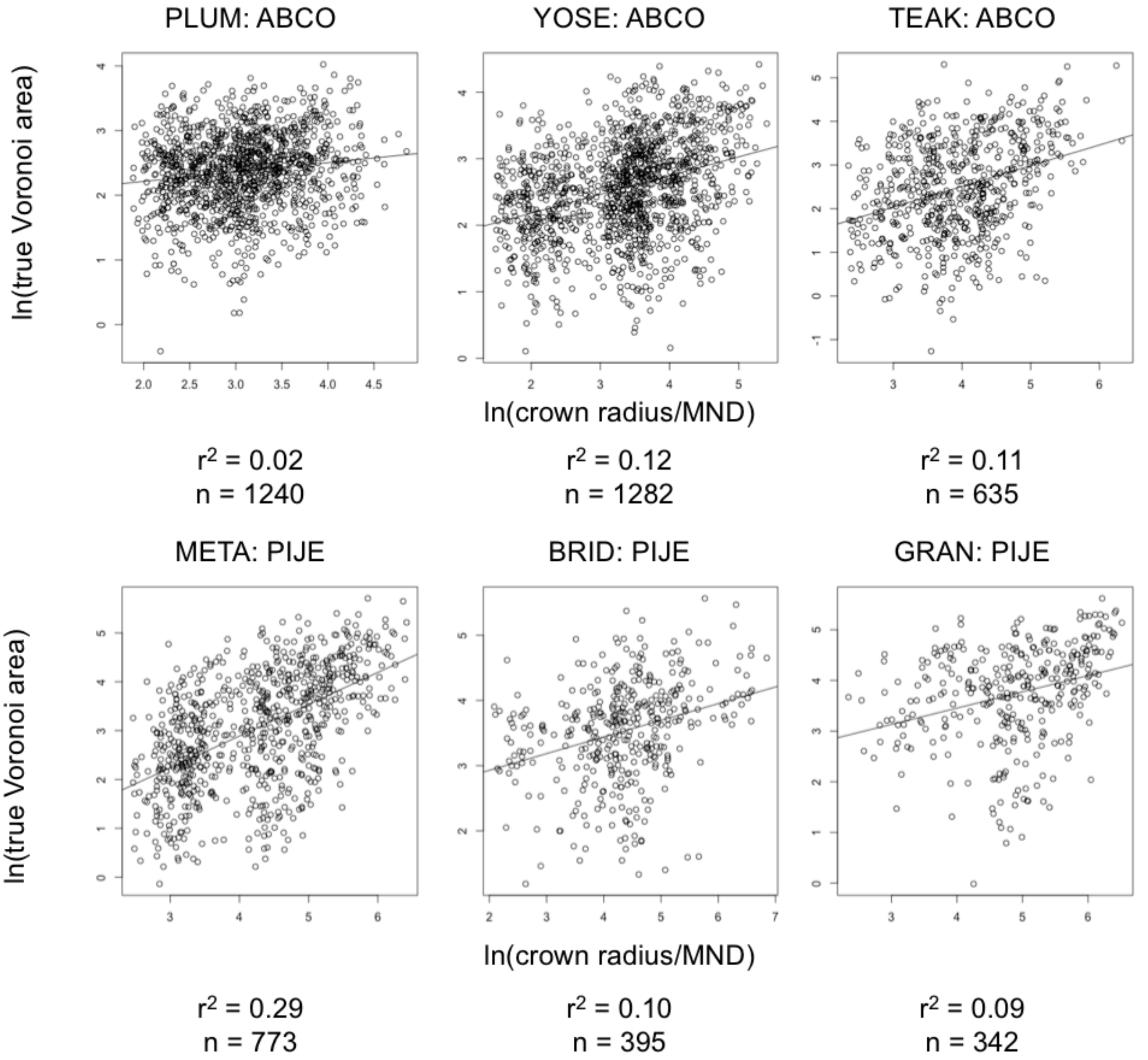


Figure 4. The relationship of true Voronoi area (VA) to crown radius (CR) for the dominant tree species at each of the six study sites. The crown radius was estimated using parameters for species-specific fits derived from Forest Health Monitoring measurements in Sierra Nevada mixed-conifer plots (PIJE, n=164; ABCO, n=746). MND is the mean neighborhood distance (see Equation 3). ABCO refers to *Abies concolor* (white fir); PIJE refers to *Pinus jeffreyi* (Jeffrey pine).

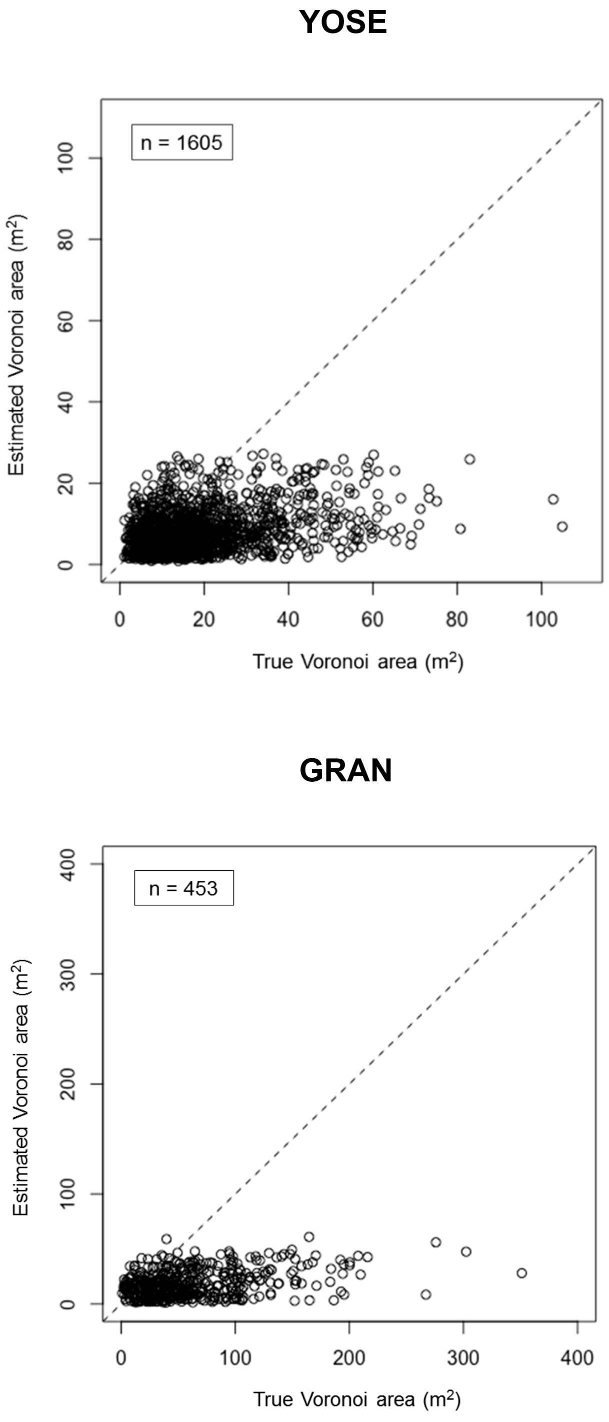


Figure 5. The relationship between the true VA and the estimated VA (i.e., MVA) in the YOSE and GRAN sites. Estimated VA was calculated using the species-specific equation parameters provided in Baker (2014) and a MND estimated from a grid of 21 sampling points with four bearing trees at each point. Results for the other stands are shown in Figure A5.

APPENDIX S1

Supplementary tables and figures

Table S1. Summary statistics of simulations for the Cottam 4nn estimator.

			Cottam (4 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	417	743	800	1478	276	0.95	0.35
		6	468	733	753	1189	184	0.93	0.23
		9	494	734	754	1087	157	0.94	0.20
		21	572	733	740	954	108	0.93	0.14
		50	623	731	735	856	81	0.93	0.10
		1000	706	731	731	756	62	0.93	0.08
YOSE	562	3	222	436	498	1116	243	0.78	0.43
		6	269	440	463	794	168	0.78	0.30
		9	290	446	462	711	149	0.79	0.27
		21	341	445	450	597	130	0.79	0.23
		50	371	444	446	541	123	0.79	0.22
		1000	425	442	443	463	120	0.79	0.21
TEAK	313	3	82	196	245	676	187	0.63	0.60
		6	96	195	217	459	137	0.62	0.44
		9	115	199	212	373	121	0.64	0.39
		21	133	197	203	301	119	0.63	0.38
		50	153	196	197	257	119	0.62	0.38
		1000	185	195	195	207	118	0.62	0.38
META	254	3	72	176	203	490	132	0.69	0.52
		6	83	166	179	344	104	0.65	0.41
		9	100	173	181	310	95	0.68	0.38
		21	117	170	173	248	91	0.67	0.36
		50	133	168	169	215	91	0.66	0.36
		1000	158	167	167	177	91	0.66	0.36
BRID	236	3	88	175	196	418	98	0.73	0.41
		6	108	178	189	329	75	0.75	0.31
		9	117	179	184	286	69	0.75	0.29
		21	135	176	179	239	65	0.74	0.27
		50	149	178	179	215	62	0.74	0.26
		1000	171	177	178	185	62	0.74	0.26
GRAN	159	3	67	133	144	299	61	0.84	0.38
		6	78	130	135	212	45	0.82	0.28
		9	87	130	133	201	40	0.82	0.25
		21	98	128	130	172	36	0.81	0.23

50	108	128	129	154	34	0.80	0.22
1000	124	128	129	134	33	0.81	0.20

Table S2. Summary statistics of simulations for the Cottam 2nn estimator.

			Cottam (2 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	329	738	868	2166	497	0.94	0.63
		6	418	734	778	1461	267	0.94	0.34
		9	455	719	757	1268	214	0.92	0.27
		21	511	721	735	1032	141	0.92	0.18
		50	579	723	727	907	105	0.92	0.13
		1000	687	721	721	755	72	0.92	0.09
YOSE	562	3	189	461	559	1570	349	0.82	0.62
		6	237	456	500	1038	216	0.81	0.38
		9	266	451	478	842	169	0.80	0.30
		21	320	453	465	683	135	0.81	0.24
		50	347	450	455	590	122	0.80	0.22
		1000	423	450	450	474	113	0.80	0.20
TEAK	313	3	70	217	297	876	391	0.69	1.25
		6	92	197	233	613	157	0.63	0.50
		9	101	199	220	476	132	0.64	0.42
		21	129	196	206	336	120	0.63	0.38
		50	148	198	200	273	117	0.63	0.37
		1000	183	197	197	211	116	0.63	0.37
META	254	3	53	181	240	828	248	0.71	0.97
		6	75	175	196	439	114	0.69	0.45
		9	86	170	185	363	101	0.67	0.40
		21	106	169	176	288	94	0.67	0.37
		50	125	167	170	226	92	0.66	0.36
		1000	156	167	167	180	91	0.66	0.36
BRID	236	3	77	182	217	624	143	0.76	0.60
		6	92	176	191	380	89	0.74	0.37
		9	107	177	187	338	78	0.74	0.33
		21	123	173	177	256	71	0.72	0.30
		50	135	172	173	222	69	0.72	0.29
		1000	163	173	173	183	66	0.72	0.28
GRAN	159	3	60	141	167	440	104	0.89	0.65
		6	69	136	146	285	58	0.85	0.36
		9	78	133	139	239	47	0.84	0.30
		21	94	134	137	199	35	0.84	0.22
		50	105	132	133	172	32	0.83	0.20
		1000	125	133	133	140	29	0.83	0.18

Table S3. Summary statistics of simulations for the Pollard 4nn estimator.

			Pollard (4 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	397	692	736	1333	249	0.88	0.32
		6	458	703	721	1083	181	0.90	0.23
		9	497	715	729	1052	153	0.91	0.19
		21	566	717	725	933	112	0.91	0.14
		50	619	721	723	843	88	0.92	0.11
		1000	698	721	721	747	71	0.92	0.09
YOSE	562	3	212	391	449	969	238	0.70	0.42
		6	257	407	428	723	179	0.72	0.32
		9	283	416	430	655	163	0.74	0.29
		21	327	419	425	551	149	0.75	0.27
		50	359	420	423	507	144	0.75	0.26
		1000	406	421	421	439	141	0.75	0.25
TEAK	313	3	72	162	204	572	178	0.52	0.57
		6	88	165	184	382	153	0.53	0.49
		9	107	172	181	315	143	0.55	0.46
		21	119	171	174	253	143	0.55	0.46
		50	135	168	170	217	145	0.54	0.46
		1000	160	169	169	178	144	0.54	0.46
META	254	3	63	152	172	391	131	0.60	0.52
		6	75	144	155	299	118	0.57	0.46
		9	88	150	158	269	111	0.59	0.44
		21	105	147	152	218	110	0.58	0.43
		50	117	147	149	188	110	0.58	0.43
		1000	140	147	148	156	110	0.58	0.43
BRID	236	3	87	162	178	380	97	0.68	0.41
		6	107	169	177	301	79	0.71	0.33
		9	114	170	175	268	75	0.71	0.31
		21	132	170	172	227	71	0.71	0.30
		50	146	171	172	204	68	0.72	0.29
		1000	166	172	172	179	67	0.72	0.28
GRAN	159	3	62	121	130	258	59	0.76	0.37
		6	76	121	126	202	49	0.76	0.31
		9	81	122	126	186	45	0.77	0.28
		21	93	123	124	165	41	0.77	0.26
		50	104	123	123	147	39	0.77	0.25
		1000	119	124	124	129	37	0.78	0.24

Table S4. Summary statistics of simulations for the Pollard 2nn estimator.

			Pollard (2 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	288	637	740	1789	405	0.81	0.52
		6	396	667	713	1290	254	0.85	0.32
		9	443	681	713	1189	207	0.87	0.26
		21	504	694	707	972	146	0.88	0.19
		50	568	703	708	872	114	0.90	0.15
		1000	677	708	709	741	84	0.90	0.11
YOSE	562	3	158	390	472	1342	312	0.69	0.56
		6	211	411	450	910	215	0.73	0.38
		9	242	411	437	748	184	0.73	0.33
		21	303	426	436	624	152	0.76	0.27
		50	332	426	431	549	142	0.76	0.25
		1000	404	429	429	451	134	0.76	0.24
TEAK	313	3	253	170	239	737	341	0.54	1.09
		6	205	161	194	535	165	0.51	0.53
		9	142	167	184	381	150	0.53	0.48
		21	110	167	176	285	144	0.53	0.46
		50	78	170	172	229	143	0.54	0.46
		1000	312	170	170	181	143	0.54	0.46
META	254	3	45	146	192	664	214	0.57	0.84
		6	64	149	165	359	122	0.59	0.48
		9	74	147	159	314	116	0.58	0.46
		21	94	146	154	248	112	0.58	0.44
		50	109	147	149	200	112	0.58	0.44
		1000	137	147	147	158	111	0.58	0.44
BRID	236	3	67	150	182	499	133	0.63	0.55
		6	86	158	171	331	94	0.66	0.39
		9	98	162	170	306	86	0.68	0.36
		21	118	162	165	236	80	0.68	0.33
		50	130	162	164	207	78	0.68	0.33
		1000	156	164	164	174	75	0.69	0.31
GRAN	159	3	52	120	142	354	88	0.75	0.55
		6	65	125	133	249	56	0.79	0.35
		9	76	126	130	219	48	0.79	0.30
		21	92	128	131	189	39	0.81	0.24
		50	101	127	129	165	36	0.80	0.22
		1000	123	129	129	136	32	0.81	0.20

Table S5. Summary statistics of simulations for the Morisita (4nn) estimator.

			Morisita (4 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	368	700	774	1610	377	0.89	0.48
		6	420	725	768	1427	251	0.92	0.32
		9	478	737	771	1241	201	0.94	0.26
		21	539	748	766	1073	135	0.95	0.17
		50	631	756	766	946	86	0.96	0.11
		1000	731	767	768	807	30	0.98	0.04
YOSE	562	3	195	448	517	1287	282	0.80	0.50
		6	251	482	523	1008	205	0.86	0.37
		9	286	499	536	954	176	0.89	0.31
		21	363	518	531	777	111	0.92	0.20
		50	407	527	535	696	79	0.94	0.14
		1000	500	531	532	568	34	0.94	0.06
TEAK	313	3	76	246	362	1389	400	0.79	1.28
		6	103	289	363	1058	293	0.92	0.94
		9	137	301	367	995	261	0.96	0.83
		21	181	335	369	749	153	1.07	0.49
		50	221	360	374	650	124	1.15	0.40
		1000	327	367	368	415	60	1.17	0.19
META	254	3	71	187	283	1027	299	0.74	1.18
		6	90	219	277	799	201	0.86	0.79
		9	108	243	286	768	173	0.96	0.68
		21	151	264	287	582	116	1.04	0.46
		50	171	270	281	447	77	1.06	0.30
		1000	253	283	284	322	31	1.11	0.12
BRID	236	3	79	171	204	520	125	0.71	0.52
		6	103	194	213	463	94	0.81	0.39
		9	115	199	214	416	80	0.83	0.33
		21	140	205	210	319	55	0.86	0.23
		50	162	210	214	290	41	0.88	0.17
		1000	199	213	213	228	27	0.89	0.11
GRAN	159	3	59	123	145	355	100	0.77	0.63
		6	73	130	142	269	64	0.82	0.40
		9	84	133	141	248	49	0.84	0.31
		21	99	136	142	227	39	0.85	0.24
		50	110	138	142	206	32	0.87	0.20
		1000	134	142	143	155	19	0.89	0.12

Table S6. Summary statistics of simulations for the Morisita (2nn) estimator.

			Morisita (2 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	218	561	751	2464	669	0.71	0.85
		6	300	639	752	2007	486	0.81	0.62
		9	337	652	759	1823	465	0.83	0.59
		21	428	693	760	1553	293	0.88	0.37
		50	515	722	757	1231	195	0.92	0.25
		1000	678	749	758	857	155	0.95	0.20
YOSE	562	3	127	385	540	1922	640	0.69	1.14
		6	185	427	571	1597	817	0.76	1.45
		9	218	474	553	1402	359	0.84	0.64
		21	293	494	552	1220	253	0.88	0.45
		50	344	506	542	913	177	0.90	0.31
		1000	481	540	545	638	45	0.96	0.08
TEAK	313	3	48	222	431	2128	783	0.71	2.50
		6	80	261	395	1593	537	0.83	1.72
		9	106	305	421	1357	452	0.97	1.45
		21	162	340	415	1081	292	1.09	0.93
		50	203	388	434	894	243	1.24	0.78
		1000	358	427	433	549	129	1.36	0.41
META	254	3	45	186	361	1749	696	0.73	2.74
		6	70	230	385	1287	481	0.91	1.89
		9	87	253	337	1093	369	1.00	1.45
		21	120	286	352	950	349	1.13	1.38
		50	171	303	336	706	170	1.19	0.67
		1000	282	335	341	432	91	1.32	0.36
BRID	236	3	51	147	229	900	280	0.61	1.17
		6	66	168	221	619	218	0.70	0.91
		9	84	183	227	646	210	0.77	0.88
		21	107	196	233	558	211	0.82	0.88
		50	134	202	220	400	92	0.84	0.38
		1000	192	223	227	295	29	0.93	0.12
GRAN	159	3	44	111	171	648	251	0.70	1.58
		6	54	123	173	537	316	0.78	1.99
		9	61	124	169	610	187	0.78	1.18
		21	82	143	165	369	84	0.90	0.53
		50	98	149	164	315	58	0.94	0.37
		1000	142	163	165	202	16	1.03	0.10

Table S7. Summary statistics of simulations for the MHVD (4nn) estimator.

			MHVD (4 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	559	917	953	1591	309	1.17	0.39
		6	619	906	924	1367	227	1.15	0.29
		9	654	907	925	1275	204	1.16	0.26
		21	742	914	916	1130	159	1.16	0.20
		50	799	913	915	1033	138	1.16	0.18
		1000	885	912	911	940	121	1.16	0.15
YOSE	562	3	355	712	664	1648	280	1.27	0.50
		6	446	750	637	1336	181	1.33	0.32
		9	474	756	642	1236	162	1.35	0.29
		21	581	778	633	1051	110	1.38	0.20
		50	651	788	630	965	88	1.40	0.16
		1000	756	790	627	831	66	1.41	0.12
TEAK	313	3	145	400	365	1437	213	1.28	0.68
		6	203	441	342	1219	132	1.41	0.42
		9	235	460	340	1087	99	1.47	0.32
		21	308	485	332	862	66	1.55	0.21
		50	359	497	328	723	43	1.59	0.14
		1000	468	506	325	551	15	1.62	0.05
META	254	3	104	315	413	1237	362	1.24	1.42
		6	132	313	359	862	210	1.23	0.83
		9	169	333	364	764	187	1.31	0.74
		21	205	335	347	565	127	1.32	0.50
		50	239	330	336	457	96	1.30	0.38
		1000	309	333	333	358	76	1.31	0.30
BRID	236	3	132	303	344	781	204	1.27	0.85
		6	174	313	333	595	146	1.31	0.61
		9	189	316	328	550	126	1.32	0.53
		21	226	314	320	447	98	1.31	0.41
		50	257	316	319	400	88	1.32	0.37
		1000	302	317	317	333	78	1.32	0.33
GRAN	159	3	85	192	216	492	124	1.21	0.78
		6	105	193	203	351	76	1.21	0.48
		9	120	193	199	319	63	1.21	0.40
		21	142	193	197	268	48	1.21	0.30
		50	157	193	194	238	39	1.22	0.25
		1000	186	194	194	203	34	1.22	0.21

Table S8. Summary statistics of simulations for the MHVD (2nn) estimator.

