

The Evolution of Long-Term Data for Forestry: Large Temperate Research Plots in an Era of Global Change

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The Evolution of Long-term Data for Forestry: Large Temperate Research Plots in an Era of Global Change

Abstract

When forest ecosystems develop over millennia, trees live five centuries, and mortality unfolds over decades, direct repeated observation (hereafter, longitudinal data) may be the only way to understand the fate of forests. Longitudinal data sets contribute greatly to our understanding, complementing experimental, modeling, and chronosequence approaches. Changing climate is changing forests, perhaps most rapidly through altered mortality regimes, and the elusive nature of integrated mechanistic understanding requires refinements and extensions to historically productive protocols. Changing climate reduces the inferential power of chronosequence techniques and changes model parameterization, and only some of the different factors contributing to tree mortality are expected to respond to climate variability and change. Because annual tree mortality rates are 5% to 1% for trees ≥ 1 cm dbh in young and old forests (respectively), detecting changes in mortality rates requires tracking thousands of trees, particularly to examine rare sub-populations of concern (e.g., large-diameter trees). And because mortality factors can be spatially aggregated and density-dependent, the causes and rates of tree mortality depend on the relationships between forest spatial structure and the direct and indirect effects of climate. Permanent plots with a combination of larger size, higher spatial precision, and greater sampling frequency will be required to further elucidate spatially explicit aspects of western forest demography. The combination of the longitudinal protocols developed by the Smithsonian Center for Tropical Forest Science, originally for studying tropical forest species diversity, and those developed by the US Geological Survey for annual tree mortality assessment together uniquely allow robust investigation of climate-mediated change in temperate forests.

Keywords: Smithsonian ForestGEO, tree mortality, tree neighborhood, Wind River Forest Dynamics Plot, Yosemite Forest Dynamics Plot

Introduction

How forest science can contribute to forest management is perhaps the most important issue facing scientists and land managers at the outset of the 21st century. Changing climate, changing disturbance regimes, and changing human use of forest ecosystems has created considerable uncertainty for scientists and managers alike. As research questions in forest ecology evolve, field and analytic methods change, often requiring more intensive data collection. Much of the earlier work in forest research was focused on growth and yield or determining communities throughout a landscape or vegetation type. For this work, smaller plots distributed throughout the study area and measured either once (e.g., Whittaker 1960) or on five-year intervals (e.g., Bechtold and Patterson 2005) were (and are) effective. But small

plot size makes some questions intractable when the study organisms are large or rare, and annual measurements are required to understand some mortality and recruitment phenomena. Here I suggest that emerging scientific questions relevant to the forests of western North America in the early 21st century can be uniquely and productively studied with large, spatially explicit monitoring plots that are sampled annually.

Large forest plots have two principal objectives: to extend what we already know about how forests work, and to help monitor the nuances of how anthropogenic change will affect forests. The rapidly changing conditions associated with anthropogenic change may require many different approaches to characterize forest community change, and large plots provide a contiguous area that allows for direct examination of heterogeneous landscapes. One goal of large plot research is to characterize and model the active ecological processes. To the extent that these processes are

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spatially autocorrelated (i.e., pathogens, insects, fire, and windthrow), large plots provide the context to analyze how these processes are changing forests and to determine how annual climate variation affects each agent of forest change. Determining the annual changes in forests due to annual climate variability (including antecedent effects [e.g., Littell et al. 2009]) will allow better prediction of the effects of climate change on forests. The differing spatial distances between individuals combined with their diversity is such that many individual trees are required to parameterize all the processes. Furthermore, rapid change makes parameterization even more difficult, as previously immaterial processes become important (i.e., water limitations in a previously energy limited forest).

Tree mortality processes are both heterogeneous and contagious, and we seek to document their differential effects on the full diversity of species and diameter classes. Mortality is perhaps the demographic process leading to most rapid forest change, particularly mortality of the largest trees. To study mortality, the scale of the sample needs to exceed the scale of the process manifold times so that there is sufficient ability to detect processes and necessary replication to confirm it. And, for purposes of attribution, particularly to changing climate, a fine-grained time dimension is required. Annual measurements can help pinpoint the causes of tree death. To the extent that our goals are to study how climate is causing mortality rates to change, measuring at least annually will become increasingly necessary.

Direct repeated observation (hereafter, longitudinal data) in forestry and forest ecology involves permanently marked plots that are periodically revisited to confirm the status and condition of tagged individual stems. The necessity and value of long-term studies in ecology has long been recognized (e.g., Franklin 1989), as exemplified by the lessons learned from the oldest set of permanent forest monitoring plots in the Pacific Northwest. The T. T. Munger plots, established in the early 20th century (Munger 1946) have provided repeated measurements of forest change in closed canopy forests using smaller, replicated

plots. Using these plots, Munger (1946) was able to develop the theory of Douglas-fir forest succession, and the data were used by Acker et al. (1998) to develop general models of the rates of biomass accumulation. Recently, the temporal depth of these plots was used to reexamine theories of forest succession in light of a century of data (Harmon and Pabst 2015). The concepts of forest succession and biomass accumulation were perhaps some of the most foundational 20th century accomplishments in forest ecology theory, and they were all tested with small permanent plots. The history of forest ecology has shown the importance of permanent plots to understanding the diversity of processes and how the different combinations of climate, disturbance, and biotic relationships act over long periods of time to produce diverse assemblages.

In this age of rapid ecosystem change (i.e., Anderson-Teixeira et al. 2014), identifying the processes which are changing will be important to coping with the long-term consequences of ecosystem alteration. In western forests, an increase in mortality rates in recent decades has already been confirmed (van Mantgem et al. 2009). However, van Mantgem et al. (2009) used data from different permanent plots sampled at different, asynchronous intervals (usually five years). The lack of annual mortality data across the western United States hindered van Mantgem et al. (2009) from clearly associating increasing mortality rate with potential environmental drivers, such as drought. In contrast, van Mantgem and Stephenson (2007), using a network of 1 ha permanent plots, linked annual observations of mortality due to stress or biotic causes to increasing indices of drought. These results highlight the need for annual measurements to better determine the mechanisms of climate-mediated mortality and suggested that future research will require larger numbers of study individuals than is usual in current studies of forest ecology to have a sufficient number of mortality events to examine. Other work into spatial patterns of old-growth forest demography (e.g., Das et al. 2011) has found that 1 ha plots may not have sufficient extent to examine some patterns of competitive mortality.

Extending the Scope of Permanent Plots

First, I identify understudied aspects of forest science, then I recapitulate the use of longitudinal data in forestry and forest ecology, then I describe the essential characteristics required for large forest dynamics plots to address grand-challenges in the 21st century. The mechanisms of rapid forest change, especially in western North America, are some of the most important unknowns facing forest scientists and how to adapt to those changes is one of the most important challenges facing managers. Our understanding of demographic processes in complex forest systems requires quantifying their context. Understanding demographic changes may require multifaceted information about the affected individuals, their sizes and species, their local neighborhoods, and the spatial aspects of dispersal and tree enemies. Whether the result of fire, insects, pathogens, or more gradual changes in demographic rates, rapid forest change is inexorably tied to tree mortality. Investigation of changing mortality rates requires data on the causes, patterns, scales, and consequences of tree death (Levin 1992, Lutz and Halpern 2006). Because tree decline and mortality is a complex process, often without a single acute cause (e.g., Manion 1981, Mueller-Dombois 1987, Waring 1987, Larson and Franklin 2010), tracking individuals over the period of their decline and examining them as soon as possible after death is necessary to determine the contributing and proximate causes of mortality as well as the consequent changes in ecosystem composition, structure, and function. The more standard forest remeasurements cycle (or even a 2–3 year cycle) cannot precisely identify the year of tree death, nor can it accurately identify the principal causes of mortality. Without knowing both the time and causes of tree death, we can still analyze the resulting compositional change in the forest composition and structure, but not why the change has occurred.