			MHVD (2 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	820	1550	1738	3626	1211	1.97	1.54
		6	959	1580	1665	2869	991	2.01	1.26
		9	1055	1571	1630	2543	922	2.00	1.18
		21	1193	1583	1616	2202	860	2.02	1.10
		50	1348	1599	1609	1934	832	2.04	1.06
		1000	1535	1601	1601	1662	811	2.04	1.03
YOSE	562	3	527	1403	1269	4152	967	2.50	1.72
		6	712	1509	1215	3572	786	2.68	1.40
		9	842	1531	1189	3128	700	2.72	1.25
		21	1062	1586	1169	2679	642	2.82	1.14
		50	1218	1625	1151	2346	604	2.89	1.07
		1000	1542	1661	1145	1796	584	2.96	1.04
TEAK	313	3	248	776	763	4426	810	2.48	2.59
		6	353	895	659	3301	466	2.86	1.49
		9	441	998	647	3193	412	3.19	1.32
		21	577	1071	628	2393	345	3.42	1.10
		50	719	1120	618	1920	318	3.58	1.02
		1000	1050	1176	614	1434	301	3.76	0.96
META	254	3	181	749	1207	4932	1929	2.95	7.59
		6	271	782	945	2632	928	3.08	3.65
		9	333	774	884	2065	773	3.05	3.04
		21	431	786	839	1497	648	3.09	2.55
		50	529	784	803	1193	570	3.09	2.25
		1000	716	787	788	870	532	3.10	2.09
BRID	236	3	235	660	849	2971	889	2.76	3.72
		6	310	660	751	1716	631	2.76	2.64
		9	365	678	729	1400	563	2.84	2.36
		21	436	670	692	1078	482	2.80	2.02
		50	502	669	679	907	451	2.80	1.89
		1000	630	679	678	725	440	2.84	1.84
GRAN	159	3	160	424	530	1510	544	2.66	3.42
		6	198	426	473	1041	382	2.68	2.40
		9	224	414	453	900	339	2.61	2.13
		21	285	430	445	677	302	2.70	1.90
		50	322	426	432	592	279	2.68	1.75
		1000	402	430	430	458	269	2.70	1.69

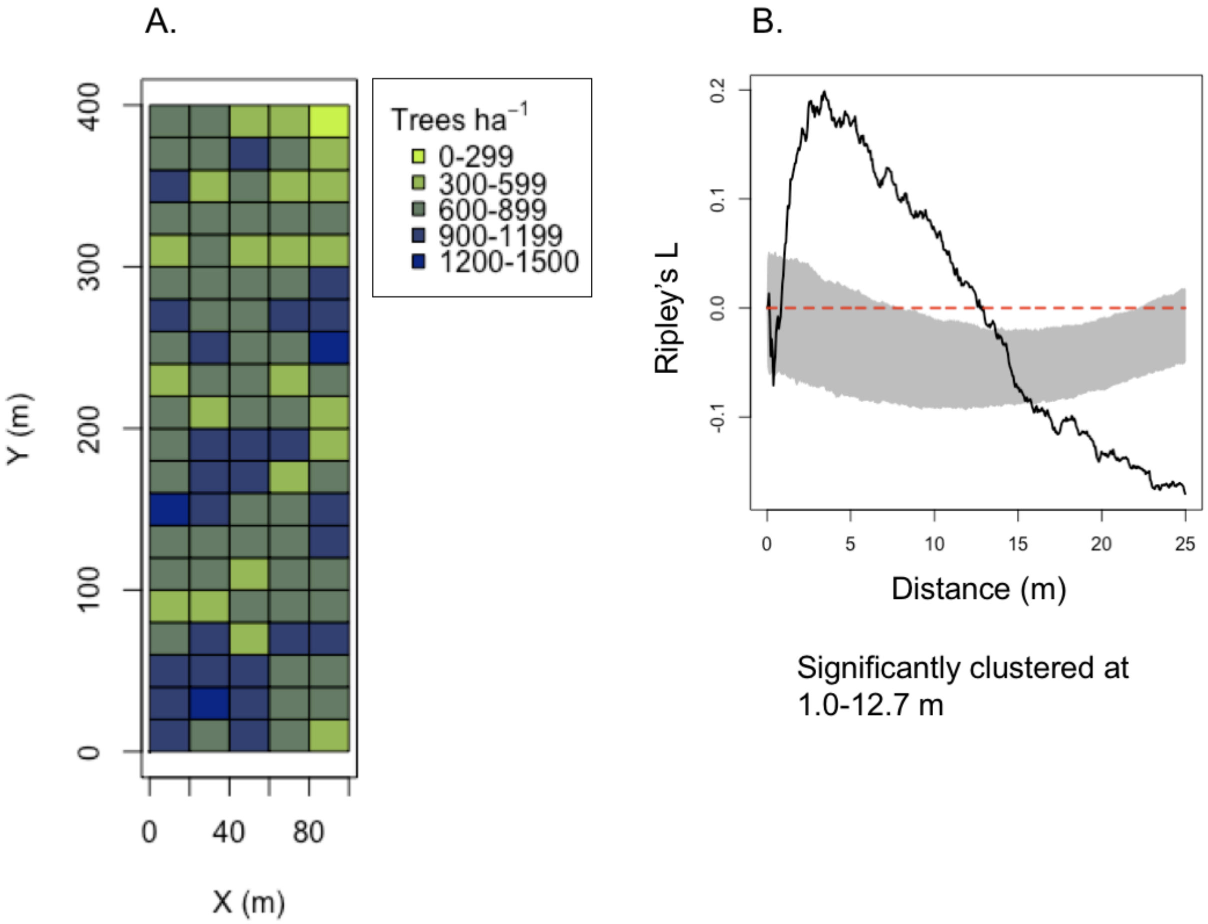
Table S9. Summary statistics of simulations for the Delincé (1nn) point density estimator.

			Delincé (1nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	384	716	789	1535	318	0.91	0.40
		6	450	748	785	1309	221	0.95	0.28
		9	495	763	787	1208	179	0.97	0.23
		21	591	773	782	1039	116	0.99	0.15
		50	650	779	786	951	78	0.99	0.10
		1000	756	785	786	819	17	1.00	0.02
YOSE	562	3	230	504	560	1226	264	0.90	0.47
		6	287	523	561	1008	196	0.93	0.35
		9	329	546	570	946	159	0.97	0.28
		21	394	548	564	816	109	0.98	0.19
		50	445	557	563	715	68	0.99	0.12
		1000	538	564	565	596	15	1.00	0.03
TEAK	313	3	86	262	344	1089	270	0.84	0.86
		6	125	304	364	931	233	0.97	0.75
		9	152	323	373	844	233	1.03	0.75
		21	192	338	364	704	137	1.08	0.44
		50	242	358	371	579	107	1.14	0.34
		1000	332	367	367	407	58	1.17	0.19
META	254	3	82	193	268	840	239	0.76	0.94
		6	105	224	273	699	159	0.88	0.63
		9	119	234	271	636	139	0.92	0.55
		21	150	250	269	499	93	0.99	0.37
		50	183	260	270	404	60	1.03	0.24
		1000	246	269	270	296	21	1.06	0.08
BRID	236	3	91	194	220	500	114	0.82	0.48
		6	116	203	227	479	98	0.86	0.41
		9	125	207	218	382	70	0.88	0.30
		21	153	211	219	328	50	0.89	0.21
		50	169	217	220	286	33	0.92	0.14
		1000	208	220	220	234	17	0.93	0.07
GRAN	159	3	66	133	157	364	105	0.84	0.66
		6	76	140	160	350	103	0.88	0.65
		9	89	144	159	333	63	0.90	0.40
		21	104	148	157	265	42	0.93	0.26
		50	117	153	159	226	29	0.96	0.18
		1000	147	159	159	173	7	1.00	0.04

Table S10. Linear regression summary statistics for the relationship of true Voronoi area to crown radius corrected for mean neighborhood distance (MND). MND was calculated using an array of 21 sampling points with four nearest neighbor trees. The MND for each individual tree was applied based on the sampling point to which the tree was located nearest. Species-specific crown radius parameters, calculated from the FHM data, were used to estimate crown radius. Species with >5% dominance in each stand are shown.

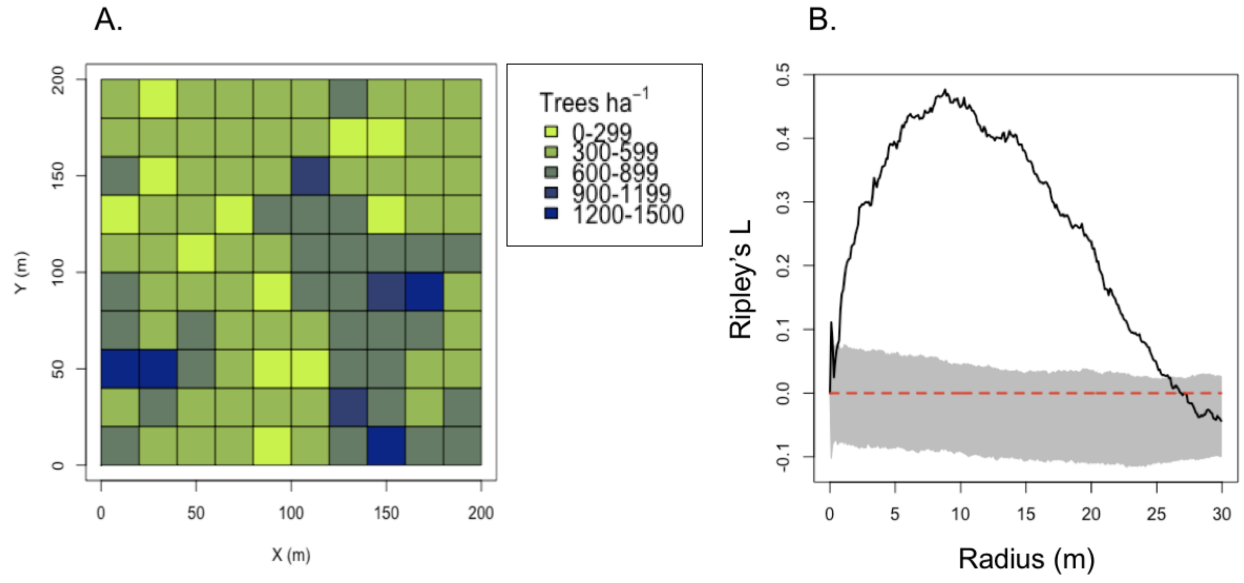
Site	Species	n	Slope (m^{-1})	Intercept	r^2	*p*-value
PLUM	Douglas-fir	574	0.20	1.64	0.050	<0.0001
	Incense-cedar	201	0.11	1.99	0.012	0.1
	White fir	1240	0.15	1.92	0.020	<0.0001
YOSE	Sugar pine	203	0.16	2.23	0.068	0.0002
	White fir	1282	0.28	1.62	0.117	<0.0001
TEAK	Incense-cedar	168	0.35	1.58	0.068	0.0006
	Jeffrey pine	97	0.42	1.59	0.146	0.0001
	Sugar pine	69	0.30	2.28	0.090	0.01
	White fir	635	0.47	0.61	0.108	<0.0001
META	Jeffrey pine	773	0.65	0.29	0.289	<0.0001
BRID	Jeffrey pine	395	0.26	2.42	0.095	<0.0001
	White fir	138	0.14	2.74	0.024	0.07
GRAN	Jeffrey pine	342	0.32	2.17	0.090	<0.0001
	White fir	73	0.05	3.69	0.003	0.6

PLUM



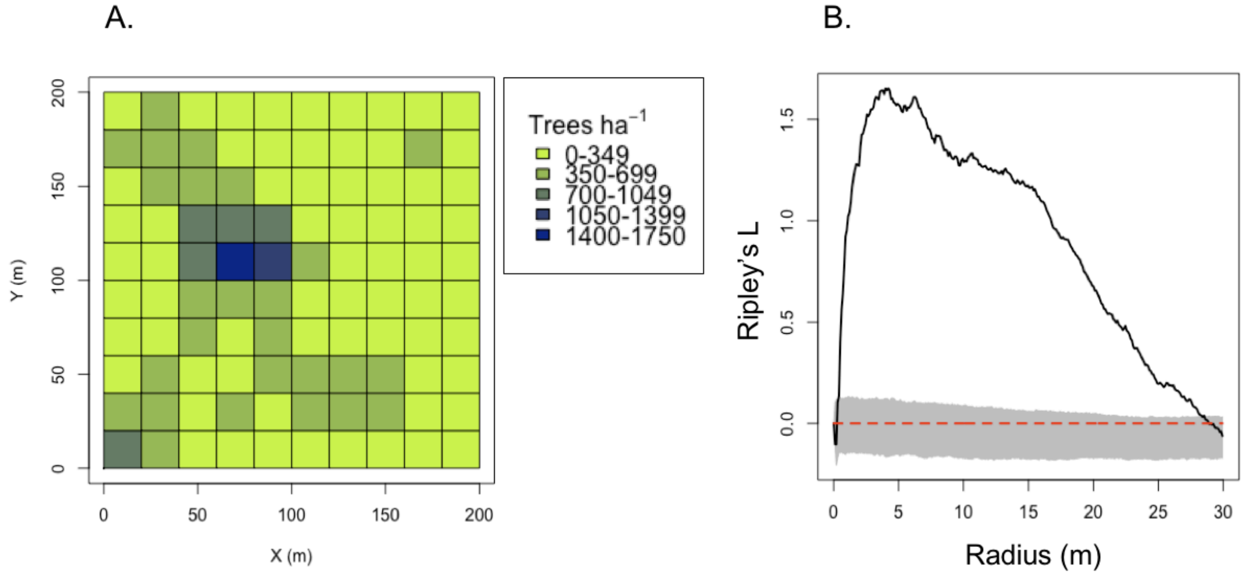
Significantly clustered at 1.0-12.7 m

YOSE



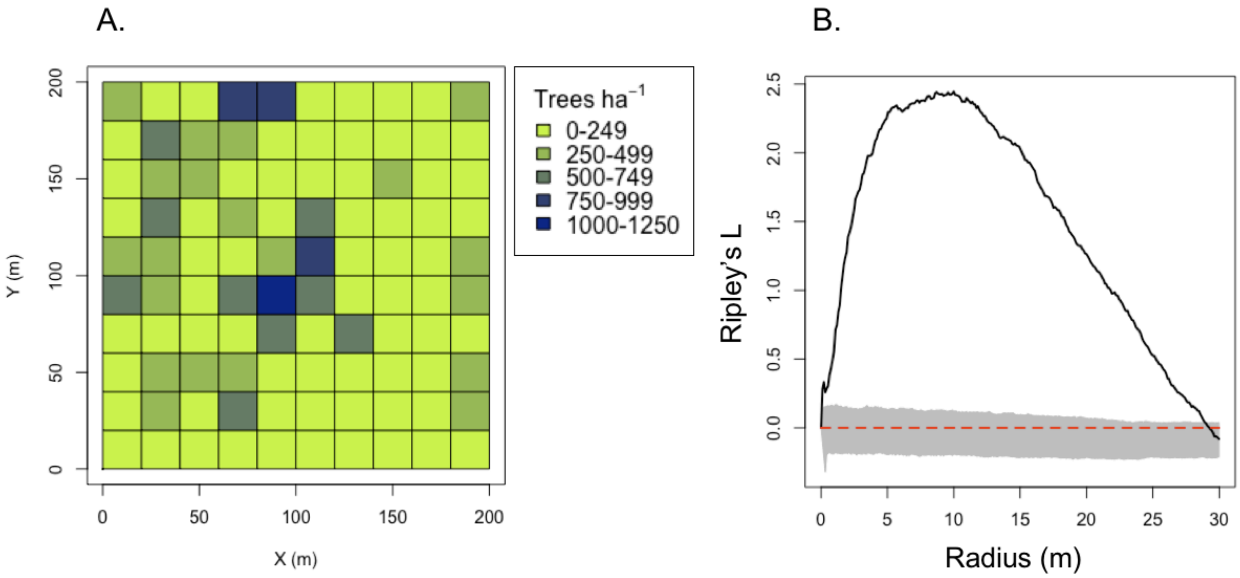
Significantly clustered at
0-0.2 m and 0.6-26.0 m

TEAK



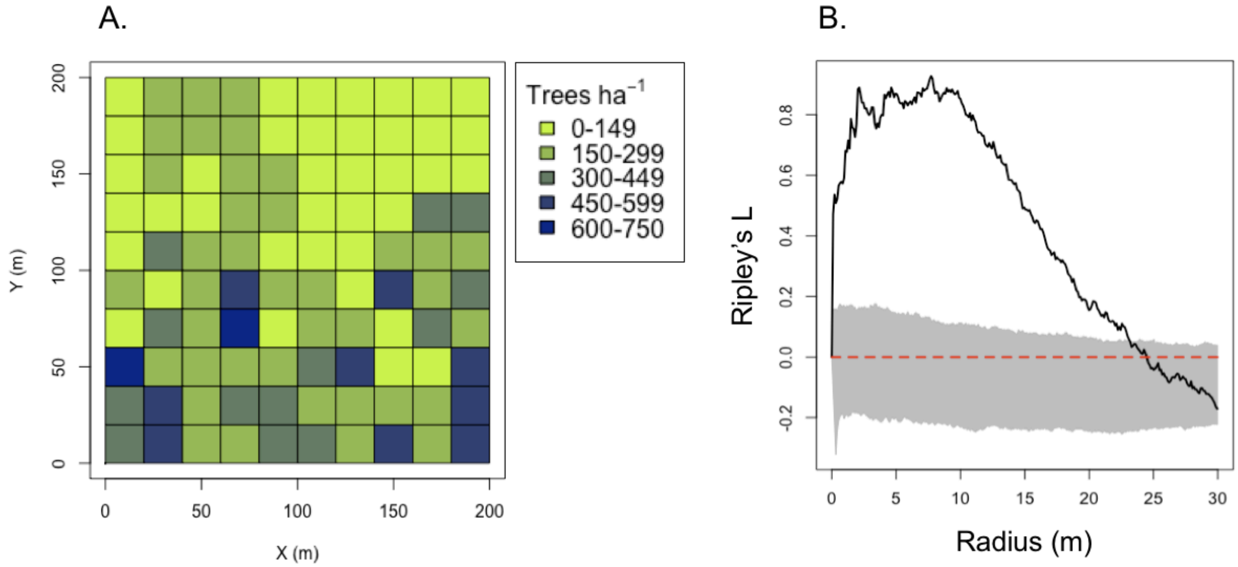
Significantly clustered at
0.3-28.5 m

META



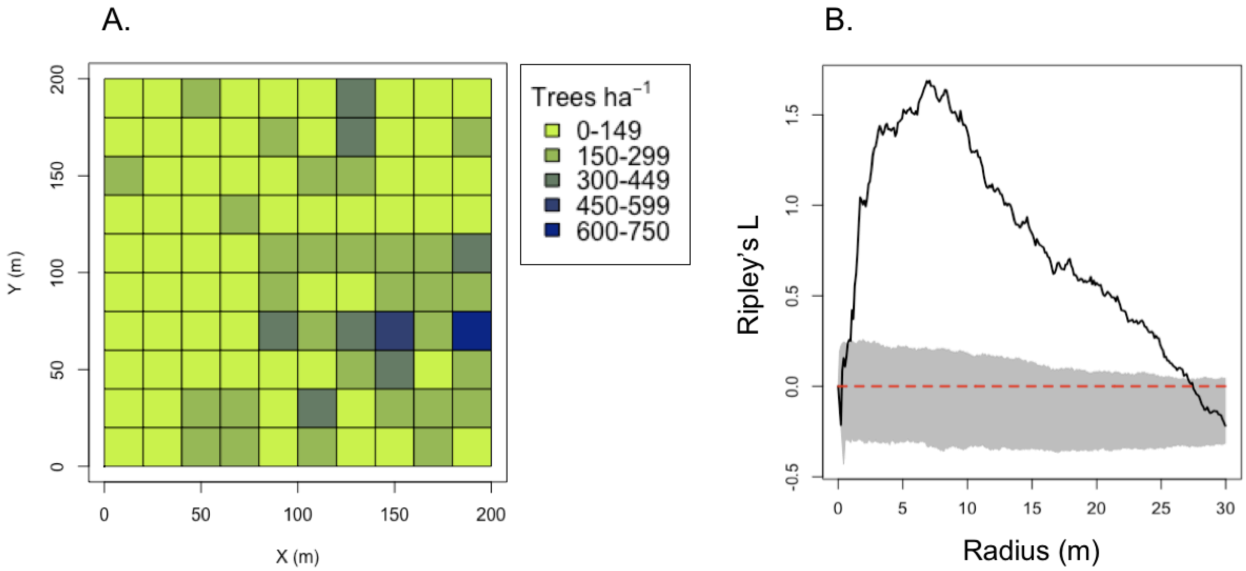
Significantly clustered at
0.0-29.0 m

BRID



Significantly clustered at
0.0-23.2 m

GRAN



Significantly clustered at
0.8-27.1 m

Figure S1. Density of trees ≥9.5 cm DBH of 20 x 20 m subplots (A) and the inhomogeneous Ripley's *L* values (B) at the range of 25 m at PLUM and 30 m at the other stands. The red lines indicate the value of a random distribution of trees and its accompanying 95% confidence interval, in gray, based on 200 simulations. A Ripley's *L* value greater than the random estimate indicates a clustered distribution.

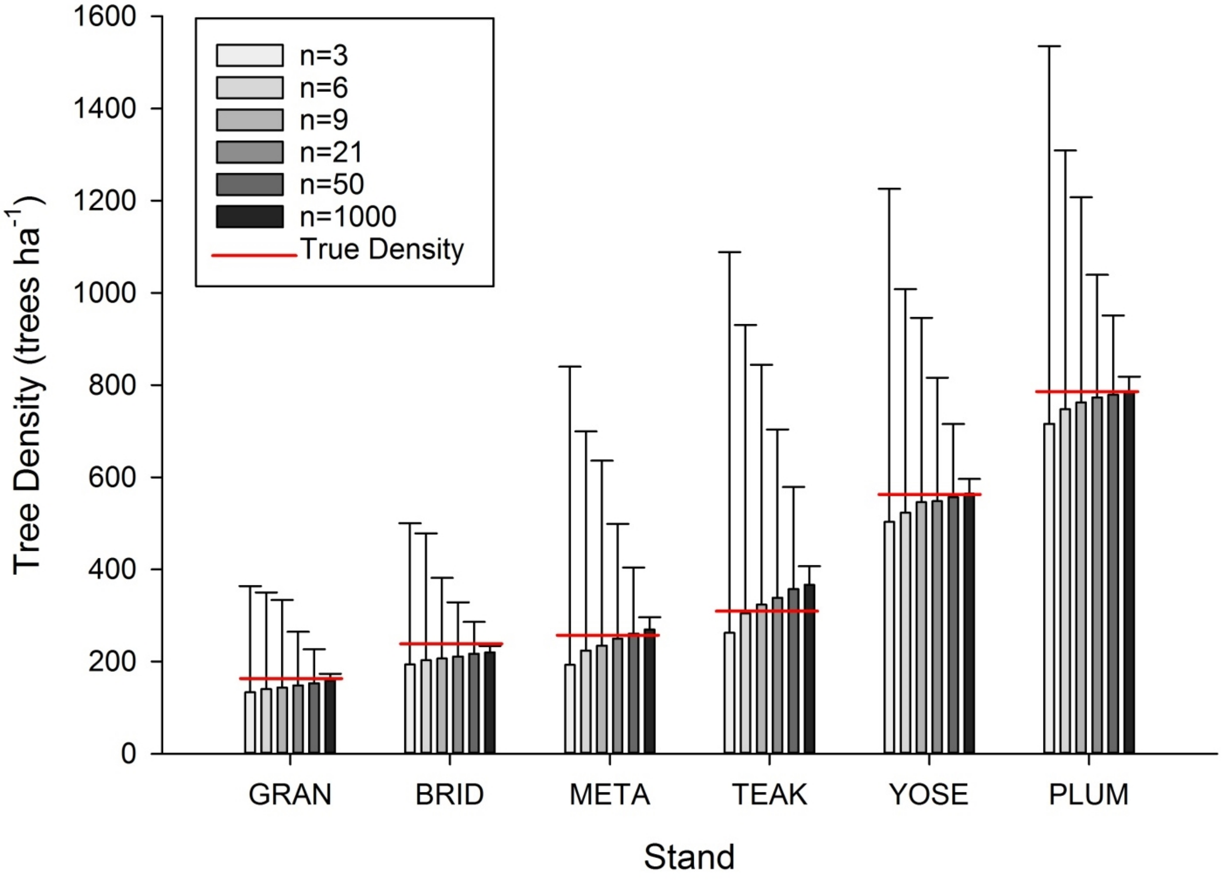


Figure S2. Results of simulations testing the effect of sampling intensity (number of sampled points) on density estimates using the Delincé PDE. Bars show the median value of 1,000 simulation runs and error bars show the 95% confidence intervals results. See Table 2 for site codes.

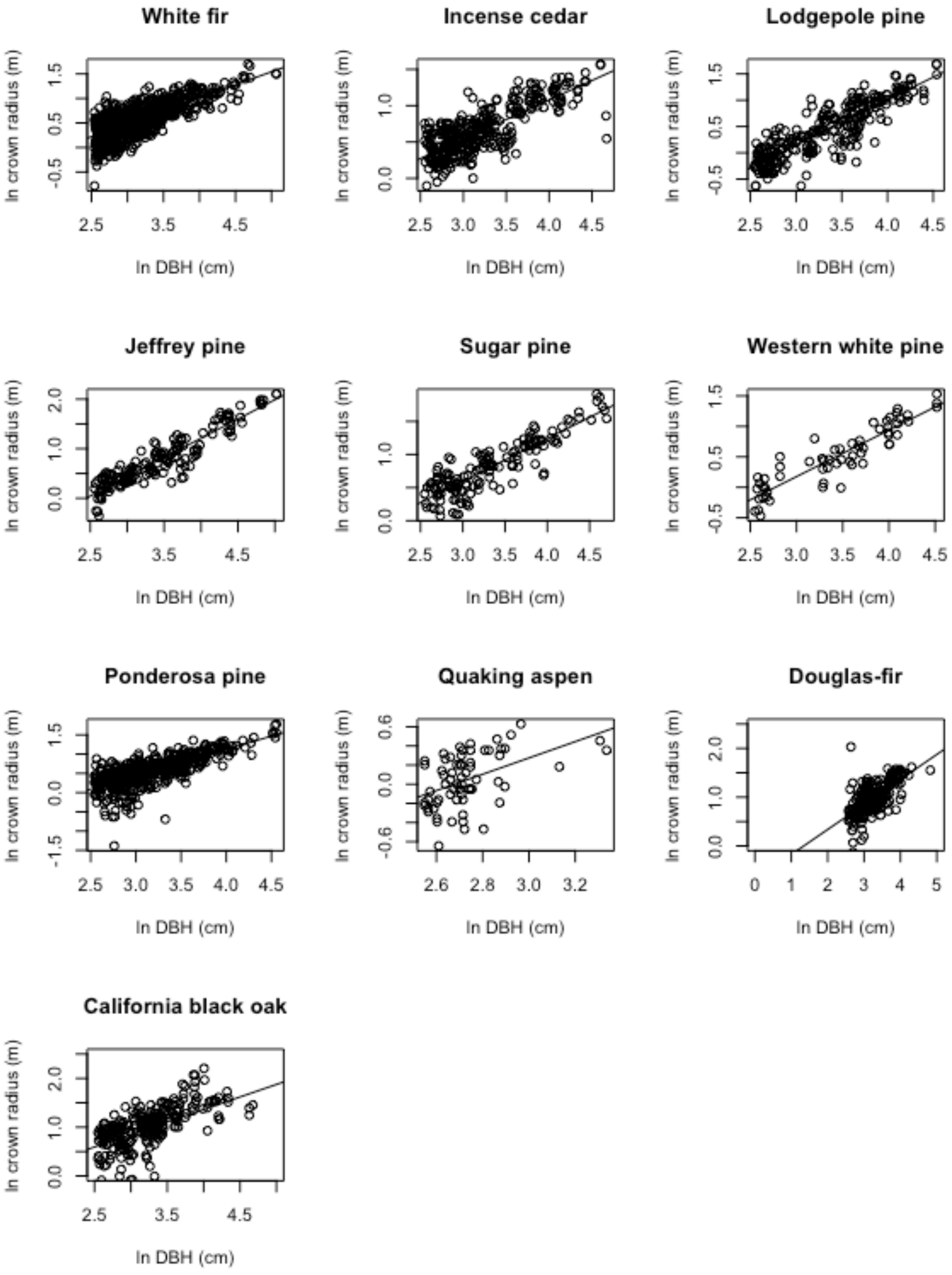
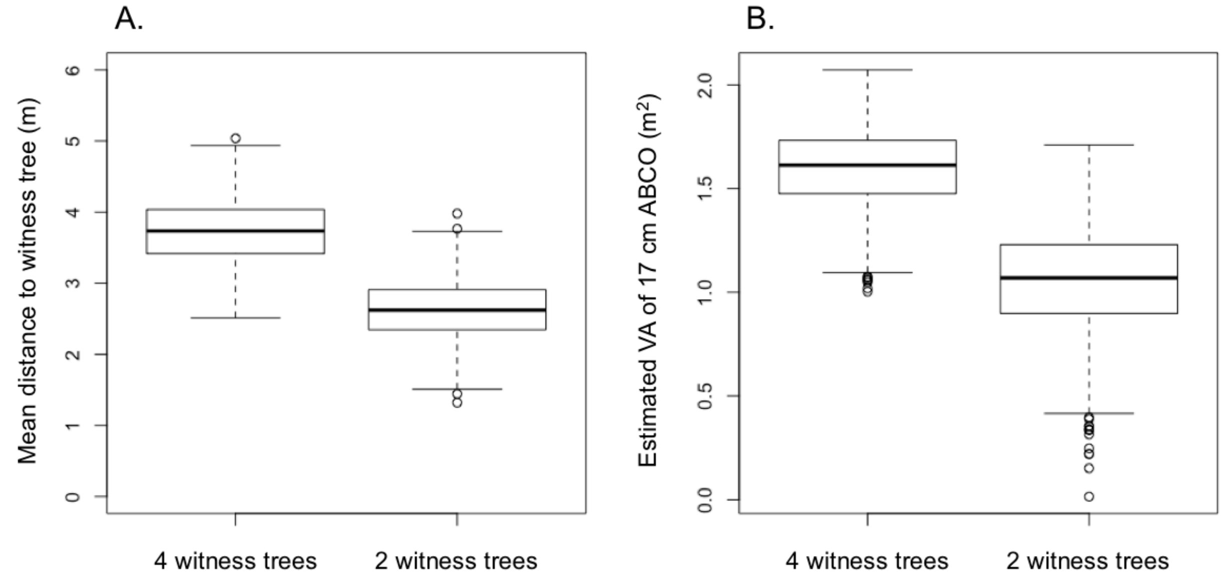
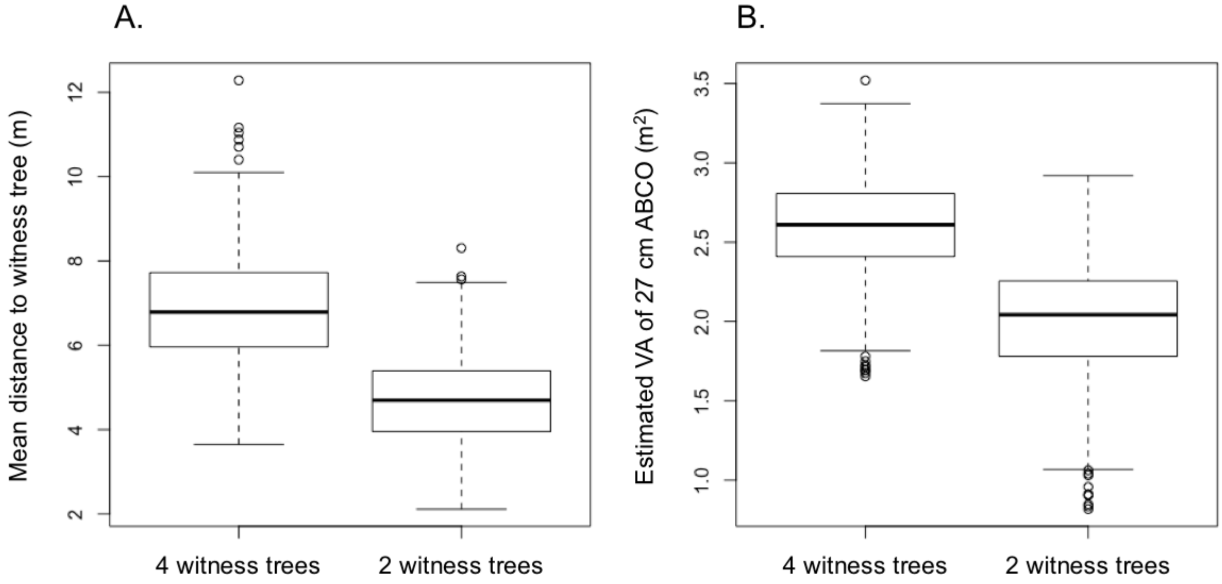


Figure S3. The relationship of crown radius (CR) to diameter at breast height (DBH; 1.37 m) for common Sierra Nevada mixed-conifer species. Values shown are from measurements taken by the Forest Health Monitoring Program in Sierra Nevada mixed-conifer stands. The r^2 values for the conifer species range from 0.43 for Douglas-fir (n=196) to 0.83 for Western white pine (n=59). The r^2 values for the hardwoods are lower, ranging from 0.22 for quaking aspen (n=65) to 0.44 for California black oak (n=254).

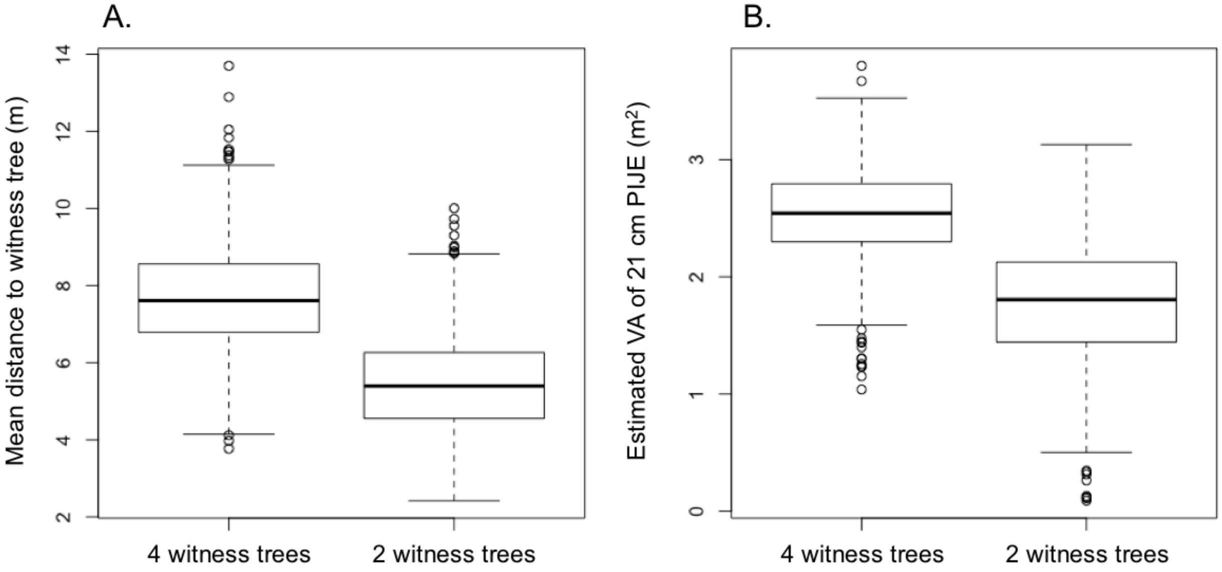
PLUM


A.
Mean distance to witness tree (m)
0
1
2
3
4
5
6
4 witness trees
2 witness trees
B.
Estimated VA of 17 cm ABCO (m^2)
0.0
0.5
1.0
1.5
2.0
4 witness trees
2 witness trees

TEAK


A.
Mean distance to witness tree (m)
2
4
6
8
10
12
4 witness trees
2 witness trees
B.
Estimated VA of 27 cm ABCO (m^2)
1.0
1.5
2.0
2.5
3.0
3.5
4 witness trees
2 witness trees

META



BRID

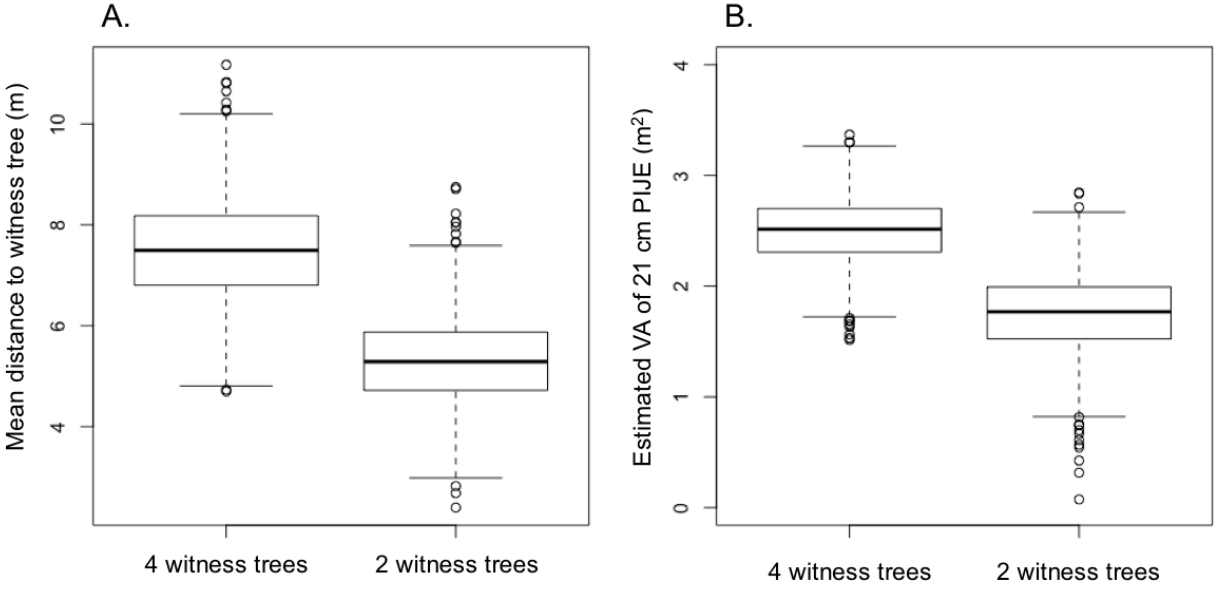
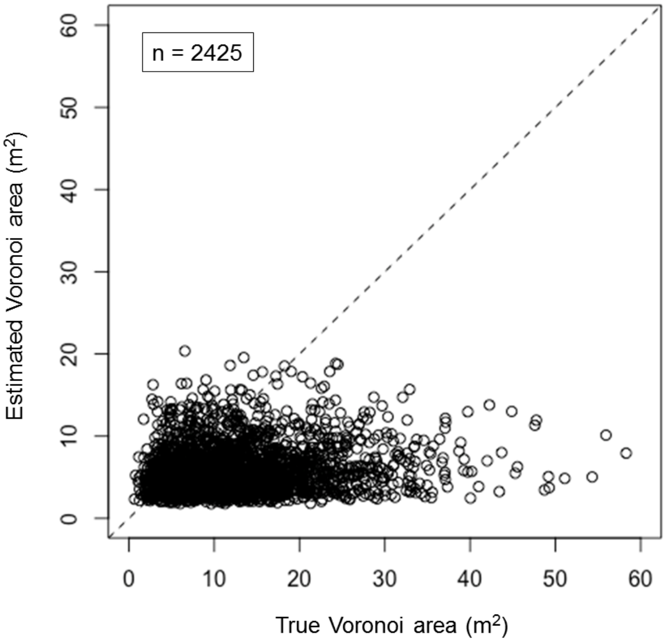
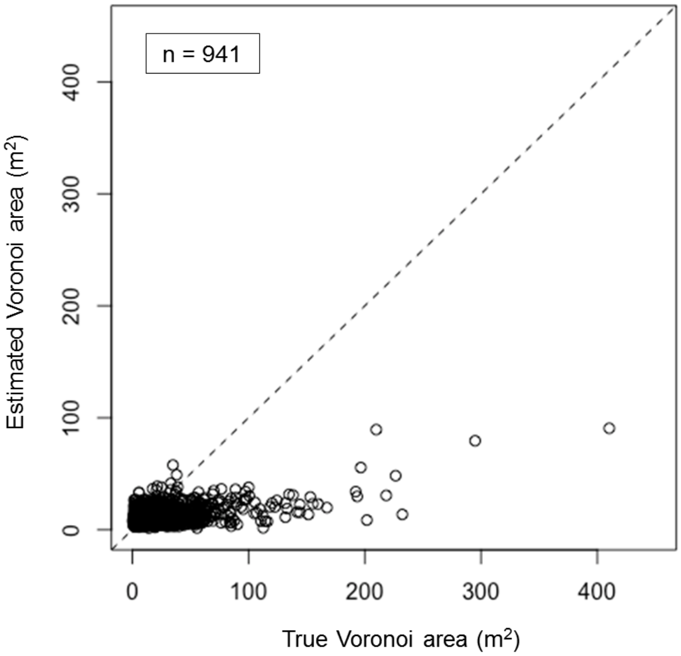


Figure S4. Simulation results (1,000 runs) of the mean neighborhood distance (A) when two nearest neighbors (2nn) or 4 nearest neighbors (4nn) are used for a 6-point sampling scheme. The discrepancy in mean neighborhood distance is reflected in the estimate of the Voronoi area of a single tree of the most dominant species at the median stand DBH (B) using the method and equation parameters in Baker (2014). ABCO refers to *Abies concolor* (white fir).

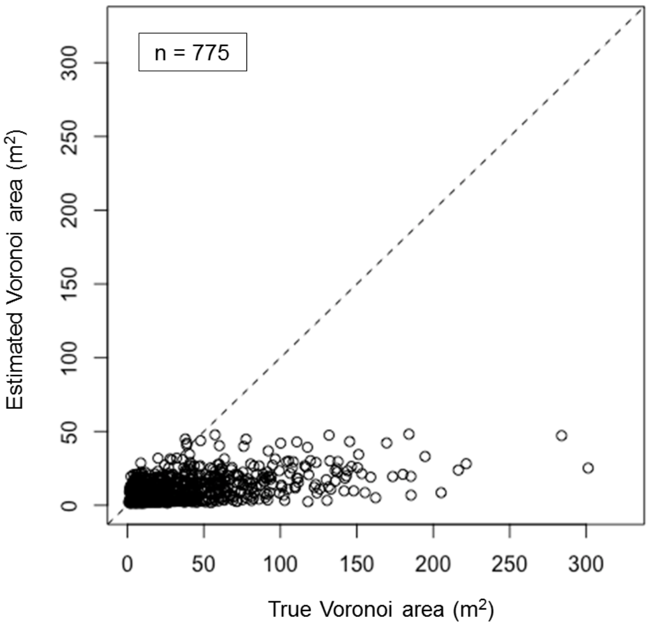
PLUM


n = 2425
Estimated Voronoi area (m^2)
True Voronoi area (m^2)
0
10
20
30
40
50
60
0
10
20
30
40
50
60

TEAK


n = 941
Estimated Voronoi area (m^2)
True Voronoi area (m^2)
0
100
200
300
400
0
100
200
300
400

META



BRID

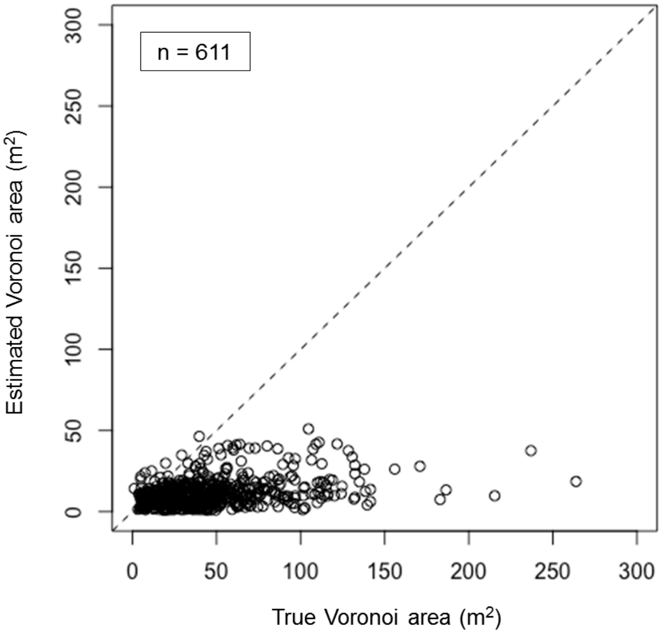


Figure S5. The relationship between the true Voronoi area estimated from the mapped Yosemite stand and the Voronoi area estimated using the method and equation parameters in Baker (2014).

APPENDIX S2

Analysis using diameter at stump height (DSH) in the place of diameter at breast height (DBH).

Introduction

The methods for the MHVD analysis presented in this manuscript follow the methods described in Baker (2014). Specifically, we used the species-specific regression parameters in Table D1 in Baker (2014) to calculate crown radius (CR) from tree diameter at breast height (DBH; 1.37 m). After submission of this manuscript for publication, it was communicated to the authors by W. Baker that an error is present in Table D1 of Baker (2014) paper. W. Baker writes that the regression parameters provided in Table D1 to calculate CR should be calculated from diameter at stump height (DSH, 0.30 m) as opposed to DBH. At the time of publication of this manuscript, this correction has not been published as an erratum. In order to address potential discrepancies arising from this error, we estimated DSH from DBH measurements using taper equations for all the trees in our analysis. We then repeated all analyses that relied on estimating the mean harmonic Voronoi density (MHVD) using DSH as opposed to DBH. We present the methods and relevant tables and figures below.