Many existing research programs involve longitudinal sampling, for example, the USDA Forest Inventory and Analysis program (Bechtold and Patterson 2005), the Long-Term Ecological Research network (Franklin et al. 1990), and the

permanent sample plot network in the Pacific Northwest (Acker et al. 1998a). These networks typically sample small plots (~ 0.1 ha) on an infrequent (~ 5 years) basis. Much of what we have learned about forests, especially in the Pacific Northwest, has been based on results from these 0.1 ha to 1.0 ha plots (e.g., Acker et al. 1998a). Plots of this scale are appropriate for a wide range of community interactions (Levin 1992) but by no means all processes (Table 1). Larger permanent plots provide a statistically relevant number of mortalities each year (i.e., ~ 500 mortalities; Table 1), providing a unique perspectives on forest change not possible with studies incorporating smaller numbers of individuals.

The USGS Sierra Nevada network (e.g., Stephenson and van Mantgem 2005) and recent monitoring networks in the National Park Service (e.g., Acker et al. 2015) incorporate medium sized plots (~ 1 ha) that are sampled annually. This spatial extent permits quantifying tree neighborhood effects at small inter-tree distances (e.g., Das et al. 2011). Annual sampling frequency allows tree death to be correlated with annual variation in climate or episodic outbreaks of insects. However, the individual plot sample size requires pooling diameter class and species data (e.g., van Mantgem et al. 2009). Covering large areas (> 10 ha), the plots associated with the Smithsonian Center for Tropical Forest Science Global Earth Observatory (ForestGEO; Anderson-Teixeira et al. 2014), as well as notable individual plots (e.g., in Georgia [Platt et al. 1988] and Germany [Holzwarth et al. 2013]), permit sampling rare species and sub-populations (e.g., Condit et al. 2000) as well as dispersal distances, modes of mortality, spatial autocorrelation, and infrequent events (e.g., Condit et al. 1994; 2012). The key advantage of these large plots is having a sampling scheme tailored to the spatial scale of the variance in the response. Thus, when trees influence each other (through dispersal, competition, facilitation, or mortality) over larger distances, plots must be large enough to capture those effects. However, most large plots are sampled on a five-year frequency, so the causes of tree mortality may be obscured, although changes in demography can

TABLE 1. Example research questions appropriate to forest plots of various sizes and measurement frequencies. As most demographic processes depend at least partly on organism size, plot sizes are given in circular equivalents scaled to canopy height. The examples numbers for plot size, number of woody stems ≥ 1 cm (n), and mortalities are for productive forests of the Pacific Slope where canopy trees average 55 m. In these forests, woody stem density ≥ 1 cm dbh in early seral communities approximates 3,000 ha⁻¹ (mortality rate 5% year⁻¹), and woody stem density ≥ 1 cm dbh in mature and old-growth communities approximates 1,500 ha⁻¹ (mortality rate 1.25% year⁻¹). Shaded cells indicate phenomenon that are understudied in western forests. Large plots provide a statistically relevant number of tree mortalities every year (bold).

		Plot size		
		Small	Medium	Large
	Data volume	radius ~ 1/5 canopy height ~ 0.04 ha <i>n</i> ~ 60 1–3 mortalities yr ⁻¹	radius ~ canopy height ~ 1 ha <i>n</i> ~ 1,500 ~ 20 mortalities yr ⁻¹	radius ~ 5 × canopy height ~ 25 ha <i>n</i> ~ 37,500 ~ 500 mortalities yr⁻¹
Measurement Interval	Once	<ul style="list-style-type: none"> Species composition and diameter distribution, when as a network of plots 	<ul style="list-style-type: none"> Species composition Spatial pattern, limited ability to analyze sub-populations 	<ul style="list-style-type: none"> Spatial pattern of species and sub-populations Model parameterization of spatial patterns Remote sensing calibration
	Five years	<ul style="list-style-type: none"> Growth and yield Some causes of mortality 	<ul style="list-style-type: none"> Demographic rates (species pooled) Effect of neighborhood on mortality 	<ul style="list-style-type: none"> Demographic rates of species and sub-populations Spatial heterogeneity and autocorrelation
	Annually	<ul style="list-style-type: none"> Seedling dynamics Causes of mortality Climate correlations without ability to distinguish neighborhood effects 	<ul style="list-style-type: none"> Variance in demographic rates (species pooled) Neighborhood effects on demographic rates at limited intertree distances Climate correlations with mortality and recruitment 	<ul style="list-style-type: none"> Variance in mortality rates of sub-populations Model parameterization of demographic rates Neighborhood effects on competition and dispersal Delayed treefall effects Differentiating neighborhood effects from climate effects