Methods for estimating DSH

The DSH of each tree was estimated from the measured DBH using taper equations. Equations for hardwood species were derived from Raile (1982) with FIA-approved species substitutions and equations for conifer species were from Wensel and Olson (1995). On average, the DSH was 3% larger than DBH for the conifer species and 22% larger for the hardwood species.

The calculation of CR from DSH was applicable to the results of the point simulations (Tables 3 and A7-A8), the comparison of the estimated Voronoi area (MVA) for a single tree of the dominant species and median DSH at each site (Figures 3 and A4), and the relationship between the true VA and MVA calculated with DSH (Figures 4 and A5).

Results

When calculated with DSH, the 95% CI of the MHVD 4nn estimator overlapped the true density at three of six sites in the 50-point simulation (Table B1). The median simulation estimate for the 50-point sampling was higher than the true density at all six sites, with relative error (RE) values ranging from 1.03-1.34 (Table B2). Estimates were moderately precise, with relative root mean square error (rRMSE) ranging from 0.13-0.40 (Table B2). The MHVD 2nn estimator overestimated density at all sites in the 50-point simulation scheme, and in no cases did the 95% CI overlap the true density. The 2nn MHVD estimator was consistently biased towards overestimating density, with RE values ranging from 1.94-3.12 (Table B3). The 2nn MHVD was less precise than the 4nn estimator, with rRMSE values ranging from 1.02-2.28 (Table B3). The bias towards underestimating the MVA when using only quarter corners (2nn) held true whether MVA was calculated with DSH or DBH (Figure B1). In both cases, the MVA for quarter corners was significantly lower than the MVA estimated with section corners. The MVA calculated with DSH consistently underestimated the true VA of the trees at all sites (Figure B2).

Discussion

Estimating MVA using DSH as opposed to DBH reduced the bias of the MHVD 4nn estimator. However, both the MHVD 2nn and 4nn estimators overestimated stand density in all cases. Additionally, the estimated VA was consistently underestimated relative to the true VA, regardless of whether VA was estimated with DSH or DBH.

Table S1. Relative performance of the MHVD density estimator for the 50-point simulations as calculated with DSH. Results are reported as relative values with the results from the 1,000 realizations divided by the true density. rRMSE refers to the relative root mean square error. Bold text indicates site estimates where the 95% CI of the simulation overlaps the true density. Results calculated with DBH are shown in Table 3.

	Site	PLUM	YOSE	TEAK	META	BRID	GRAN
Measure (nn trees)	True density (trees ha^{-1})	784	562	313	254	236	159
MHVD (4 trees)	2.5% CI	1.01	**0.92**	**0.82**	**0.96**	1.09	1.00
	Median	1.16	**1.10**	**1.03**	**1.31**	1.34	1.23
	97.5% CI	1.32	**1.32**	**1.32**	**1.84**	1.71	1.54
	rRMSE	0.17	**0.14**	**0.13**	**0.40**	0.38	0.27
MHVD (2 trees)							
	2.5% CI	1.66	1.63	1.49	2.13	2.17	2.05
	Median	2.02	2.01	1.94	3.12	2.89	2.71
	97.5% CI	2.44	2.49	2.62	4.69	3.94	3.55
	rRMSE	1.04	1.05	1.02	2.28	1.98	1.77

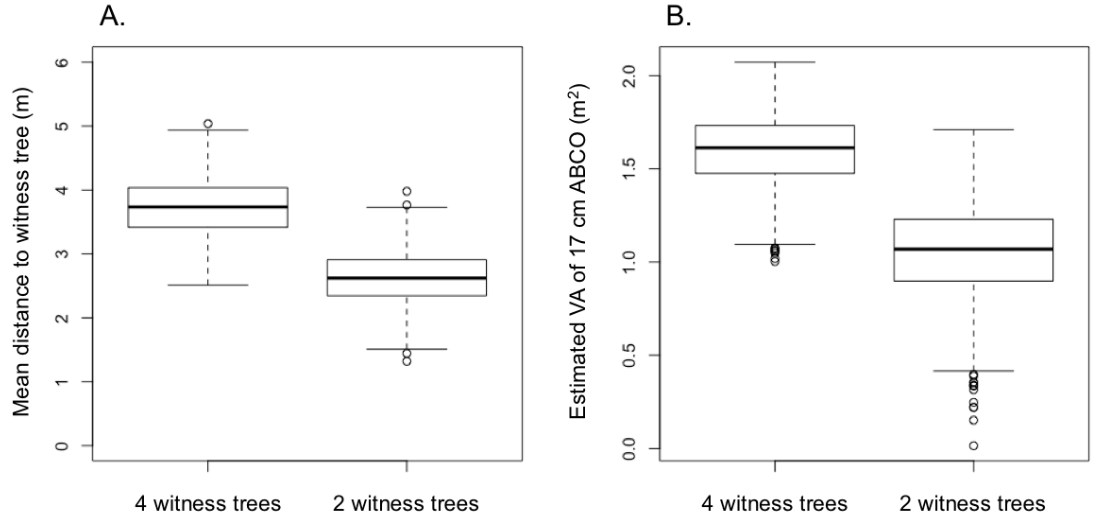
Table S2. Summary statistics of simulations for the MHVD (4nn) estimator calculated using DSH. Results calculated with DBH are shown in Table A7.

			MHVD (4 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	533	896	935	1557	304	1.14	0.39
		6	605	896	916	1312	228	1.14	0.29
		9	663	895	909	1208	189	1.14	0.24
		21	733	903	908	1115	159	1.15	0.20
		50	794	906	906	1033	136	1.16	0.17
		1000	878	902	903	931	119	1.15	0.15
YOSE	562	3	321	607	665	1264	274	1.08	0.49
		6	376	619	644	1050	195	1.10	0.35
		9	411	616	632	948	155	1.10	0.28
		21	476	619	625	810	105	1.10	0.19
		50	517	616	620	740	80	1.10	0.14
		1000	594	618	618	641	57	1.10	0.10
TEAK	313	3	130	320	364	885	206	1.02	0.66
		6	168	318	341	652	129	1.01	0.41
		9	182	316	332	568	100	1.01	0.32
		21	222	320	326	478	65	1.02	0.21
		50	255	322	323	414	41	1.03	0.13
		1000	305	323	323	341	13	1.03	0.04
META	254	3	106	313	425	1448	403	1.23	1.59
		6	144	329	377	875	228	1.29	0.90
		9	164	336	358	733	175	1.32	0.69
		21	206	332	346	561	129	1.31	0.51
		50	243	333	338	467	101	1.31	0.40
		1000	312	337	337	362	84	1.33	0.33
BRID	236	3	136	311	361	908	230	1.32	0.97
		6	178	313	330	562	141	1.33	0.60
		9	195	308	325	519	124	1.31	0.53
		21	221	312	318	430	98	1.32	0.41
		50	257	316	319	404	91	1.34	0.38
		1000	302	316	316	333	81	1.34	0.34
GRAN	159	3	90	196	216	457	112	1.23	0.70
		6	110	194	206	383	82	1.22	0.51
		9	121	193	200	323	67	1.21	0.42
		21	143	194	197	269	49	1.22	0.31
		50	158	195	197	244	43	1.23	0.27
		1000	186	195	195	204	36	1.23	0.23

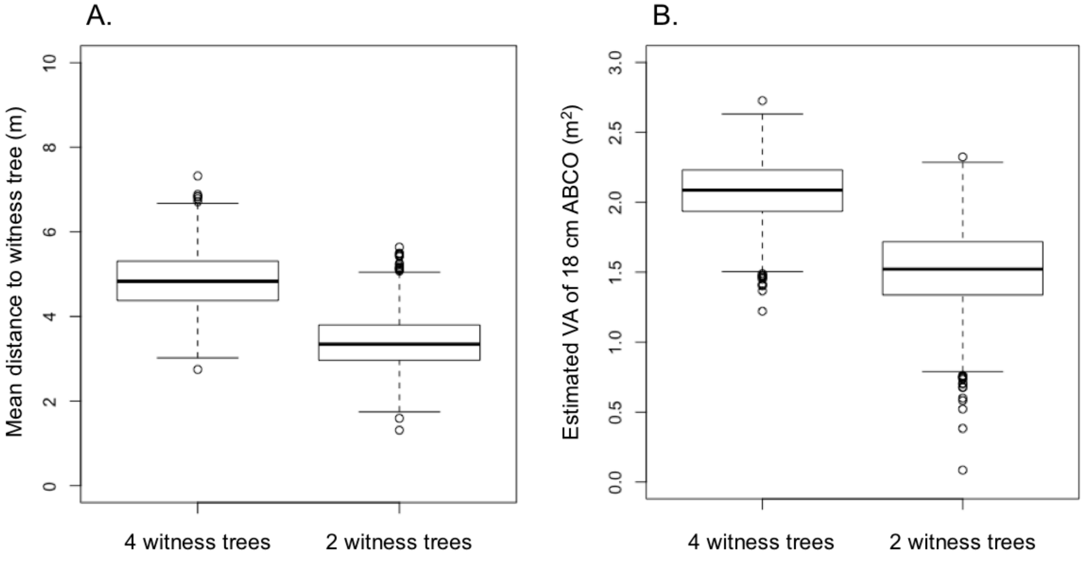
Table S3. Summary statistics of simulations for the MHVD (2nn) estimator calculated using DSH. Results calculated with DBH are shown in Table A8.

			MHVD (2 nn)						
Site	True density (trees ha^{-1})	Points sampled	2.5% CI	Median	Mean	97.5% CI	RMSE	RE	rRMSE
PLUM	784	3	745	1577	1697	3423	1140	2.01	1.45
		6	964	1557	1662	2991	1013	1.99	1.29
		9	1025	1579	1622	2473	916	2.01	1.17
		21	1207	1596	1616	2135	865	2.04	1.10
		50	1298	1581	1584	1913	815	2.02	1.04
		1000	1522	1586	1587	1656	803	2.02	1.02
YOSE	562	3	493	1157	1294	2859	999	2.06	1.78
		6	623	1134	1199	2265	763	2.02	1.36
		9	666	1111	1162	1928	682	1.98	1.21
		21	819	1129	1152	1635	625	2.01	1.11
		50	915	1132	1138	1401	590	2.01	1.05
		1000	1071	1128	1128	1188	566	2.01	1.01
TEAK	313	3	213	605	753	2145	726	1.93	2.32
		6	266	584	652	1421	454	1.86	1.45
		9	316	603	649	1342	417	1.93	1.33
		21	397	607	634	997	356	1.94	1.14
		50	465	606	617	819	318	1.94	1.02
		1000	568	607	608	654	296	1.94	0.95
META	254	3	185	752	1165	4501	1643	2.96	6.47
		6	278	784	972	2940	1020	3.09	4.02
		9	312	800	920	2211	837	3.15	3.30
		21	443	787	840	1571	652	3.10	2.57
		50	540	793	809	1191	579	3.12	2.28
		1000	727	796	797	866	544	3.13	2.14
BRID	236	3	232	654	819	2336	891	2.77	3.77
		6	307	659	740	1646	610	2.79	2.59
		9	352	681	730	1460	570	2.88	2.41
		21	431	678	700	1098	494	2.87	2.09
		50	513	681	691	930	468	2.89	1.98
		1000	637	679	680	724	444	2.88	1.88
GRAN	159	3	151	411	541	1756	600	2.58	3.77
		6	205	414	469	1075	382	2.61	2.40
		9	237	433	466	870	349	2.72	2.20
		21	278	429	442	674	301	2.70	1.89
		50	326	431	434	564	282	2.71	1.77
		1000	405	431	431	459	273	2.71	1.72

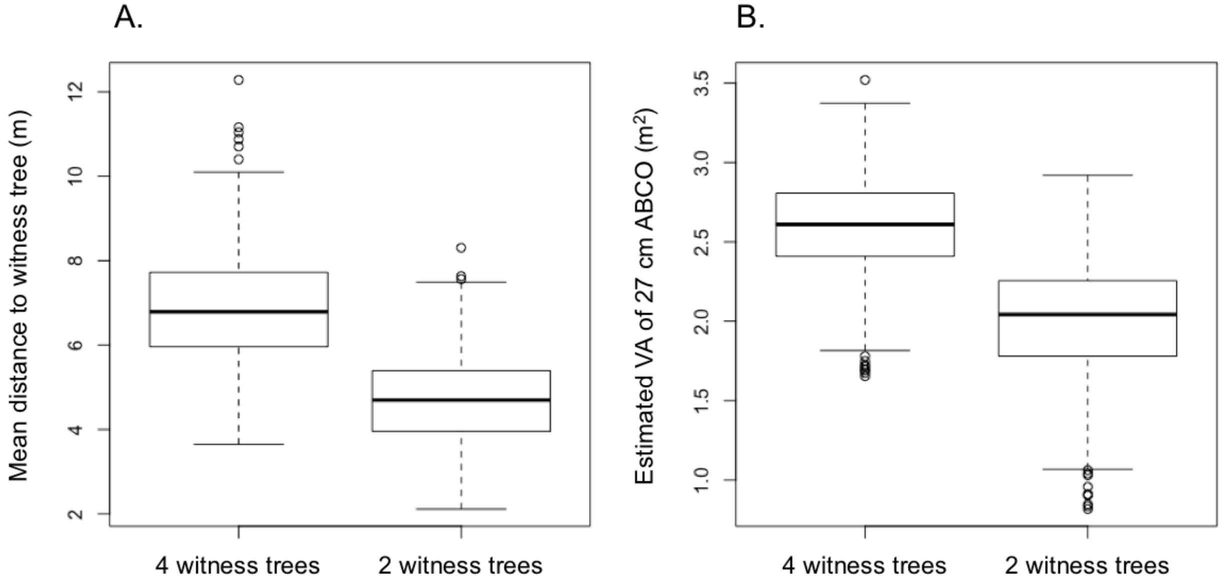
PLUM


A.
Mean distance to witness tree (m)
0
1
2
3
4
5
6
4 witness trees
2 witness trees
B.
Estimated VA of 17 cm ABCO (m^2)
0.0
0.5
1.0
1.5
2.0
4 witness trees
2 witness trees

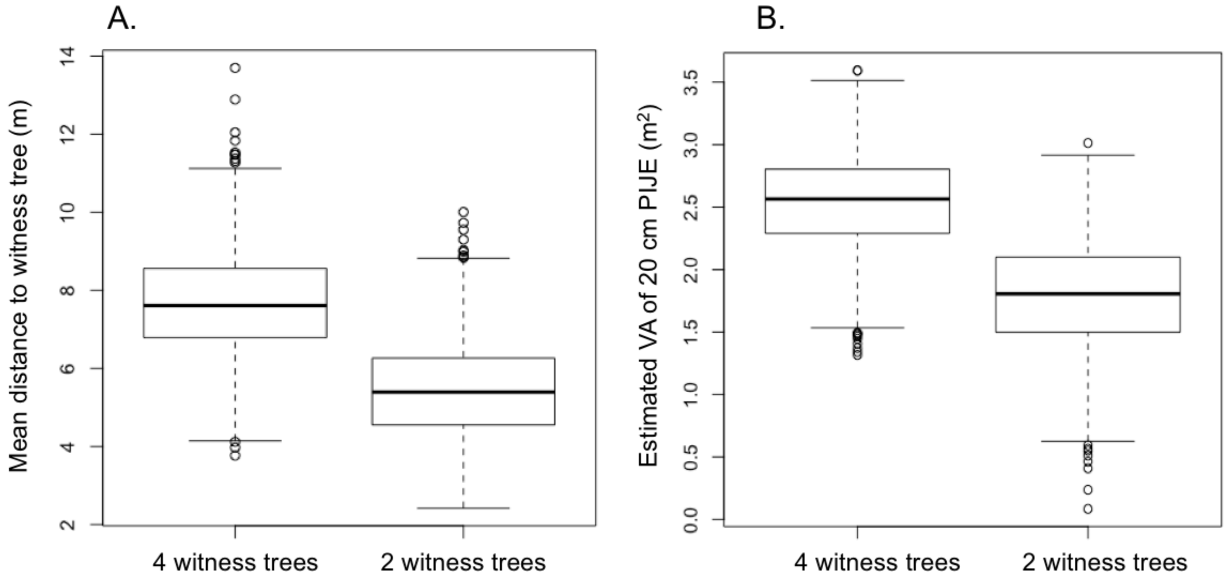
YOSE


A.
Mean distance to witness tree (m)
0
2
4
6
8
10
4 witness trees
2 witness trees
B.
Estimated VA of 18 cm ABCO (m^2)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
4 witness trees
2 witness trees

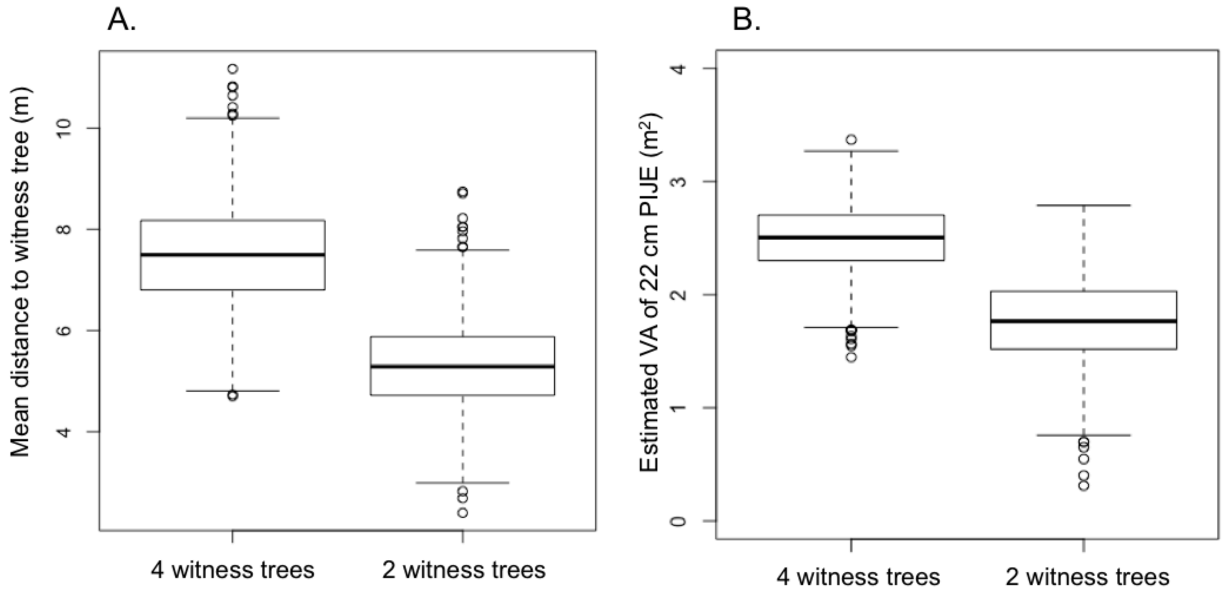
TEAK


A.
Mean distance to witness tree (m)
2
4
6
8
10
12
4 witness trees
2 witness trees
B.
Estimated VA of 27 cm ABCO (m^2)
1.0
1.5
2.0
2.5
3.0
3.5
4 witness trees
2 witness trees

META


A.
Mean distance to witness tree (m)
2
4
6
8
10
12
14
4 witness trees
2 witness trees
B.
Estimated VA of 20 cm PIJE (m^2)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4 witness trees
2 witness trees

BRID



GRAN

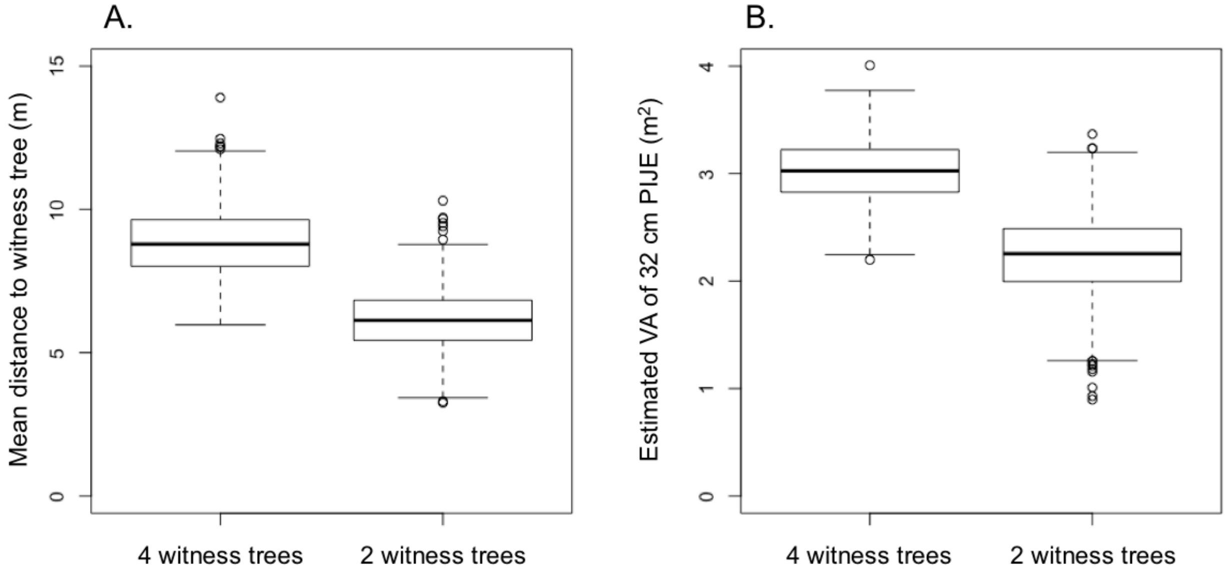
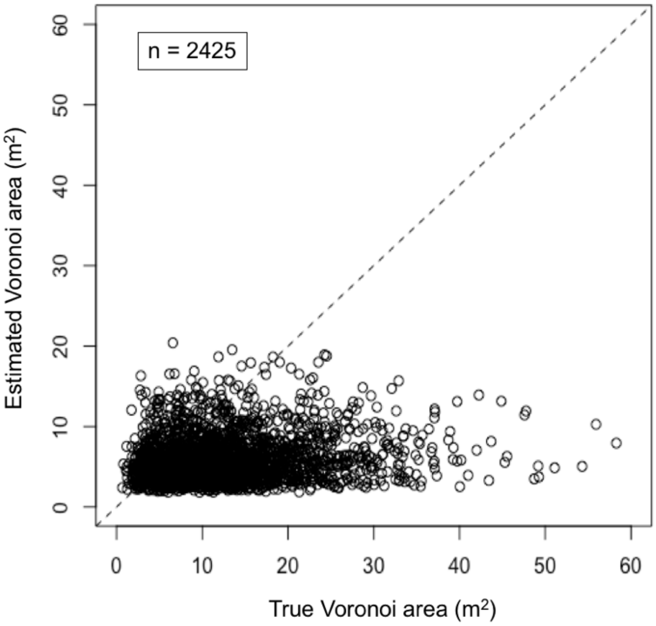
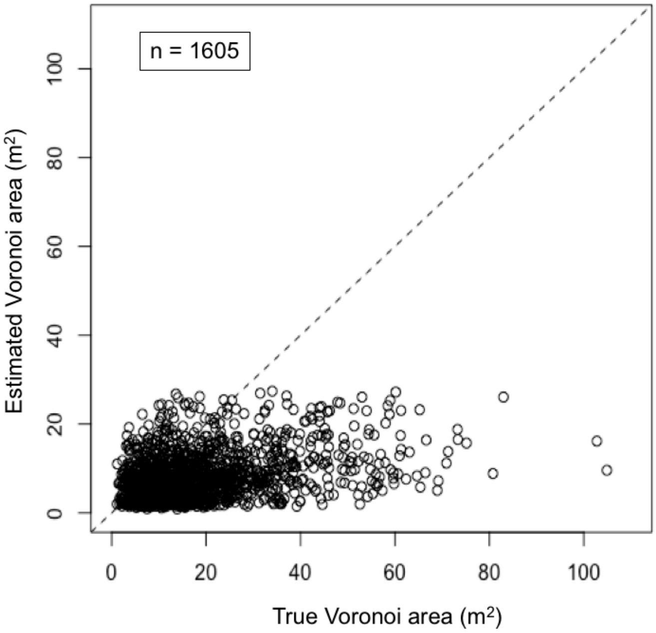


Figure S1. Simulation results (1000 runs) of the mean neighborhood distance (A) when two nearest neighbors (2nn) or 4 nearest neighbors (4nn) are used for a 6-point sampling scheme. The discrepancy in mean neighborhood distance is reflected in the estimate of the Voronoi area of a single tree of the most dominant species at the median stand DSH (B) using the method and equation parameters in Baker (2014). Crown radius is calculated from DSH. Results calculated with DBH are shown in Figures 3 and A4.

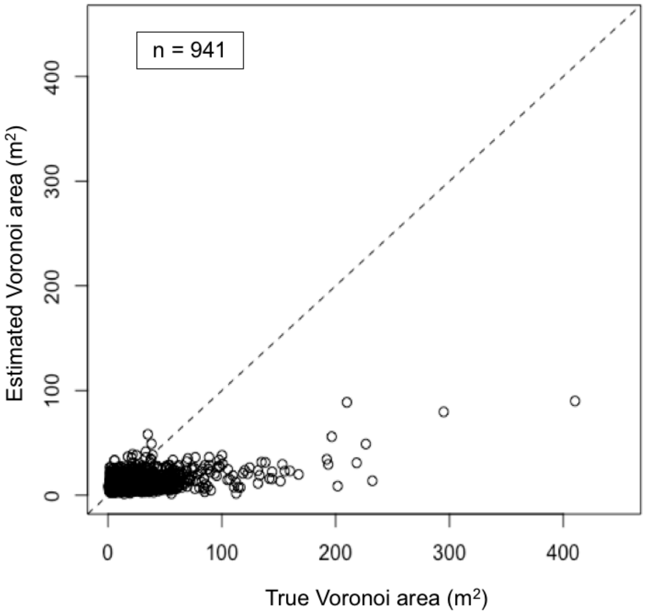
PLUM


n = 2425
Estimated Voronoi area (m²)
True Voronoi area (m²)
0
10
20
30
40
50
60

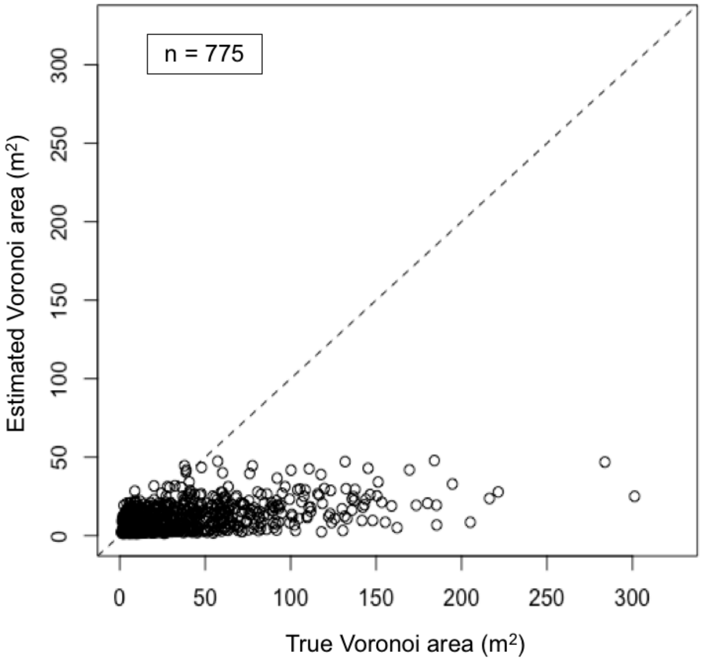
YOSE


n = 1605
Estimated Voronoi area (m²)
True Voronoi area (m²)
0
20
40
60
80
100

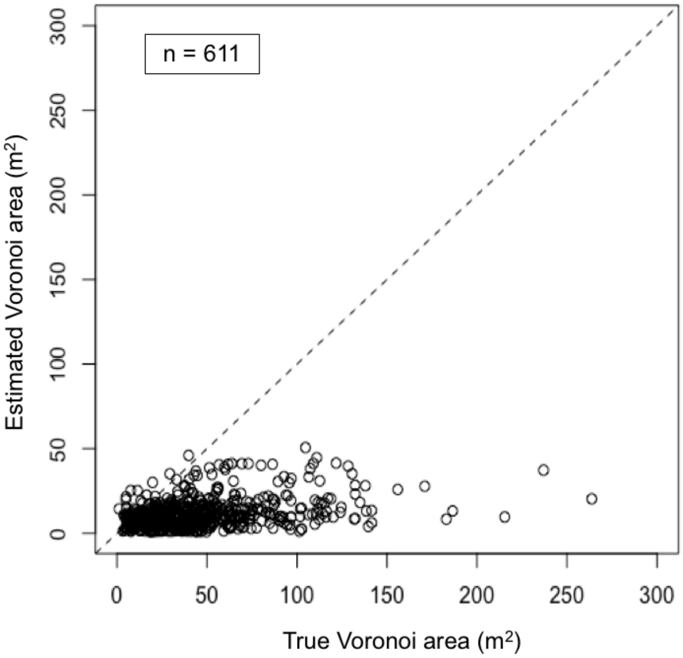
TEAK


n = 941
Estimated Voronoi area (m²)
0
100
200
300
400
True Voronoi area (m²)
0
100
200
300
400

META


n = 775
Estimated Voronoi area (m²)
0
50
100
150
200
250
300
True Voronoi area (m²)
0
50
100
150
200
250
300

BRID



GRAN

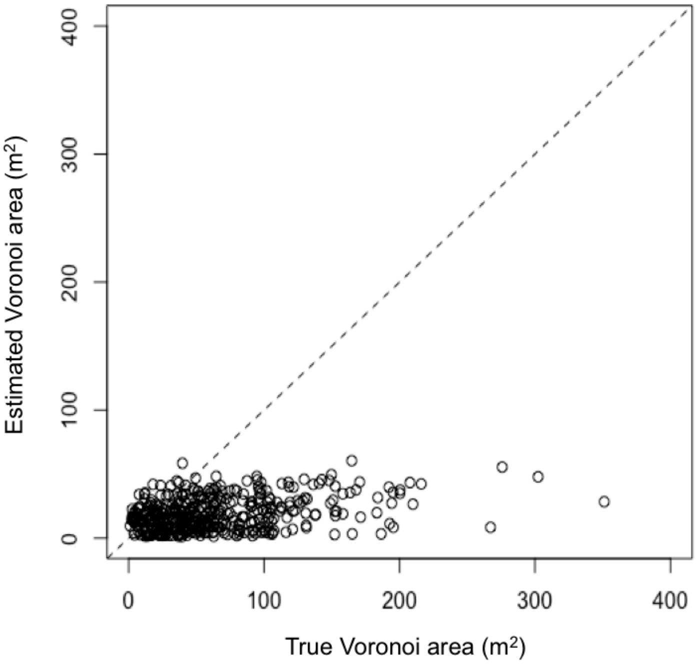


Figure S2. The relationship between the true Voronoi area estimated from the mapped stands and the Voronoi area estimated using the method and equation parameters in Baker (2014). Crown radius is calculated from DSH. Results calculated with DBH are shown in Figures 4 and A5.

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CHAPTER 3 Defining the dimensions of resilience to inform forest management

ABSTRACT

Forest resilience is often cited as a management goal in a variety of silvicultural and forest ecology contexts. While the area of resilience theory is well developed, explicit metrics for the measurement of resilience are typically missing. I develop a framework for operationalizing the resilience of forested systems, which is focused on enhancing the resilience properties of resistance to disturbance and recovery from disturbance. I outline four dimensions of resistance and recovery that can be used to measure and monitor resilience: heterogeneity at the patch scale, complexity at the multi-patch scale, quality of individuals and populations, and reserves of nutrients, carbon, and propagules. These dimensions are grounded in four core disciplines within ecology: community ecology, landscape ecology, population biology, and ecosystem ecology. I review studies that have measured aspects of forest resilience in order to assess key measurements and analyses that can be used to quantify the four dimensions of resilience in the context of resistance and recovery. The framework proved to be flexible enough that the main principles could be applied in three temperate forest systems that encompass a range of spatial scales and management jurisdictions. Though the resilience framework does not provide an absolute estimate of resilience for a single point in time, it can be used to outline monitoring plans that measure relative changes in forest resistance and recovery over time.

INTRODUCTION

Maintaining the resilience of forests in an era of global change is a priority for both conservation and management (Millar et al. 2007a, Nagel et al. 2017). The development of the theory of ecological resilience has spurred calls to incorporate resilience into stewardship plans, including directives from federal agencies (NPS 2010, USDA 2012). A major challenge for these initiatives is the lack of explicit metrics to assess progress towards goals of increasing resilience (DeRose and Long 2014).

Resilience is an aggregate property of systems that maintains the system's composition, structure and function when faced with a disturbance. Holling (1973) introduced the concept of resilience to ecology. His paper marks a notable shift in perspective from an emphasis on equilibrium conditions to a focus on transient dynamics. Specifically, Holling argued that not all ecological systems persist in a stable equilibrium and that a system may persist in different configurations (i.e., alternate states). Holling (1973) also noted the potential value of resilience to inform resource management, but commented that it was unlikely that researchers would have enough information to measure resilience in a meaningful way (Holling 1973). It has been more than the four decades since Holling described the missing link between resilience and management. Since then, the empirical support of resilience theory has focused on laboratory microcosm studies (e.g., Allen-Morley and Coleman 1989, Scheffer et al. 2003, Lee and Brown 2001, Chase 2003) and small-scale, self-contained field experiments (e.g., Scheffer et al. 1993, Handa et al. 2002, Scheffer et al. 2003, Paine and Trimble 2004, Schmitz 2004). There remains a lack of theory for the practice of applying resilience metrics to complex ecosystems such as forests.

The main challenge inherent in using resilience to inform management and conservation is the multitude of definitions and jumble of concepts that have been developed over the past several decades (Grimm and Wissel 1997). At the same time, the application of resilience concepts to management and conservation activities must be consistent with theory (Carpenter et al. 2001). Brand and Jax (2007) describe the transition from a specific but descriptive ecological term to a broad and general concept used by multiple disciplines to refer to the dynamics of environmental and social-ecological systems. A benefit of the wider definition is that it can be used to foster communication across disciplines and lead to successful interdisciplinary practice. However, the vague application of the term, particularly in applied contexts, does little to guide quantifiable practices and management decisions in order to improve the resilience of forests to disturbances. The application of resilience for identifying management targets can seem conceptually straightforward; the challenge for managers lies in identifying specific metrics that can be used to quantify resilience and monitor change over time.

The objective of this paper is to define a useful framework for quantifying resilience of complex ecosystems. This framework connects existing resilience theory with forest management principles in order to outline a strategy that uses quantitative analyses to assess resilience of forest ecosystems. First, I define the terms used in the development of the framework and its application. This paper does not introduce new resilience terms, but rather brings to light the ways that existing resilience theory can be applied in a forest management context. Next, I outline a framework for measuring resilience in forest ecosystems. This conceptualization recognizes the two key processes in resilience, namely resistance and recovery, as well as four dimensions of resilience by which resistance and recovery are assessed: heterogeneity, complexity, quality, and reserves. I then provide an overview for applying the framework. Next, I describe the methods and results of a review of current methods for measuring and analyzing metrics of resistance and recovery. This review highlights a range of potential measurements that can be used to quantitatively assess the four dimensions of resilience. I then give examples of the resilience framework and measurements applied to three unique temperate forest ecosystems. These three case study systems include sites that span a range of spatial scales and measurement jurisdictions. These case studies also highlight three disturbance agents that are common to temperate forests: high-severity fire, an invasive pest, and exposure to chronic pollution. Finally, I summarize the results of the literature review and the case study assessments and describe the benefits and limitations of the resilience framework for quantifying resilience of forest systems.

Definitions

Resilience theory as it has developed over the more than 40 years since Holling’s seminal paper has traversed a wide swath of ecology including disturbance dynamics, community assembly, population persistence, invasion biology, and ecosystem restoration. Thus many aspects of resilience (e.g., alternative states, stability, persistence) have multiple meanings. Indeed, the term resilience itself has been used in a variety of ways. The resulting ambiguity hinders the understanding and application of resilience (Grimm and Wissel 1997). Thus in creating this framework for operationalizing resilience concepts, I carefully describe terms in a context appropriate for forest management.

Resilience definitions have historically included ideas about both an assemblage's resistance to disturbance and/or its recovery after disturbance. For example, Holling's (1973) definition of "ecological resilience" emphasized resistance to disturbance. In contrast, Scheffer (2009) took a more inclusive perspective defining resilience as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks." The phase "absorb disturbance" implies resistance while the term "reorganize" implies recovery.

My approach follows Scheffer (2009) in that I considered resistance and recovery as essential but separate components of resilience. Specifically, resistance is used in the sense of Walker and Salt (2006): "the capacity of a system to absorb disturbance, undergo change, and still retain essentially the same structure, function, and feedbacks." I derived the definition for recovery from Westman (1978), who described the "degree, manner, and pace of restoration of initial structure and function in an ecosystem after disturbance." This definition encompasses both the speed and extent of recovery following disturbance.

Questions regarding the resilience of systems require defining the scale, both spatial and temporal, of the system being investigated (Holling 1973, Connell and Sousa 1983, Turner et al. 1993). It can be difficult to generalize from experimental manipulations to ecological theory (Trumbore et al. 2015). Additionally, differences in scale may lead to quite different assessments of the resilience of an ecological system (Turner 2010). The resilience framework outlined below relies on a determination of scale that matches the scale of a management unit, where the appropriate scale are determined by considering management goals and constraints on management activities. I use the terms "patch" and "stand" to describe dynamics at the scale of communities (Seymour and Hunter 1999). In wildland forests, stands may be differentiated by species composition, age and size structures, or edaphic factors such as elevation, slope, or soil parent material. In managed forests, stands may be differentiated by management regime. I use the term "landscape" to refer to spatial scales that encompass multiple patches or stands (Seymour and Hunter 1999).

When defining both spatial and temporal scope, considering the scale of disturbance experienced by the site is important (Carpenter et al. 2001, Scheffer 2009, DeRose and Long 2014). Typically, the spatial scale of a management unit will be large enough to incorporate both stand-scale dynamics and landscape-scale processes. The spatial scale that managers are considering when addressing resilience of forests will also be intrinsically tied to the management unit. For example, private landowners are likely to be managing smaller areas than managers of federally-owned lands, and thus may consider dynamics relevant to enhancing forest resilience at a finer scale. In general, the spatial scale relevant to conservation and management will range from the stand or patch scale to the landscape scale, which includes many patches and potentially many different communities.

The temporal scale considered in the framework described below includes temporal scales relevant to both the ecological dynamics of the forested system and the management plan.

Typically, the benchmark of the temporal scale required for assessing the resilience of an ecological system is considered to be the turnover time of the longest-lived species in the assemblge (Connell and Sousa 1983). This metric is important when the management plan is focused on maintaining a specific population or assemblage of species. However, management plans may also target certain forest functions rather than specific assemblages, in which case the relevant temporal scale would be defined by the processes that maintain function. Additionally, management plans typically must consider ecosystem processes at more restricted temporal scales than the centuries-length timescales of tree lifespans. Examples may include the temporal scale related to seedling regeneration, harvesting, regeneration of an overstory cohort, time for a new cohort to reach reproductive maturity, or regeneration response after disturbance. Thus, the relevant temporal scale considered under this resilience framework will be determined both by the temporal effects of disturbance and the relevant management goals.

Disturbance is known to play a vital role in structuring ecosystems and mediating species interactions (Dayton 1971, Sousa 1984, White and Pickett 1985). Disturbance agents may be biological or physical (Sousa 1984). I consider disturbance in the sense of pulse and press perturbations (*sensu* Bender et al. 1984). The original concept of press and pulse perturbations was defined in a community ecology framework and referred to an alteration of the density of one or more species in a system, where pulse disturbances are a short-term alteration of species density from which the system is able to recover quickly, while press perturbations are sustained alterations of species densities that result in a new configuration of species interactions (Bender et al. 1984). While the original derivation of the concept of press and pulse perturbations was related to concepts of system equilibrium, the terms are now generally used to define the temporal scale of a perturbation (i.e., short and punctuated versus long and sustained; Lake 2000). Examples of press perturbations typically experienced by forests include chronic pollution, introduced pests and pathogens, fire suppression, and prolonged drought and increased temperatures resulting from anthropogenic climate change. Pulse disturbances are defined in the sense of White and Pickett (1985), as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.” Examples of pulse perturbations typically faced by forests include insect outbreaks, fires, logging, and storm-related mortality events such as ice storms, hurricanes, and microbursts. Silvicultural treatments may qualify either as press or pulse disturbances. For example, a light thin or fuel treatment would not result in changes in species composition and would therefore be a pulse treatment. A harvest that initiated a new cohort, such as a group selection or a clearcut, could be considered to be a press disturbance. This paper includes examples of both press and pulse perturbations as the defining disturbance of a system.

This paper considers compounded disturbances in the sense of Paine et al. (1998), as the interacting effects of multiple disturbances which may delay recovery compared to single perturbations. While Paine et al. (1998) focus on the effects of compounded disturbances on the speed of recovery, this same concept can also be applied to resistance, in the sense that resistance may be lowered in the presence of multiple disturbance agents. Anticipating disturbance type, disturbance scale (both spatial and temporal), and the interacting effects of multiple disturbances will be involved in assessing appropriate variables to measure resistance and recovery.

Dispensing with alternate stable states

The concept of resilience is intrinsically tied to the concepts of stability and alternate stable states in ecology. The concept of stability is often linked to resilience and, like resilience, has taken on many different definitions and meanings in ecology (Ives and Carpenter 2007). Holling's (1973) definition of stability, "the ability of a system to return to an equilibrium state after a temporary disturbance" is typically cited. When a system can support two or more assemblages as a result of differing starting conditions, these are termed alternative stable states (Lewontin 1969, Holling 1973, Scheffer et al. 2001). Ten years after Holling's paper, Connell and Sousa (1983) proposed criteria for demonstrating stability of natural systems, with the underlying premise that if stability cannot be demonstrated, neither can the existence of alternate stable states. Much research subsequent to Connell and Sousa (1983) was focused on demonstrating or disproving the existence of alternate stable states in natural systems, particularly related to alternate stable states that arose in the face of anthropogenic effects (Peterson 1984, Beisner et al. 2003, Chase 2003, Scheffer and Carpenter 2003, Scheffer et al. 2003, Pain and Trimble 2004, Petraitis and Dudgeon 2004). These studies typically attempt to determine whether two existing states in a system conform to a strict definition of alternate stable states, as well as whether a system is self-sustaining over at least one complete turnover of the individuals of the dominant species (Connell and Sousa 1983). The concept of alternate stable states has also been extended to the fields of conservation and restoration ecology, where threshold models inclusive of complex, non-linear dynamics have been proposed to address habitat management (Suding and Hobbs 2009). However, when these threshold models are applied, the existence of alternate stable states cannot be determined in a strict sense. Thus these models are used largely as heuristic devices rather than quantitative guides (Bestelmeyer 2006, Briske et al. 2006).

Because of the assumption of equilibrium states, it can be difficult to apply resilience theory to complex systems. A definition of stability such as Holling's (1973) described above, which relies on the existence of equilibrium states, is too narrow for the purposes of this paper. While noting the historical importance of Holling's (1973) definition and its pervasiveness in the literature, I define stability in the sense of Thompson et al. (2009), as "the capacity of an ecosystem to absorb disturbance and remain largely unchanged over time." This definition highlights the relationship between stability and resistance to disturbance. In this sense, highly stable states have higher barriers to state shifts (Ives and Carpenter 2007). There is still little consensus on how stability can be measured in natural systems (Grimm and Wissel 1997, Petraitis 2013), thus the framework outlined below focuses on measuring the dimensions of resilience rather than attempting to estimate the absolute stability of forest systems. I consider forested systems able to persist in multiple configurations and I dispense with a strict test of stability in this framework of resilience.

In the resilience framework described below, target states serve as the metric by which to measure resilience, as opposed to stable states. I define the target state for a forest system as a state that meets the criteria specified by the goals of the management plan. The criteria for determining the target may be purely ecological, including variables such as forest structure, composition, and function. The criteria may also include other factors specified in management plans, such as recreational, aesthetic, or economic considerations. Focusing resilience goals on target states rather than alternate stable states is in keeping with the idea that ecosystem states may be dynamic and change over time (Gunderson 2000). For the purpose of achieving and maintaining target states, it is not necessary to demonstrate the existence of strictly-defined stable states to determine state shifts in the precise manner of the theoretical concept, or to determine whether a system is strictly self-sustaining in order to manage for resilience; instead, this framework proposes that metrics of resistance and recovery be the focus of resilience-oriented management goals.

A FOREST RESILIENCE FRAMEWORK

The framework outlined below can be used both to quantify the status of forest resilience at a particular site and to develop monitoring plans to measure progress toward improved resilience for that site. The framework includes principles derived from four key areas of ecology that form the basis of resilience theory: community ecology, landscape ecology, population biology, and ecosystem ecology. In general, this resilience framework focuses on measures of tree characteristics and dynamics, due to their important role in defining the structure and function of forested systems (Ellison et al. 2005). This framework is general enough to be applied to a range of forested systems. It is also important that the framework be adaptable to a range of management jurisdictions. In order to be helpful for managers, in addition to addressing ecological considerations, management plans must be economically and legally feasible. The framework focuses on explicit, measurable forest attributes and processes that can be used to quantify four resistance and recovery dimensions.