still be examined to some degree with multiple measurements (e.g., Hubbell 2005).

Large spatial extent was first systematically combined with longitudinal studies at the Smithsonian research plot on Barro Colorado Island, Panama (BCI; Condit 1998, Hubbell et al. 1999, Hubbell 2005). Until recently, spatially-explicit research plots in temperate forests were mostly limited to 1 ha to 4 ha (e.g., North et al. 2002). Larger plots were thought to be primarily necessary to investigate species diversity in the tropics, and as species diversity is lower in temperate forests, a lesser area should be required to examine local species diversity. However, recent emphasis on climate change, invasive species, and sub-populations (e.g., large-diameter trees) suggest that larger (> 10 ha) plots may be useful in temperate forest research (Table 1). Sub-populations of

large-diameter trees are rare on the landscape, analogous to the rare species of tropical census plots. In forests of the Pacific Slope (west of the crest of the Cascade Range and the Sierra Nevada), the density of trees ≥ 100 cm dbh is 10 ha⁻¹ to 20 ha⁻¹. And when large trees are defined in a relative sense (i.e., trees larger than the 99th percentile in diameter), 1 ha monitoring plots do not include a sample large enough of those individuals for statistical analysis. With the pair correlation function, commonly used in spatial analysis (Wiegand and Moloney 2004), between 100 and 400 individuals constitute an appropriate population for analysis, implying a total forest sample size between 10,000 and 40,000 individuals to examine large-diameter tree patterns. Tree recruitment (into the ≥ 1 cm dbh class) and mortality are relatively rare events in forests with trees exceeding 500 yrs. With

mortality and recruitment rates in older forests of $\sim 1.5\%$ per year, a total forest sample size of $>10,000$ individuals is required to generate enough data to examine changes in recruitment and mortality rates. Furthermore, local neighborhoods vary tremendously in forests. Although competitive interactions and facilitation occur, they are probably limited to inter-tree distances less than 10 m (e.g., Das et al. 2011, Lutz et al. 2014a, but see Wang et al. 2011), the effects of tree-fall extend to approximately the height of the tallest trees. The large number of individuals in a Smithsonian-affiliated plot (generally $>20,000$; Anderson-Teixeira et al. 2014) allows examination of forest structure and forest structural change as well as spatially explicit aspects of tree demography.

General Characteristics of Forest Monitoring Plots

Forest research designs involving repeated measurements that attempt to examine the specific effects of tree neighborhoods and environmental variation have five general requirements: 1) sufficient spatial extent to include rare species or subpopulations of interest, 2) sufficiently broad size representation of individuals to detect ecosystem fluxes, 3) sufficient sampling frequency to isolate causal factors, 4) sufficient spatial accuracy to determine and model spatial correlations, and 5) logistics that are financially and organizationally

sustainable. Smaller plots with different sampling frequencies (e.g., more than once a year for seedlings and five years for growth and overall change) will still continue to play the major role in forest research. However, future work aimed at isolating the effects of spatial pattern and environmental dynamics will require all of these factors to be addressed simultaneously, and to a degree rarely attempted to date (Table 1).