In this conceptual framework, resilience is comprised of two components: resistance and recovery. As defined above, resistance is the ability of the system to absorb the impact of disturbance without experiencing changes to overall structure, composition, or function. The goal of managing for resistance is to promote ecosystem processes that maximize the target state's resistance to changes in forest structure and function in response to disturbance. Recovery is the ability of the system to return to the structure and function of the target state after experiencing a disturbance. The goal of managing for recovery is to promote ecosystem processes that enhance response strategies for anticipated disturbances, in order to maximize the speed and extent of recovery of the target state. Resistance prevents loss of energy, biomass, and nutrients from the system. Recovery rebuilds these resources.

Dimensions of resilience

This conceptual framework defines four dimensions that contribute to overall resilience: heterogeneity, complexity, quality, and reserves (Figure 1). The first dimension of resilience is heterogeneity at the forest stand scale, which is akin to a forest patch, as defined above. Heterogeneity relates to the discipline of community ecology and encompasses measurements related to compositional and structural diversity and species interactions, such as competition. Heterogeneity of forests can refer to the structure and composition of the dominant vegetation as well as the available habitats for establishment and regeneration. Structural heterogeneity includes heterogeneity in tree diameter, tree height, or in the spatial arrangement of trees. Compositional heterogeneity refers to both species richness and evenness.

Heterogeneity has long been noted to be an important determinant of a system's resistance to disturbance, both in the sense of species diversity and diversity of habitats available for colonization (Goh 1975, Peterson et al. 1998, Bertness et al. 2002, Ives and Carpenter 2007). Often the influence of heterogeneity on resistance is described as the influence of heterogeneity on stability. Early studies demonstrated that spatial heterogeneity conferred stability in simple modeled systems (Goh 1975). Later models described multiple ways that heterogeneity in species composition promotes stability, extending the theory of heterogeneity-stability models beyond a simplistic model where increased heterogeneity leads to linear increases in stability (Peterson et al. 1998). The influence of greater species diversity on resistance to disturbance has been highlighted specifically for forested systems (Larsen 1995).

Heterogeneity has also been noted to enhance recovery after disturbance. For example, heterogeneneous forests include a variety of structural elements that support a range of different light and soil conditions, which can provide regeneration sites for species with varying regeneration requirements (Dale et al. 2001). A structurally heterogeneous stand will also have saplings and understory trees that may be available to fill gaps after disturbance.

The second dimension of resilience is complexity at the multi-patch or landscape scale. Complexity is the dimension of resilience that relates to the discipline of landscape ecology. Complexity is similar to heterogeneity in that it includes aspects of diversity, but complexity operates at a larger spatial scale than heterogeneity. Complexity includes landscape-level species diversity (i.e., gamma diversity) and structural diversity. The four key components of forest structural complexity have been defined as live-tree size distribution, vertical foliage distribution, horizontal pattern, and coarse woody debris (Spies 1998). Additionally, complexity includes the diversity of trophic interactions, food web topology, and landscape-scale dynamics of trees, such as dispersal and recruitment. Landscape-scale homogenization has been shown to lead to impaired ecosystem function in a wide range of ecosystems and often this loss of complexity results in feedbacks that make the homogenized state resilient to restoration (Lindenmayer et al. 2011).

Complexity is often linked to resistance to disturbance in similar ways to heterogeneity, but at a landscape scale. Gamma diversity is often considered to be an indicator of resistance to disturbance due to the increase in functional diversity that accompanies an increase in species richness, though this relationship is often complex (Ives and Carpenter 2007, Tilman 1996, Tilman et al. 1996). To describe the relationship between resistance and complexity, ecologists often reference the fact that the variance of an aggregate variable (e.g., community biomass) is lower than the variance of the components (e.g., the biomass of individual species; Doak et al. 1998, Tilman et al. 1998, Tilman 1999). This concept is modeled after a principle from economics demonstrating that diverse portfolios are more stable, and thus is termed the "portfolio effect" (Tilman 1999). There is also a scale-dependent effect of complexity on resistance, where diversity within and between scales leads to greater resistance to disturbance due to overlapping functions of redundant species (Peterson et al. 1998). From a management perspective, maintaining landscape-scale complexities which may prevent or slow the spread of disturbances such as disease or fire will be important for increasing resistance.

The influence of complexity on recovery after disturbance has been less studied than the influence of complexity on resistance; however, landscape-scale complexity also contributes to recovery in important ways. The role of complexity in the recovery of forests after disturbance is strongly tied to the dimension of reserves. One pathway in which complexity mitigates recovery from disturbance is via the presence of seed sources distributed across the landscape. Complexity in species composition implies that seed source trees will be distributed throughout the landscape rather than concentrated in a single area. This is particularly important for trees with seeds that are primarily wind-dispersed, because these seeds are typically not dispersed further than 50 m from their source trees (Nathan and Muller-Landau 2000). Additionally, landscape-scale complexity promotes habitat for a greater diversity of animal species relative to less complex forests and seed dispersal by animals may be even more influential than wind dispersal, even for trees with seeds adapted for wind dispersal (Vander Wall 2008). Finally, structural complexity may contribute to recovery from disturbance due to the distribution of saplings and understory trees. The ingrowth of established saplings and understory trees after disturbance may prevent a shift to a non-forested landscape. For example, in mixed-conifer forests of the Sierra Nevada shrubs can often outcompete regenerating tree seedlings after high-severity fires (Collins and Roller 2013, Coppoletta et al. 2016).

The third dimension of resilience is the quality of individuals and populations. Quality is associated with the discipline of population biology. In the application to forest management, we are typically referring to individuals and populations of tree species, as these are the dominant organisms in forested landscapes (Ellison et al. 2005). Individual quality refers to the vigor, growth increment, and fecundity of individual trees, while population quality refers to the size and rate of growth of the population. Quality encompasses aspects of the concept of forest health, and both are terms which may refer to individual trees or to the broader forest ecosystem (DellaSala et al. 1995, Woodall et al. 2011). While forest health may be defined by cultural or economic indices rather than scientific metrics (Woodall et al. 2011, Sulak and Huntsinger 2012), quality is specifically tied to individual and aggregated measures of tree physiology, demography, and productivity.

Quality is important for resistance to disturbance because individuals with decreased vigor are more likely to face injury or mortality as a result of disturbance (Franklin et al. 1987, Das et al. 2007). Additionally, low quality can leave trees vulnerable to multiple interacting disturbances where healthy individuals would be better able to resist these effects (Paine et al. 1998, Johnstone et al. 2016). For example, in California, drought effects lower resistance to beetle infestation (Jones et al. 2004, Millar et al. 2007b) and increase mortality in high-severity fires (Westerling and Swetnam 2003).

Quality is important for recovery mostly in the sense that it is related to the ability of forests to regrow after a disturbance. High quality individuals that resist mortality during a disturbance event will contribute to the recovery of forest biomass directly through their own growth. High quality individuals also contribute to recovery indirectly through propagule dispersal, an important dynamic needed for recovery after disturbance (Nathan and Muller-Landau 2000). Fecundity is positively related to tree growth (Green and Johnson 1994) and thus high quality individuals are generally likely to contribute more propagules for regeneration after disturbance.

The fourth dimension of resilience is comprised of the reserves of carbon, nutrients, fungal symbionts, and propagules stored within the ecosystem. Propagule reserves may be stored in the soil seed bank or the tree seed bank. I also consider the understory seedling and sapling bank to be a reserve of individuals that would be available for regeneration in the event of gap openings. Reserves are associated with the discipline of ecosystem ecology and this dimension addresses belowground-aboveground interactions and interactions of the biotic community with abiotic resources. Reserves of soil nutrients, carbon, and water help to maintain soil biota and forest fauna, which increases the strength of trophic interactions and overall forest biodiversity. Reserves also maintain individual and population quality trees. A decrease in the availability of reserves may also result in a shift in the species richness and evenness of forested systems mediated by species-specific responses to a shift in a particular reserve. For example, decades of acidic deposition in the northeastern US resulted in the depletion of base cation nutrients from soils. As a consequence, species with high requirements of calcium (Ca), such as *Acer saccharum* (sugar maple) and *Picea rubens* (red spruce), showed declines in growth and recruitment as a result (Driscoll et al. 2001, Eagar and Adams 1992).

The resistance to disturbance that reserves promote is mediated by the dimension of quality. Reserves of soil carbon and nutrients contribute to the maintenance of high quality individuals and populations, which are less prone to mortality when faced with disturbance.

In general, reserves are much more strongly tied to recovery after disturbance than to resistance. Reserves provide many of the resources needed for establishment and rapid growth post-disturbance. An adequate supply of propagules, seedlings, and saplings promotes regeneration after disturbances open available sites for regeneration. Adequate soil pools of nutrients are essential for regeneration, regrowth, and wound healing after disturbance. Reserves of fungal symbionts in the soil promote recovery after disturbance by serving as partners for regenerating tree seedlings.

General approach to evaluating resilience of a forested system

For a particular site, the resilience framework can be applied to assess changes in resilience over time, to help develop a monitoring protocol to address current and projected threats to resilience, and to measure the baseline resilience metrics when implementing monitoring protocols. The relevant dimensions of resistance and recovery are likely to differ from one site to another, even in similar forest types, due to differences in target state, scale, disturbance regime, and landscape characteristics. The influence of site-specific disturbance agents, management jurisdictions, and management priorities necessitate evaluating resilience on a case-by-case basis. The steps involved in evaluating resilience at a site include:

1. Identifying key *disturbances* (natural and anthropogenic) common to the site, disturbances predicted to change in frequency or duration in the future, and potential compounding disturbances.

2. Identifying the *target state*, including ecological, economic, aesthetic, or recreational criteria and potential management constraints or considerations.

3. Identifying the dimensions of *resistance* relevant to the heterogeneity, complexity, quality, and reserves of the individual system.

4. Elements that *promote* resistance and metrics to measure them

5. Elements that *weaken* resistance and metrics to measure them
6. Potential management actions that can *promote* resistance
7. Identifying dimensions of *recovery* (rate and extent) relevant to the heterogeneity, complexity, quality, and reserves of the individual system.
8. Elements that *promote* recovery and metrics to measure them
9. Elements that *weaken* recovery and metrics to measure them
10. Potential management actions that can *promote* recovery
11. Prioritize management actions that promote identified elements promoting resistance and recovery.

MEASURING RESISTANCE AND RECOVERY: A REVIEW

While there have been calls to incorporate estimates of forest resilience in research and management plans (NPS 2010, USDA 2012), it is not always clear how resilience metrics should be quantified. To assess the current state of resilience quantification, I reviewed papers that measured forest resilience or aspects of forest resilience in order to compile a comprehensive list of metrics and analyses that have been used previously to estimate resilience (Table 1). I conducted the review by searching the terms "resilience" and "forest" on the Google Scholar search engine. The resulting papers were sorted by relevance within the Google Scholar search engine and the title and abstract of the first 5000 results were scanned. After approximately 3500 entries there were very few relevant results, indicating that I had identified all or very nearly all of the papers relevant to this review. I included all papers that described original research addressing measures of terrestrial forest resilience, including boreal, temperate, and tropical forests; papers addressing kelp forests were not included. I also included meta-analyses if these studies used quantitative metrics to measure resilience. I did not include review papers or papers that described management practices to improve resilience without also providing metrics and analyses to measure the impacts of these proposed management practices. I also did not include studies that addressed issues related to resilience (eg. forest health, vigor, and vulnerability) but did not explicitly state that the goal of the study was to measure forest resilience. I included all studies that addressed forest resilience generally, but I did not include studies that addressed the resilience of a single component of the forest ecosystem. Examples of studies I rejected for this criterion included analyses of the resilience of an individual tree species in a forest matrix, the resilience of forest soil microbiota, and the resilience of forest avifauna. I found 37 studies that met the inclusion criteria, ranging in publication date from 1988-2015.

I was interested in assessing which components of resilience (resistance and/or recovery) were addressed in these studies, as well as which dimensions (heterogeneity, complexity, quality, and/or reserves) were quantified in these studies. I was also interested in documenting the metrics used to measure resilience and the analytical tools used to evaluate resilience. For each of the 37 studies that met the inclusion criteria, I recorded the component(s) of resilience addressed, the dimension(s) of resilience addressed, the metrics used to measure resilience, and the analyses used to evaluate the resilience metrics (Table 1). Heterogeneity and complexity were differentiated using a plot size cut off, where the dimension was defined as heterogeneity for studies that used plots <1 ha and complexity for studies that used plots or study areas ≥ 1 ha. While this strict empirical definition of heterogeneity vs. complexity does not exactly correspond to the ecological definition used for the resilience framework, it seemed reasonable to assume that studies with replicated plots ≥ 1 ha would encompass more than one community type and this fit the ecological definition of complexity.

I found that a majority of the papers assessed resilience by measuring only recovery after disturbance (20 papers, 54%). Twelve papers (32%) measured both resistance and recovery. Five papers (14%) assessed resilience by measuring only resistance to disturbance. Most papers (27 papers, 73%) measured the dimension of heterogeneity in order to quantify resilience, either measuring heterogeneity alone (11 papers) or in combination with another dimension (18 papers). Complexity was measured in 12 papers (32%) and reserves and quality were each measured to define resilience in nine papers (24%). Two studies measured three dimensions: heterogeneity, quality, and reserves. No studies included all four dimensions of resilience as defined by this resilience framework.

Methods for quantifying and analyzing the four dimensions of resilience ranged from quite simple to complex; however, I found that most measurements and analyses used to quantify resilience relied on basic ecological techniques (Table 1). Heterogeneity was typically assessed by estimating species richness, diversity, and abundance. The methods used to analyze these datasets were also common to ecology and included diversity indices such as the Shannon diversity and evenness indices, null hypothesis tests such as *t*-tests, analysis of variance tests (ANOVA), linear regressions, and ordination methods such as principal component analysis, detrended canonical correspondence analysis, and non-metric multidimensional scaling. Note that while diversity indices are in themselves a type of measure of richness, I consider them as analyses for this review because they are derived from the more basic field measurement of species counts per area. More complex non-linear models were also used in some studies of heterogeneity, but in general, the analyses used to measure heterogeneity were straightforward. Measures of complexity included many of the same measures as heterogeneity, such as species richness and species percent cover. Studies of complexity also used paleoecological records and remotely sensed data. Methods used to analyze complexity were frequently similar to those used for heterogeneity (eg. ANOVA and linear regression), and more complex modeling methods were used to assess the larger datasets and less traditional data structures required to measure landscape-scale complexity. Quality was typically assessed by comparing individual growth rates and ecosystem productivity over time or between experimental treatments. The analytical methods used to quantify changes in quality were also basic to ecology and included linear regression models and ANOVA to assess change over time and treatment effects. Reserves were typically quantified by measuring soil nutrient concentrations (typically Ca, nitrogen (N), phosphorus (P), carbon (C), magnesium (Mg), and potassium (K)) or by the density of seeds and seedlings. Like quality, analyses focused on basic estimates of change over time or treatment effects. Reserves were most frequently measured in studies of recovery after disturbance.

Overall, the results of this review indicate that resilience can be measured using familiar metrics and statistical analyses. Studies of resilience can effectively make use of these methods for quantification and analysis, and the most compelling studies will address both components of resilience (resistance to and recovery from disturbance) and all four dimensions of resilience.

RESILIENCE FRAMEWORK APPLIED

Case study examples

To explore the application of the proposed resilience framework and metrics for quantifying resilience, I selected three temperate forests in the continental US to serve as case studies: eastern hemlock forests of the mid-Atlantic and northeastern US, northern hardwood forests of the Northeastern US, and mixed-conifer forests of the Sierra Nevada in California. By necessity, potential case studies were limited to well-studied forests. However, these three forests span a range of biophysical settings and community dynamics. They also encompass different management jurisdictions, including private ownership, federal management under the US Forest Service, and federal management under the National Park Service. The variation in ecologies and management among the cases will demonstrate the versatility of the framework. For each case study, I outline the site description, the key disturbances, the target state, and management considerations based on site and scale. These are outlined in the mode that would be required when designing a research or monitoring plan to address resistance and recovery within the proposed resilience framework. In two cases, multiple sites are included for the forest type in order to highlight differences in target state or management implications based on management jurisdiction or site scale.

Each case study is also supplemented with a brief example of an application of one or more metrics that can be used to measure resistance and/or recovery of the four resilience dimensions at that site. These examples are not meant to be an exhaustive exploration of the resilience dimensions of each forest type. Instead, they illustrate common ecological analyses that can be applied in the context of the resilience framework for each forest type and their associated key disturbances. The examples were chosen to illustrate methods ranging from quite basic and ubiquitous (species and structural diversity and evenness indices) to relatively advanced (population-level vulnerability indices). These examples briefly illustrate ecological and management-related considerations related to measured resilience metrics.

Case Study #1: Eastern hemlock forest

Site description

The eastern hemlock systems that I consider in these case studies are located at two sites: the Delaware Water Gap National Recreation Area (DEWA) and the Harvard Forest. DEWA is a 27,800 ha park located along the Delaware River in western NJ and eastern PA administrated by the National Park Service. The primary management focus of this National Recreation Area is the preservation of scenic, scientific, and historic resources for recreational use by the public (Delaware Water Gap General Management Plan 1987). Forests cover approximately 80% of the DEWA and are dominated by *Quercus rubra* (red oak), *Acer saccharum* (sugar maple), *Quercus prinus* (chestnut oak), *Acer rubrum* (red maple), *Betula lenta* (black birch), *Betula alleghaniensis* (yellow birch), *Tsuga canadensis* (eastern hemlock), and *Pinus strobus* (eastern white pine; Eschtruth et al. 2006).

The Harvard Forest is a 1,500 ha forest located in north-central Massachusetts privately owned by Harvard University. The primary management focus of the Harvard Forest is for use as a center for research and education in forest biology and conservation, with recreation and forest management activities used to support the primary goals (O'Keefe et al. 2008). The dominant tree species at the Harvard Forest are red oak, red maple, black birch, white pine, and eastern hemlock, with eastern hemlocks dominating areas with poorly drained soils (Ellison et al. 2010).

Eastern hemlocks grow in dense stands that exert strong control over microsite habitat by limiting light conditions and depositing acidic litter. These conditions exclude establishment of other understory and tree species, resulting in monodominant stands that are typically found in nutrient-poor, moist soils in spatially patchy stream ravines and north-facing slopes (Rogers 1978, Eschtruth et al. 2006). The monodominance of hemlock stands makes them unique to the oak-maple hardwood matrix that composes the majority of the forest cover where eastern hemlock stands are found.

Key disturbances

Hemlock decline represents the most significant threat to the eastern hemlock system and is main the focus of management efforts in these forests. Hemlock decline is due to the introduction of the hemlock woolly adelgid, a nonnative insect that feeds on the hemlock's parenchyma cells, causing bud mortality and needle loss (Young et al. 1995). Hemlock stands show no resistance to the adelgid and there is no effective biological control agent. Ultimately, the adelgid causes complete mortality of infested stands in 4-6 years (McClure 1991). At the DEWA, eastern hemlock was historically abundant across the landscape of the park, but currently composes only 5% of forest cover (Myers and Irish 1981, Young et al. 2002). It has been estimated that 80% of the park's hemlocks were dead or at varying stages of decline (Evans 2004).

Target state

The target state for the eastern hemlock system is a hardwood forest matrix that includes monodominant patches of eastern hemlock. The DEWA management plan has designated hemlock stands as "outstanding natural features" having "high intrinsic or unique values" (NPS 1987), underscoring the important role of hemlock stands for maintaining biodiversity and contributing to the recreational experience of the park (Evans 2004). However, due to a lack of genetic resistance to the pest, a lack of effective biological control agents, and the prohibitive cost of chemical control, guidelines for managing effects of the hemlock woolly adelgid are focused primarily on monitoring and minimizing impacts rather than eliminating threats (Evans 2004, Ward et al. 2004).

Management considerations

The eastern hemlock forests of the DEWA and the Harvard Forest have considerable differences due to their spatial scale and their management jurisdiction. However, despite this contrast, in both cases there are few management options for restoring and maintaining the target state of monodominant hemlock stands throughout the landscape. The combination of the lack of resistance of eastern hemlocks to the hemlock woolly adelgid and the lack of any effective insecticide treatments or biological controls for managing adelgid infestation has left few effective management options for mitigating hemlock decline at these sites (Ward et al. 2004). Some trees may be treated with a chemical control; however this strategy is cost-prohibitive at large scales (Ward et al. 2004). At the DEWA, management of the hemlock woolly adelgid has primarily focused on monitoring the effects of the invasive pest due to the nature of allowable intervention on National Park Service land (Evans 2004). In contrast, at Harvard Forest, long-term monitoring has been paired with experimental tests of the effect of hemlock removal on ecosystem processes (Ellison et al. 2010).

At both sites, evidence suggests that ultimately there are few processes in place that will be able to promote the persistence of monodominant hemlock stands throughout the landscape. As a result, this may be a case where the target state must be adjusted to reflect the constraints of the available management options. At these sites, a primary management question in the face of the lack of eastern hemlock resistance to the hemlock woolly adelgid is whether another species can successfully replace of eastern hemlocks. Overstory species such as white pine, red oak, red maple, and black birch may all be available to replace eastern hemlock (Orwig et al. 2012). However, as eastern hemlock stands decline and light availability increases, these stands may also be replaced by shrubs and herbaceous species, including non-native species (Eschtruth and Battles 2011, Orwig et al. 2012). If the target state is adjusted from specifically preserving monodominant hemlock stands, a reasonable alternative might be to focus management goals on maintaining a forested landscape. This may preserve some of the ecological and aesthetic functions of the eastern hemlock forest, such as nutrient cycling capacity and wildlife habitat in order to promote resistance to future disturbances (Block et al. 2012, Ward et al. 2004). Management approaches can be adjusted to promote processes that allow for the establishment of hardwood and pine species in former eastern hemlock stands and may include planting of desired species mixes that best achieve management objectives at individual sites (Ward et al. 2004).

Measuring structural heterogeneity in the eastern hemlock forest

Structural heterogeneity may be an indicator of stand growth and also promotes forest biodiversity across trophic scales (Staudhammer and LeMay 2001, Önal 1997), which can play a role in conferring resistance to disturbance and recovery after disturbance. A structurally heterogeneous forest has an increased ability to recover from disturbance due to the presence of both large, mature trees that are able to provide seeds for recovery (Green and Johnson 1994) and small-diameter understory trees that are able to fill canopy gaps that result from disturbance-induced mortality. Quantifying stand structure distribution is a simple method for assessing potential for resistance to disturbance or recovery after disturbance. Structural heterogeneity of forests is defined by an uneven stand structure.

The Gini coefficient is a measure of the diversity of a distribution and is defined by values ranging from 0-1, where a smaller Gini coefficient implies a more homogeneous population (Gini 1912, Ceriani and Verme 2012). The Gini coefficient can be used to assess the diversity of tree sizes in a forest stand and has been employed specifically to measure forest resilience

(Lafond et al. 2014). Using the mean absolute difference between individuals, the Gini coefficient is defined as:

$$Gini = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}|x_i - x_j|}{2n\sum_{i=1}^{n} x_i} \qquad \text{(Eq. 1)}$$

where n is the number of trees, x_i is the diameter of tree i, and x_j is the diameter of tree j (Handcock and Morris 1999). Alternately, the Gini coefficient can be defined by diameter classes rather than individuals (Duduman 2011, Cordonier and Kunstler 2015). While the original application of the Gini coefficient was to assess income inequality in economic studies, it can also be used to quantify size distribution of forest stands and can serve as a unit of measurement for structural heterogeneity (Duduman 2011). The Gini coefficient has been found to be an efficient method of comparing stand structure relative to other structural diversity indices (Lexerod and Eid 2006, Duduman 2011, Lafond et al. 2014). A lower Gini coefficient will indicate a decreased structural heterogeneity. Because the Gini index is unitless, comparisons of increases or decreases can be used to assess relative changes in structural diversity.

I estimated the Gini coefficient for forest inventory plots at the Harvard Forest, where stand conditions have been monitored to assess the effects of the introduction of the hemlock woolly adelgid to the region (Orwig and Foster 1998; data available at http://harvardforest.fas.harvard.edu/harvard-forest-data-archive). I utilized tree size data (DBH; diameter at breast height (1.37m)) from five plots where the DBH of tagged trees was measured during inventories which took place from 1999-2004. The prevalence of hemlock woolly adelgid increased over this time period in the central Massachusetts region in which Harvard Forest is located (Orwig et al. 2012). The plots included one 120m x 60m plot (designated HF31; n ranging from 451-636 trees) and four 30m x 30m plots (designated PH2, PH7, SC10, and SC09; n ranging from 74-130 trees). Plot HF31 was measured in 1990, 1999, 2009, and 2014. Plots PH2, PH7, SC10, and SC09 were measured in 1995, 2002, and 2012. Each of the five plots was treated as an independent sample.

The Gini coefficient declined in all plots from 1990-2014 (Figure 2). Though the overall decreases in the Gini coefficient are small, the pattern was consistent in all plots over the entire monitored period. This indicates a pattern of homogenization of stand structure in this forest as a result of a decrease in the number of small diameter trees due to mortality induced by the hemlock woolly adelgid. In this case, the effect of this homogenization of stand structure is likely to result in the decreased ability of the forest to recovery after disturbances compounded with the hemlock woolly adelgid, such as the effect of storms, pollution, increased temperatures, or other invasive pests and pathogens.

Case Study #2: Northern hardwood forest

Site description

The northern hardwood forest I consider in these case studies are located at the Hubbard Brook Experimental Forest (HBEF), a 3,160 ha reserve in the White Mountain National Forest of north-central New Hampshire. Elevation at the HBEF ranges from 222 to 1,015 m. Overstory vegetation at the HBEF is dominated by northern hardwood trees; 80% of the forest basal area is composed of sugar maple, *Betula alleghaniensis* (yellow birch), and *Fagus grandifolia* (American beech). At higher elevations, vegetation also includes red spruce, *Abies balsamea* (balsam fir), and *Betula papyrifera* (paper birch; Battles et al. 2014). The HBEF is owned and managed by the USDA Forest Service Northern Research Station. Management goals of the WMNF include using current scientific knowledge to sustain healthy forests and restore forest systems with a focus on ecosystem viability, providing recreation opportunities to the public, and supporting local economies by maintaining a natural-appearing landscape (USDA 2005). The HBEF is home to long-term ecological research and monitoring, including continuous hydrological measurements since the 1950s and large-scale watershed manipulation experiments.

Key disturbances

Much of the long-term research at the HBEF has been directed towards addressing the impacts of acidic deposition on the northern hardwood forest ecosystem and the trajectory of recovery from these impacts since the passage of the Clean Air Act in 1970 (Likens et al. 1996). Acidic deposition directly impacts the health of sensitive tree species such as red spruce and sugar maple (Eagar and Adams 1992, Long et al. 2009, Schaberg et al. 2011). Overall forest health and productivity are also impacted by acidic deposition due to the leaching of soil nutrient cations such as Ca and magnesium (Mg), which results in decreased soil fertility (Battles et al. 2014). At HBEF, a decrease in soil Ca as a result of acidification was found to be driving decreases in biomass accumulation (Battles et al. 2014). Productivity is an important aspect of the dimension of individual and population quality, which confers the ability to both resist and recover from disturbances. Additionally, differential species responses to acidic deposition have the potential to result in decreased species heterogeneity, an important dimension of forest resistance to disturbance. For these reasons, focusing on impacts of acidic deposition is one of the main management objectives for the northern hardwood forest system.

Target state

The target state for the northern hardwood system is a mature second-growth post-agricultural forest which maintains a landscape-level patch mosaic of successional stages. The mosaic of successional stages contributes to structural and compositional heterogeneity and complexity. The primary management objectives for maintaining and enhancing this target state are to ensure persistence of species that are sensitive to disturbances such as acid deposition and invasive pests and pathogens.

Management considerations

In the northern hardwood forest, the major management focus is on maintaining nutrient reserves to support the system's ability to resist and recover from disturbance. A watershed-scale Ca amendment experiment at the HBEF demonstrated that a deficit of a soil nutrient was responsible for lower individual and population-level quality (Hawley et al. 2006, Haggett et al. 2007, Battles et al. 2014), thus limiting resistance to disturbance and recovery from disturbance. Liming is a frequently used method for addressing acidification effects in forests and is likely to be a feasible management option for stand-scale and watershed-scale restoration (Smallidge et al. 1993). The results of the Ca amendment study indicate that individual quality of sensitive species such as sugar maple and red spruce were most compromised by the soil Ca deficit. Other than large-scale Ca amendments, management activities may focus on other methods of promoting the quality of these sensitive species. At the HBEF, the combination of the landscape-scale management unit and the designation as an experimental forest has allowed for other such large-scale experimental manipulations that explore the impacts of disturbances such as clear cut harvesting, ice storms, warming winter temperatures, and decreases in snowpack predicted under future climate scenarios on forest resilience.

Measuring compositional heterogeneity in the northern hardwood forest

Species diversity is a simple metric that can be used to assess differences in compositional heterogeneity over space or time, and is frequently used in forestry as a quantitative measure of diversity (Staudhammer and LeMay 2001). In the northern hardwood forest, there is concern that species richness and evenness are declining due to species-specific shifts in relative dominance that in turn contribute to the noted decline in forest-wide biomass (van Doorn et al. 2011). This would have the effect of decreasing heterogeneity.

To measure change in heterogeneity, I relied on data collected at HBEF. Specifically, I obtained measures of trees >10 cm diameter at breast height (DBH) collected in 29 25 x 25 m monitoring plots in a northern hardwood forest (data available http://www.hubbardbrook.org/data/dataset_search.php). I used two indices, the Shannon diversity index (*H'*) and the Shannon evenness index (*E*) to measure changes in diversity and evenness at the local scale over a 20-year period at the HBRF, in order to assess changes in heterogeneity in the system over time. The Shannon index is commonly used to quantify diversity and is useful because it accounts for both species richness and abundance. The evenness index describes the equitability of species presence (Oksanen 2017). The indices are defined as:

$$H' = -\sum_{i-1}^{S} p_i \ln p_i \qquad \text{Shannon diversity} \qquad \text{(Eq. 2)}$$

$$E = H'/\log(S) \qquad \text{Shannon evenness} \qquad \text{(Eq. 3)}$$

where p_i is the proportion of species i, and S is the number of species (Shannon and Weaver 1949, Oksanen 2017).

Over a 20-year period (1992-2012), species diversity and evenness declined in a majority of plots over this period (Figure 3). The Shannon diversity index (*H'*) was greater in 1992 than 2012 in 25 of 29 plots (86%), indicating a decrease in diversity over time. The evenness index (*E*) was greater in 1992 than 2012 in 26 of 29 plots (90%), indicating a decrease in evenness due to a decline of rarer species and an increase in more abundance species. At HBRF, these dynamics were largely due to an increase in American beech, at the expense of less dominant species including sugar maple, white birch, and yellow birch. This shift is a result of the influence of beech bark disease, which has caused high mortality of large beech followed by infilling of small stems (Forrester et al. 2003), and is an important management concern in these forests. A loss of species richness and evenness would move the northern hardwood forest away from the target state of a late-successional, compositionally heterogeneous forest.

Case Study #3: Sierra Nevada mixed-conifer forest

Site description

The Sierra Nevada mixed-conifer forests that I consider in these case studies are located at two sites: Blodgett Forest Research Station (BRFS) and the Last Chance study area. Both BRFS and Last Chance are located in CA on the western slope of the Sierra Nevada with vegetation dominated by the mixed-conifer forest type (York et al. 2003, Collins et al. 2011b). Vegetation is dominated by *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), *Calocedrus decurrens* (incense-cedar), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (ponderosa pine), and *Quercus kelloggii* (California black oak). BFRS is located on the Georgetown Divide in the northern Sierra Nevada, adjacent to the Eldorado National Forest. The 1,728 ha forest ranges from 1,200-1,500 m in elevation. BFRS is privately owned by the University of California, Berkeley and the primary objectives of the forest are research and instruction in forestry and related wildland resources (Blodgett Management Plan 2012). The Last Chance study area is located within the Tahoe National Forest in the northern Sierra Nevada. The 4,300 ha study area ranges from 800-2,200 m in elevation (Collins et al. 2011b). In accordance with the USDA Forest Service mission, the resource management objectives of the Tahoe National Forest include managing resources in a sustainable manner, providing goods and services for the public and protecting forest ecosystems (USDA 1990).

Key disturbances

Key disturbance agents affecting Sierra Nevada mixed-conifer forests include increased prevalence of high-severity fire, prolonged drought and increased temperatures resulting from anthropogenic climate change, and increased prevalence and severity of pests and pathogens (Perry et al. 2011, Hessburg et al. 2016, van Mantgem and Stephenson 2007). Historically, Sierran mixed-conifer forests were considered to be resilient to ecological disturbances due to their heterogeneous structure and composition (Fulé 2008, North et al. 2009). A century of fire suppression coupled with timber harvesting and livestock grazing has resulted in forest conditions that have been estimated to diverge greatly from pre-settlement forest structure and composition (Collins et al. 2011a, Dolanc et al. 2014). The differential responses by species to fire exclusion and climate change appear to be contributing to a species reordering of fire-adapted California forests, where shade-tolerant fir species are exhibiting greater growth and recruitment than pine species in densifying forests (Levine et al. 2016). In addition, the interaction between pest and pathogen outbreaks and increased prevalence and severity of drought conditions is also contributing to the decline of pine species (Hicke et al. 2016). Loss of species heterogeneity at multiple scales can impact the system's ability to reorganize after disturbance (Peterson et al. 1998). This reordering potentially represents the first phase of a transition from a well-mixed, resilient forest to a less diverse community that is more susceptible to catastrophic loss due to fire, pests, or pathogens. Management activities to address this potential reordering are focused on restoring complex landscapes that maintain native species assemblages and characteristic processes (North et al. 2009).

Target state

The target state considered for Sierra Nevada mixed-conifer forests is typically a stand structure, composition, and density that generally resemble the characteristics of this forest type prior to European settlement of the Sierra Nevada region. Several lines of evidence, including historical inventories, public land survey records, and reconstructions using fire scars, stumps, and tree-rings (Stephens et al. 2015, Taylor 2004) suggest that frequent, low-severity fires maintained a structurally and compositionally heterogeneous landscape with dominance shared among several conifer species (van Mantgem et al. 2011). BFRS considers this target state but due to its role as a research and teaching site, also considers additional target states at the stand scale. BFRS contains stand-scale compartments that have undergone a range of experimental forest management treatments. The target state at BFRS is to maintain certain stands at densities and compositions similar to pre-settlement conditions, as well as maintaining control reserve stands and stands that achieve resilience via a range of age classes, high within-stand species diversity, and high between-stand structural diversity.

Management considerations

In Sierra Nevada mixed-conifer forests, frequent, low-severity fires historically maintained canopy gaps resulting from small patches of mortality due to fire, disease, and insects. However, these gaps are largely absent in contemporary, fire-suppressed forests (Larson and Churchill 2012). These uniformly dense forests are at an increased risk of severe fires because of altered fuel characteristics (Stephens and Moghaddas 2005, Taylor et al. 2014). Conferring resistance by reintroducing complexity at the landscape scale is a top management priority in order to achieve and maintain the system's target state and to increase resistance catastrophic fire or pest outbreaks (North et al. 2009).

The BFRS and Last Chance sites differ considerably due to their spatial scale as well as their management jurisdiction. As described above, the difference in management jurisdiction impacts not only the target state, but also the available methods to implement the target state. In the Sierra Nevada mixed-conifer forest, intensive fuel reduction treatments are necessary for increasing resistance to high-severity wildfires and for restoring densified forests to low-density target state (Stevens et al. 2014). Large-scale fuel manipulation treatments are an important management tool to achieve lower tree densities and gap openings for regeneration. It has been possible to implement these treatments at the Last Chance site using strategically placed area treatments (SPLATs) to increase complexity of forest structure and reduce fuel loads (Fry et al. 2015). SPLATs are discrete treatment units arrayed throughout a landscape with the goal of increasing resistance to disturbance by slowing fire spread and moderating fire risks (Finney 2001). Implementing SPLATs requires a site large enough to include a full fireshed, as well as a management jurisdiction that allows for large-scale fuel reduction treatments. Management approaches at the BFRS are undertaken at the stand scale rather than the landscape scale, due to the arrangement of compartments used for research and timber harvesting. Gap-based approaches have been implemented at the BFRS to promote resistance to disturbance by reducing fuel loads and to promote recovery by providing suitable sites for pine regeneration (York et al. 2012). This method is effective when management treatments are conducted at the stand scale.

Measuring quality in the mixed-conifer forest

Quality confers resistance in mixed-conifer forests because individuals with decreased fitness are more likely to be vulnerable to injury or mortality when they experience disturbances. Patterns in tree growth increment can be used to assess quality as it relates to the probability of mortality of individual trees (Das et al. 2007). A vulnerability index (VI) is a metric ranging from 0-1 that can be used as a relative quantitative measure of stand forest quality (Das et al. 2007). VIs predict species-specific mortality rates based on survival probabilities estimated from measurements of tree growth over decadal timescales (Collins et al. 2014). VIs are quantified via a four-step process. First, tree ring data are used to develop models of individual tree survival probabilities. Next, these models are applied to individual trees from a separate sample. Plot data is then used to simulate a population with matching structure and composition for simulation and an average mortality rate is calculated for the simulated populations, allowing for estimates of mean mortality rates with bounding errors (Collins et al. 2014). VIs can then be used to target management activities towards improving conditions for at—risk species.

In Sierra Nevada mixed-conifer forests, pine vulnerability is of primary concern because pines have decreased in dominance relative to white fir, Douglas-fir, and incense-cedar due to the presence of pests and pathogens, a lack of regeneration sites in densified forests, and a history of logging. At BRFS, a study was conducted to assess the vulnerability of pines relative to white fir, Douglas-fir, and incense-cedar (Collins et al. 2014). VIs were developed for the five major overstory tree species present at the site: white fir, incense-cedar, sugar pine, ponderosa pine, and Douglas-fir. For this study, tree survival probability models were derived from cores collected from live and dead trees at the Last Chance site, located approximately 22 km north of BFRS. Mortality probability models were estimated, following methods described in Das et al. (2007). Population-level VIs were calculated using data from 20-31 cores per species that had been collected at BFRS and 1000 simulations were run to estimate the mean and 95% confidence intervals (CI) of the indices for the five species and for all species. Non-overlapping 95% CIs were used as a conservative metric for identifying significant differences in the vulnerability indices of the five species.

Ponderosa pine appeared to be highly vulnerable to mortality, with a mean VI value of 0.11 (Figure 4). The VI of ponderosa pine ranged from 300%-2100% higher than the VI of the other four species. White fir, incense-cedar, and sugar pine had similar mean VIs which ranged from 0.019-0.025, with the white fir VI being significantly higher than the VI of incense-cedar and sugar pine. Douglas-fir had a very small mean VI, 0.0048, relative to the other species. The results of this study imply that ponderosa pine is potentially at high risk of mortality events, particularly relative to the other four overstory species. This finding, in combination with evidence that pines are showing lower growth and recruitment than firs at a similar northern Sierra Nevada mixed conifer site (Levine et al. 2016) indicates that promoting the quality of pine populations should be a management priority. Increased pine quality would promote resistance by maintaining a population that is less vulnerable to injury and mortality when faced with drought-induced beetle outbreaks and fire. In order to achieve the target state of a structurally and compositionally heterogeneous landscape with dominance shared among conifer species, pine persistence on the landscape is an important management goal.

Quality confers recovery in mixed-conifer forests by promoting growth and productivity after disturbance. Additionally, decreased fitness may negatively affect fecundity, leading to a decrease in propagules available for regeneration. The vulnerability study investigated the effects of prescribed fire on the VI of the five major tree species, simulating recovery of individual quality after disturbance. A difference in vulnerability between control and burned plots indicates a difference in that species' ability to recover from low-severity fire. Prescribed fire is often used as a management strategy to restore mixed-conifer forests to their target state by reducing fuel loads and decreasing density of small-diameter trees. However, fire is also a potential disturbance agent in these systems and may adversely impact the quality of trees that remain after prescribed burning. At BRFS, the VI for the overall community ("All species"; Figure 4) was not significantly different between burned and control plots, and most species showed little difference in VI between the burned and control plots. The exception to this was the VI of Douglas-fir, which was 360% higher in burned plots than control plots, which indicates that Douglas-fir mortality may be a concern when managing for recovery trajectories after prescribed fire (Collins et al. 2014). The results of this study also serve as a reminder that while recovery typically refers to the recovery of the forest towards the target state, individual species are likely to have unique responses to disturbance and recovery will be influenced by differences in species recovery trajectories.

SUMMARY

Measuring resilience is a challenge for forest ecologists and managers. The novel resilience framework (Figure 1) outlined above uses our best knowledge of theoretical resilience principles combined with management considerations to outline a comprehensive method for quantifying resilience. By grounding this framework in the disciplines of community ecology, landscape ecology, population biology, and ecosystem ecology, I provide a flexible framework for incorporating resilience theory into management. In applying this approach to three temperate forest systems that encompass a range of target states, disturbance regimes, and management entities, I found this framework provided an adaptable system for identifying the target state, the primary management priorities, and potential metrics to address the dimensions of resilience.

Quantification of forest resilience requires a framework that addresses both resistance to disturbance and recovery from disturbance, as well as an understanding of the dimensions of resilience. A majority of the studies I reviewed defined and measured resilience as the speed and extent of recovery from disturbance. Although this type of study lends itself more easily to the structure of ecological studies (eg. testing treatment effects of disturbance or measuring change over time since disturbance in a chronosequence), a comprehensive quantification of resilience will include both measurements that assess the system's ability to resist disturbance and its ability to recover its structure and function post-disturbance.

To be comprehensive, a quantitative resilience assessment must extend beyond simply measuring heterogeneity at the local scale. As shown in the review of forest resilience papers, studies often explicitly measure heterogeneity. The innovation of the new framework is to extend the scope of resilience measurements beyond heterogeneity and to be inclusive of integral ecosystem processes such as demography, competition, and nutrient cycling. The review of forest resilience papers demonstrated that holistic measurements of forest resilience are not out of reach. These studies typically relied on measurements and analyses that are foundational to ecology and familiar to most ecologists and practitioners. The challenge is not in inventing complex methods for measuring and analyzing resilience, but in identifying a comprehensive group of metrics that addresses the scope of the four resilience dimensions identified in the resilience framework described above. Measurements must be chosen purposefully with and understanding of the resilience metrics they will represent. This process will ensure a holistic understanding of forest resilience, rather than addressing individual resilience metrics and assuming that they represent total forest resilience.

One important limitation of the approach outlined in this resilience framework is that there is no single estimate defining “forest resilience” that can be derived to quantitatively compare resilience across sites or times. Instead, resilience measurements will be most effective when assessed on a relative and system-specific basis. This type of framework lends itself more to estimating changes in resistance and recovery over time, rather than quantifying a resilience estimate at a single point in time. Thus, I recommend that that this framework be used to inform the planning of monitoring protocols for repeat measures through time in order to best quantify the relative estimates of resistance and recovery.

Since I have now established the flexibility of this framework to be used in a range of forest types and management jurisdictions, future work will apply this framework in a single site, where resistance and recovery measurements can be used as baseline resilience estimates for future monitoring. In the literature review, I identified two studies that included metrics for heterogeneity, quality, and reserves (Herbert 1999, Drobyshev et al. 2013). However, no studies included all four resilience dimensions. Complexity was likely left out because it requires measuring metrics at large spatial scales. However, there are several long-term ecological study sites in the US and internationally where ecological measurements have been collected over spatial scales required for measuring complexity. These sites would be good candidates for the first applications of the full framework at a single site.

Measures of resistance and recovery must be evaluated in a holistic context. Particular attention should be paid in cases where promoting feedbacks of one resilience dimension may negatively impact a different resilience dimension. This framework can be considered to be a roadmap for assessing the current status of resilience, determining metrics for measuring change in resilience over time, outlining strategies for determining major likely disturbances, and evaluating feedbacks to focus management on to increase resistance and resilience.

TABLES

Table 1. A comprehensive list of methods used to measure the resilience of terrestrial forest ecosystems. Only studies that explicitly state the goal of measuring resilience were included. Heterogeneity and complexity were differentiated using a plot size cut off, where the dimension was defined as heterogeneity for studies that used plots <1 ha and complexity for studies that used plots or study areas ≥ 1 ha.

Abbreviations: DBH = diameter at breast height (1.37 m); C = carbon; N = nitrogen; P = phosphorous; K = potassium; Ca = calcium; Mg = magnesium; Fe = iron; Al = aluminum; ANOVA = analysis of variance; MANOVA = multivariate analysis of variance.

‡ Indicates that this dimension was measured indirectly rather than directly.