Sufficient Spatial Extent

Longitudinal data needs to be taken at a spatial extent that captures a sufficient level of the variation in the ecological properties of the system (Whittaker 1960, Levin 1992). An example is treefall, which eventually affects every tree in the forest. In forests with 65 m emergent trees (those in the highest canopy positions), common on the Pacific Slope, an emergent tree growing in the middle of a 1 ha plot would fall partially outside the study area (Figure 1). The effects of treefall (e.g., crushing mortality, deformation, shading by debris) are often delayed, with neighboring trees declining or becoming more vigorous over time. Therefore, not only do measurements need to encompass the spatial extent of the process (in this case the area of the tree gap and the area crushed by the tree remains), but measurements need to be made multiple times (see Sufficient Sampling Frequency, below). When plots are sufficiently large (Table 1) or numerous then single measurements can

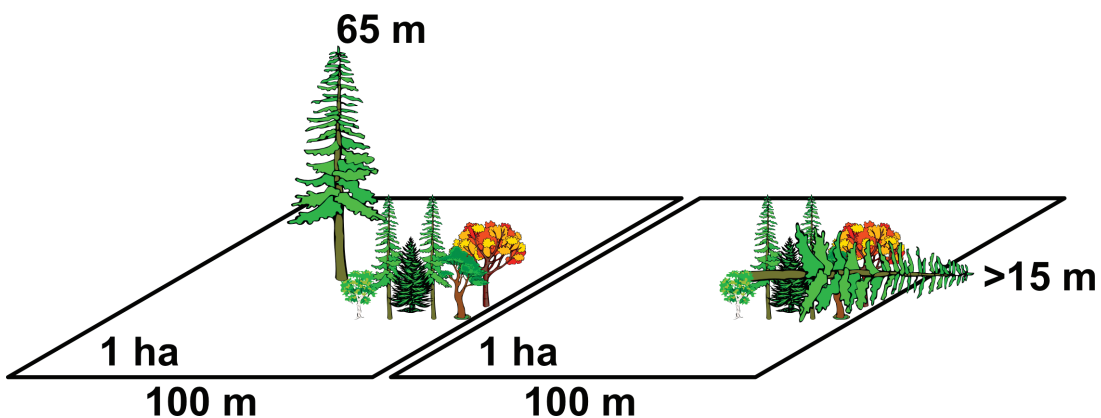


Figure 1. Illustration of the effect of a single tree falling in a 1 ha plot (100 m \times 100 m). A tree that was 65 m tall, even if exactly in the middle of the plot (left), would extend at least 15 m outside the plot boundary if it fell (right), precluding the examination of immediate and delayed crushing mortality.

determine spatial patterns (for large plots [e.g., Platt et al. 1988, Chen et al. 2004]) and distribution of species (for smaller plots [e.g., Whittaker 1960]), allowing inference of past disturbances, as well as modeling of canopy and understory conditions (North et al. 2004, Sprugel et al. 2009, Freund et al. 2014). However, sufficient *contiguous* extent allows the variation among tree neighborhoods to be considered. With large numbers of trees in a contiguous plot, even infrequent measurements (5 to 15 years) can demonstrate some mechanisms of change (e.g., Larson and Franklin 2006, Lutz et al. 2014a). Inter-tree relationships, to the extent that they determine tree spatial pattern, can be examined as far as one quarter of the minimum plot dimension (Wiegand and Moloney 2004).

Examining the community effects of environmental conditions on individual trees also requires considerable contiguous spatial extent. Droughtiness, or any manifestation of climate variability, is inherently a “supply side” phenomenon. Water, light and temperature are provided to a site relatively uniformly (with fine-scale differences based on variation in topography and soils). Increased environmental stress on individual trees is inherently a “demand side” phenomenon, and its relative impact is tied to the local tree neighborhood. If droughtiness increases in one year, most trees will experience increased stress (excepting

those accessing deep water reserves [e.g., Hubbert et al. 2001]), but not equally. If conditions become droughtier, potentially only the trees in local neighborhoods where water demand is very high (or soil water storage capacity is lower) may exhibit increased mortality (Figure 2). Trees growing in less dense local neighborhoods might not experience stress levels contributing to elevated mortality. Study areas with a diversity of local neighborhoods will help us understand more about how stressors affect individuals. Smaller plots (Table 1) cannot fulfill this goal, because they do not encompass a complete tree neighborhood (considering an 8–10 m interaction distance [Das et al. 2011, Tatsumi et al. 2013]) for any but the most central trees, and spatial analyses of these smaller plots are dominated by edge effects (Wiegand and Moloney 2004). Small plots may also be subject to biases due to small-scale environmental features (soil conditions) or past treefall events extending over the plot (Condit 1998, Hall et al. 1998, Clark and Clark 2000). If spatial heterogeneity within forests creates pockets of instability where trees experience elevated sensitivity to climate-induced mortality, understanding the variability in local spatial structure may be necessary to understand the effects of interannual climatic variation on tree mortality rates and causes. In addition to the effect of local neighborhood on water availabil-

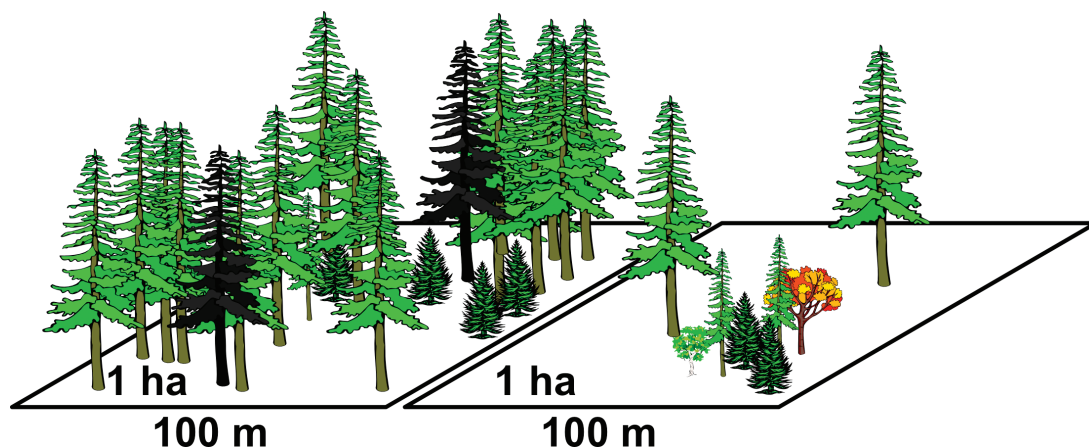


Figure 2. Illustration of the effect of droughtier conditions mediated by local tree neighborhood. In a crowded local neighborhood (left) high levels of water demand could contribute to higher rates of tree mortality (black trees, left) than would be the case in a less crowded local neighborhood (right). The spatial variation in most temperate forests requires a large spatial extent to develop statistically significant quantification of neighborhood effects.

ity, the distribution of light in temperate forests is complex throughout the day and the growing season (e.g., Sprugel et al. 2009), which influences forest regeneration (e.g., Taylor and Halpern 1991). Because the canopies of trees one tree height away can influence light availability, modeling these processes requires plots with radii larger than one tree height. Small plots are therefore likely to be inadequate for describing temporal changes in forest dynamics.

Sufficiently Broad Size Representation

The breadth of a sampling scheme includes the species representation and the size representation. Much forestry research has been conducted with lower diameter limits based on economically useful tree sizes, often 10 cm dbh (although many studies have used lower diameter limits, e.g., Chen et al. 2004, Knapp et al. 2013). However, where studies have investigated smaller diameter classes, it has been common to use a sub-sampling scheme for smaller diameter stems (e.g., Knapp et al. 2013), which limits the spatial statistics that may be applied. Any subsampling scheme introduces spatial discontinuities in the data set that preclude evaluating processes over contiguous intertree distances. Subsampling prevents analysis of relationships between smaller individuals and larger individuals that may be influencing the smaller ones from greater distances (e.g., Lutz et al. 2014a). Extending a sampling scheme to include more individuals requires a tradeoff between labor requirements and expected results. However, changes in populations are first apparent at smaller diameter classes, and at diameter classes < 10 cm dbh, tall shrubs become increasingly abundant in some forests. These shrubs can strongly influence tree communities (i.e., Lutz et al. 2014b), so small-diameter stem dynamics may be an important contributor to forest change. Inclusion of smaller stems may reveal processes such as density-dependent mortality and also type conversion between tree-dominated and shrub-dominated ecosystems. In old-growth Pacific Slope forests, changing the sampling protocol from trees ≥ 10 cm dbh to woody stems ≥ 1 cm dbh approximately doubles the number of stems in the data set (Lutz et al. 2012, 2013). This doubling of the number of stems changes