Dimension(s) of Resilience	**Resistance and/or Recovery?**	**Measured Variable**	**Analysis Type**	**Study Location**	**Reference**
Heterogeneity, Reserves	Resistance and recovery	% cover of forest understory species	Detrended correspondence analysis	Oregon, USA	Halpern 1988
Heterogeneity,	Resistance	Shrub percent cover; herb percent cover; seedling percent cover	Detrended correspondence analysis	Quebec, Canada	de Grandpré and Bergeron 1997
Heterogeneity, Quality, Reserves	Resistance and recovery	Aboveground net primary productivity; litterfall; DBH increment, fine live root biomass; litter decomposition rate; leaf area index; reduced leaf mass per unit leaf area; foliar P; foliar N	Linear regression for disturbance effects, ANOVA	Hawaii, USA	Herbert 1999

Heterogeneity, Reserves	Recovery	Species richness; plant density; seed count; soil moisture; soil pH; total N, P, K, Ca, and Mg	ANOVA; Mann Whitney *U*-test; Wilcoxon sign rank test	Savaii, Samoa	Elmqvist et al. 2001
Complexity	Recovery	Normalized difference vegetation index	ANOVA; multiple regression	Catalonia, Spain	Díaz-Dalgado et al. 2002
Heterogeneity, Reserves	Recovery	Slope; aspect; heat index; soil depth (minimum, median, and maximum); convexity; canopy density index; soil moisture; loss on ignition; pH; soil species composition	Local nonmetric multidimensional scaling; Bray-Curtis compositional dissimilarity index; detrended correspondence analysis ordination; ANOVA and MANOVA; Wilcoxon signed rank tests	Høgkollen, Norway	Rydgren et al. 2004
Heterogeneity, Quality‡	Recovery	Aboveground biomass; stand density; size distribution; number of stems per plant; growth form composition	Logistic regression	Amazonas, Brazil	Gehring et al. 2005
Heterogeneity, Reserves	Resistance	Soil total C, N, and P; Bray-extractable P; tree DBH; tree species richness; mortality rate; recruitment rate; turnover rate	Fisher's alpha; Shannon diversity index; linear regression; contingency tables; Mann Whitney *U*-test; t-test	Eastern Jamaica	Tanner and Bellingham 2006
Complexity	Recovery	Forest cover	Linear regression	Quebec, Canada	Girard et al. 2008

Heterogeneity	Resistance and recovery	Species richness; species percent cover; modal height of conifers, shrubs, dwarf wood plants, herbs, and mosses; vegetation volume production	Stepwise linear and non-linear least squares regression; Bray-Curtis distance measure; second-order jack-knife diversity estimator	British Columbia, Canada	Hamilton and Haeussler 2008
Heterogeneity, Quality	Recovery	Annual DBH increment; species richness; stem density; stem basal area; stem mortality and recruitment rates; litterfall	Chi square, linear regression, non-statistical comparisons	Grande-Terre, Guadeloupe	Imbert and Portecop 2008
Heterogeneity	Recovery	Species density; species richness; density; canopy height; total crown area; total crown area	Nonlinear models; nonmetric multidimensional scaling ordination; % recovery of mature forest mean values; Shannon diversity; Shannon evenness	Oaxaca, Mexico	Lebrija-Trejos et al. 2008
Heterogeneity	Recovery	Species richness; tree height; crown diameter; wood density; sprouting ratio; recruitment rate; mortality rate	SEIB-DGVM plant structure and function model	Okinawa Island, Japan	Fujii et al. 2009
Complexity	Recovery	Species richness; species density; Chao-Jaccard abundance-based estimator; seedling abundance; sapling abundance	Non-metric multidimensional scaling; Horn similarity index	Heredia Province, Costa Rica	Norden et al. 2009
Heterogeneity	Recovery	Species richness	ANOVA	Middle Urals, Russia	Trubina 2009

Heterogeneity	Resistance and recovery	Compositional turnover; return time to former diversity and composition after disturbance	Principal component analysis, redundancy analysis, detrended canonical correspondence analysis	Southeastern Madagascar	Virah-Sawmy et al. 2009
Heterogeneity, Quality	Recovery	Wood net primary production; leaf area index; stem mortality	Linear regression; Simpson's diversity index	Michigan, USA	Gough et al. 2010
Heterogeneity, Quality	Resistance and recovery	Number of dead trees; number of seedlings; species richness; topographic variation; distance from seed source; tree growth	Mixed model; general additive model; non-linear least squares model; multi-level model	Yukon, Canada	Johnstone et al. 2010
Heterogeneity	Recovery	Annual biomass increment	T-test	Santa Cruz, Bolivia; Manaus, Brazil; Rondonia, Brazil; Zona Bragantina, Brazil; S. Yucatan, Mexico; W. Kalimantan, Indonesia	Lawrence et al. 2010
Heterogeneity, Complexity	Resistance and recovery	Parent rock material; slope; vegetation cover; vegetation type; volume of woody vegetation; % woody vegetation cover; pine density; % legume cover; % legume	Multi-criteria evaluation method	Attica Peninsula, Greece	Arianoutsou et al. 2011

		contribution; % annual colonizers; fire interval			
Heterogeneity, Complexity	Resistance and recovery	Vascular plant structure; species composition; forest-floor invertebrate faunal composition; bird nesting success; ship rat abundance; livestock presence/absence	System dynamics model	Waikato, New Zealand	Dodd et al. 2011
Complexity	Resistance	Tree cover, annual precipitation	Latent class analysis to measure multimodality, logistic regression	Tropical and subtropical zones of Africa, Australia, and South America	Hirota et al. 2011
Complexity, Reserves	Recovery	Tree density; basal area; leaf area index; canopy height; stand age; soil respiration; soil temperature; soil moisture; fine root nonstructural carbohydrate concentration; fine-root turnover; fine-root biomass; forest floor N availability; soil N gas flux; soil N leaching; foliar C and N; net ecosystem CO_2 exchange;	Principal component analysis; ANOVA and t-test	Michigan, USA	Nave et al. 2011

		gross primary productivity; ecosystem respiration			
Complexity	Resistance and recovery	Forest:grassland ratio; oxygen isotope ratio; magnetic susceptibility; macro-charcoal influx	Pearson correlation coefficient; redundancy analysis; quantile regression; Mann Whitney *U*-test	Kerala, India	Bhagwat et al. 2012
Heterogeneity	Resistance and recovery	Forb percent cover; rock percent cover; graminoid percent cover; coarse woody debris percent cover; bare ground percent; moss percent cover; aspen density	Random forests and regression trees	Colorado, USA	Buma and Wessman 2012
Complexity	Resistance and recovery	Probability of fire spread	Comparison of distributions, Moran's I spatial autocorrelogram	NA; modeled forest	Kitzberger et al. 2012
Heterogeneity, Reserves	Recovery	Sapling density; seedling presence/absence; economic valuations (cost of planting, cost savings accrued by seed disperser activities)	Generalized linear model	Norrtheastern Spain	Puerta-Piñero et al. 2012
Quality	Recovery	Aboveground net primary productivity, biomass accumulation	T-test	New Hampshire, USA	Reiners et al. 2012

Heterogeneity	Recovery	Species richness; seedling density; coarse woody debris; standing dead tree DBH and height; total C	Bootstrap model comparison	Colorado, USA	Buma and Wessman 2013
Heterogeneity, Complexity	Resistance and recovery	Species composition; diameter distribution; stand density index; amount and size of openings	Global and local point pattern analyses	Washington, USA	Churchill et al. 2013
Heterogeneity, Quality, Reserves	Resistance and recovery	Tree DBH; species richness; tree density; tree growth; soil organic layer depth; soil organic layer volumetric content; mineral soil texture; soil organic layer moisture; mineral soil particle size analysis; mineral soil total C, N, P, and S; pH	Mann-Whitney *U*-test; redundancy analysis; Chi square test	Quebec and Ontario, Canada	Drobyshev et al. 2013
Heterogeneity, Quality	Recovery	Species by diameter class; tree status; seedling regeneration	Kolmogorov-Smirnov test	Montana, USA	Larson et al. 2013
Complexity, Quality	Recovery	DBH; tree height; aboveground biomass; belowground biomass; relative mortality rate; relative recruitment rate; growth rate; age composition; sap flow	Least squares regression	Guangdong, China	Zhou et al. 2013

Heterogeneity	Resistance	Basal area; proportion of large trees (DBH > 42.5 cm); density of small trees (DBH ranging from 7.5 - 17.5 cm); % spruce	Gini index, Clark-Evans aggregation index	Modeled European spruce-fir forest	Lafond et al. 2014
Complexity	Recovery	Total ecosystem C storage; rumple index of canopy complexity; presence of late seral species; spatiotemporal patterning of early-, mixed-, and late-seral patches; species richness	Kruskal-Wallis test; Wilcoxon signed-rank sum test; ANOVA; MANOVA; squared Mahalanobis distance; Simpson diversity index	Oregon, USA	Seidl et al. 2014
Heterogeneity	Resistance	Bare ground cover; woody debris cover; litter (needle) cover; litter depth, and soil moisture; percent cover for each ground cover class, including basal vegetation, litter, bare ground, rocks, and woody debris (>2 cm diameter); litter depth to the O horizon; soil moisture; tree seedling abundance; shrub seedling abundance; shrub cover %; basal area; tree density; crown base height; canopy closure; tree cover	Non-metric multidimensional scaling	California, USA	Stevens et al. 2014

Heterogeneity, Reserves	Recovery	Species richness; DBH; tree height; canopy openness; species richness; soil organic C; total N; available P, K, Ca, Mg, Fe, pH and Al; percentage of the different particle sizes (sand, silt, and clay); linear distance to old-growth forest	Principal component analysis; Shannon and inverse-Shannon species richness; mixed-effects models with maximum-likelihood parameter estimation; Pearson correlation	Central Amazon, Brazil	Jakovac et al. 2015

FIGURES

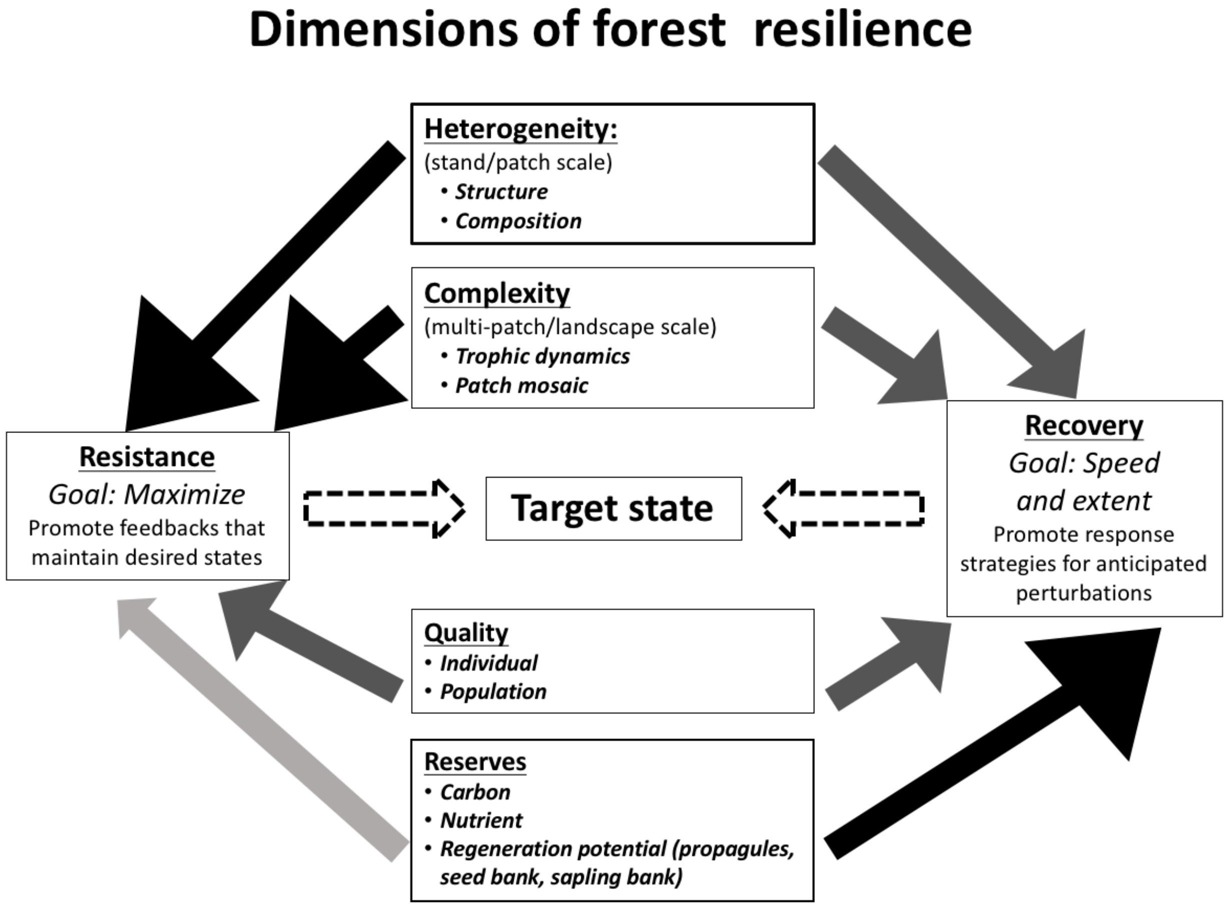

Figure 1. Dimensions of forest resilience. The strength of the relationship between the dimension (heterogeneity, complexity, quality, or reserves) and the component of resilience (resistance or recovery) is signified by color and size of arrows. Larger, darker arrows signify a strong relationship. Smaller, lighter arrows signify a weaker relationship. Resistance and recovery maintain the target state in the face of disturbance.

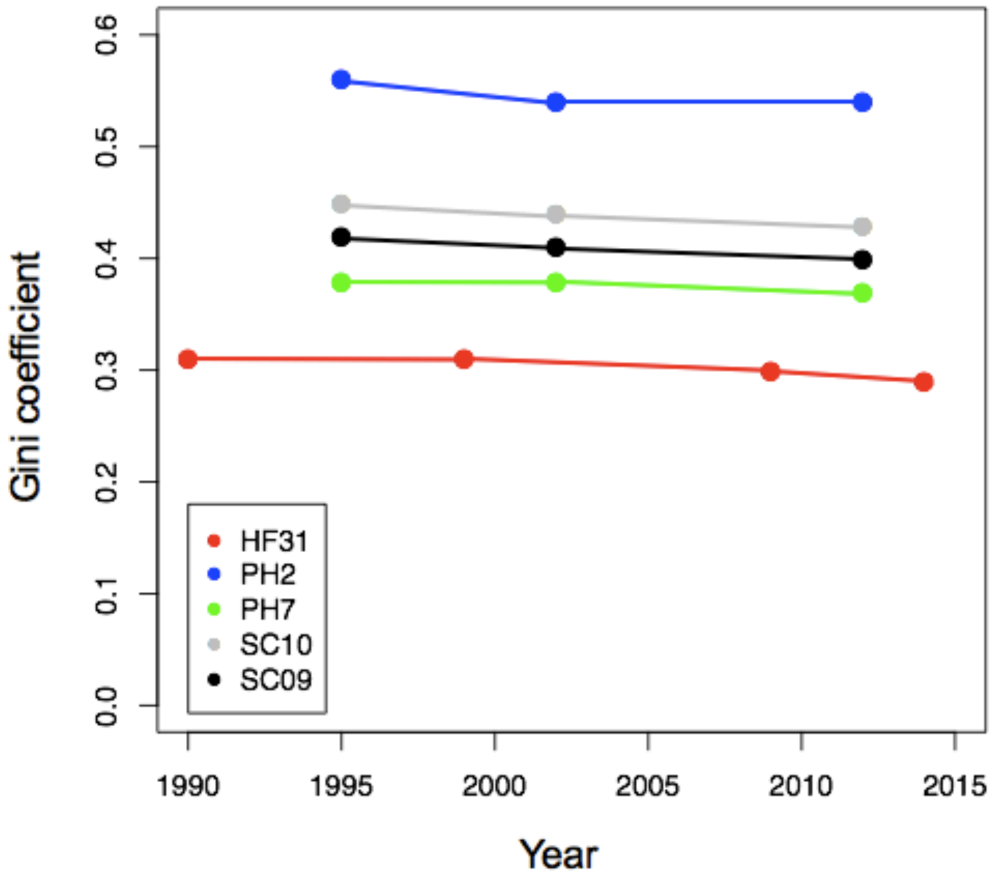

Figure 2. Gini coefficient for one 120m x 60m stand (HF31; *n* ranging from 451-636 trees) and four 30m x 30m plots (PH2, PH7, SC10, and SC09; *n* ranging from 74-130 trees) at the Harvard Forest, 1990-2014.

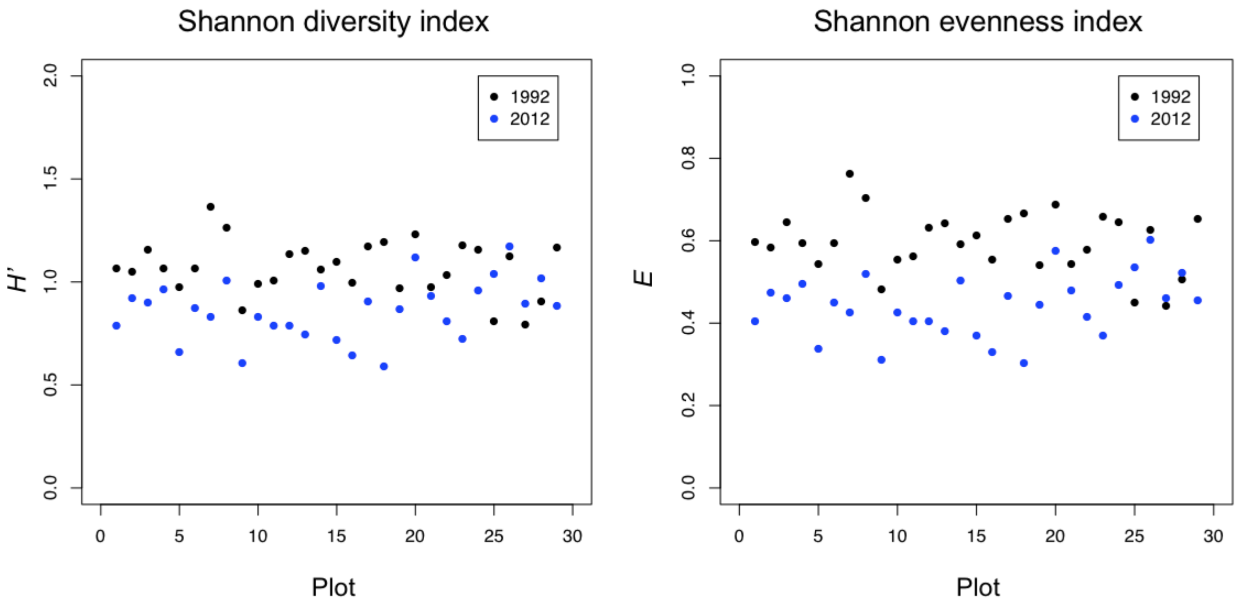

Figure 3. Change over a 20-year period in Shannon diversity index and Shannon evenness index for 29 northern hardwood plots at the Hubbard Brook Research Forest.

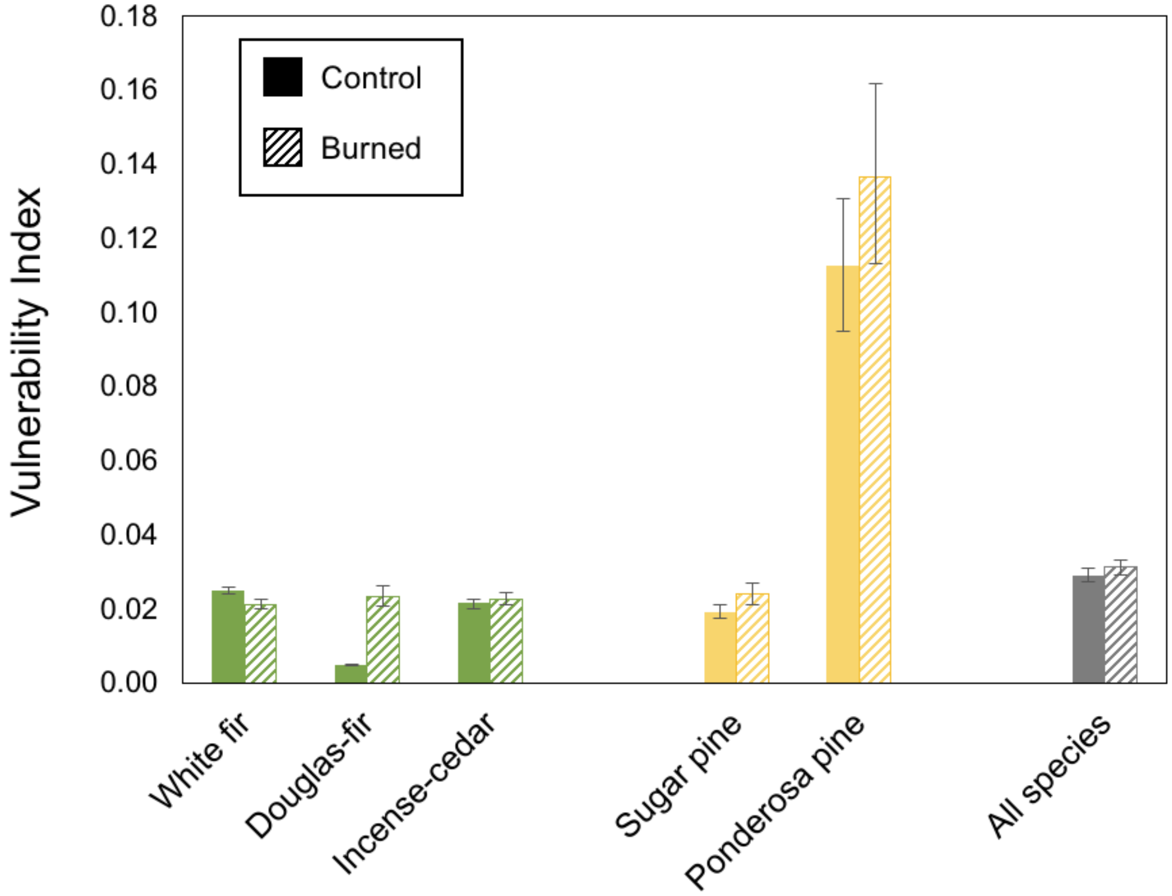

Figure 4. Vulnerability indices for five mixed conifer species and for all species at the Blodgett Forest Research Station. Error bars represent the 95% confidence interval of 1000 simulations. Figure redrawn from Collins et al. 2014.

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