the perception of species diversity (plot level α -diversity and sub-plot β -diversity), rare species occurrence, and allows earlier identification of species colonizing the plot. A logical extension to the need to include younger woody individuals is seedling studies that are informed by extensive characterization of the forest canopy (Hille Ris Lambers et al. 2002, Comita and Hubbell 2009). Although determination of seedling mortality rates do not require large-permanent plots *per se* (e.g., Larson 2013), understanding seedling demography requires *a priori* understanding of the surrounding forest structure. Within the context of the surrounding forest, seedling studies can elucidate dispersal limitations, density dependent mortality, and Janzen-Connell type limitations.

Sufficient Sampling Frequency

Much forest research has concentrated on growth and yield, or long-term demographic trends, which do not require annual sampling (Acker et al. 1998b, Harmon and Pabst 2015, Munger 1946). However, mechanistic attribution of the correlations between demographic changes (i.e., mortality and recruitment) and climate-driven events such as climatic variation and climate-mediated mortality factors (e.g., fire or insects), requires at least annual measurements. And as climate in the West has considerable interannual variability, an annual sampling frequency is required to analyze how climate affects the mechanisms of forest change, arguably the most important set of questions in the coming decades. Changes in forest turnover rates (e.g., Stephenson and van Mantgem 2005) may be the first indication of forest change. Annual measurements of mortality allow correlations between climate and changes in demographic rates (van Mantgem and Stephenson 2007), and evaluation of interannual differences in mortality rates (Acker et al. 2015). Furthermore, some field observations must be conducted on at least an annual basis to avoid ambiguous data. For example, bark beetles (family Curculionidae, subfamily Scolytinae), an important disturbance agent in forests of western North America, both cause tree mortality and infest trees that have died from other causes. Although some species predominantly attack living trees (e.g., *Dendroctonus ponderosae* [Furniss and

Carolin 1977]), some attack both living and newly dead trees (e.g., *Dendroctonus pseudotsugae* and *Scolytus ventralis* [Furniss and Carolin 1977]). The difference between a post-mortality bark beetle infestation and a bark beetle-caused mortality can be readily determined early in the season following mortality, but the timing of the creation of the beetle galleries will be obscured after two years. Similarly, common pathogenic fungi such as *Armillaria* spp. are facultative necrotrophs (Baumgartner et al. 2010). They colonize living tissue, but continue to spread following the death of the host. With rates of spread from 0.7 to 1.3 m yr⁻¹ (Peet et al. 1996), an infection that is not severe enough to contribute materially to tree mortality could be misinterpreted as a factor associated with death if observed five years after tree death. The nature of disturbances in the forests of western North America requires annual sampling frequencies to reduce uncertainty in causes of mortality.

Sufficient Spatial Accuracy

Considerable forest research has used spatially non-explicit plots, but almost every ecological phenomenon exhibits spatial autocorrelation (i.e., bark beetles, pathogens, fire, and windthrow). The ground size of plots must reflect both the size of the organisms and the degree of spatial autocorrelation in the ecological processes. Complete inclusion of treefall gaps requires plot sizes with linear dimensions at least twice the height of the vegetation (Table 1). Usually relative accuracy at short inter-organismal distances is most important, while accurate mapping of large distances may have less ecological relevance. However, as modern remote sensing techniques such as LiDAR, small footprint satellite, and aerial data are increasingly used in forest research, establishing a precise correspondence between ground data and remotely sensed data is important. The ability to scale up from intensively studied model ecosystems to landscape and planetary scales requires ground plots that are both much larger than satellite footprint size (e.g., Réjou-Méchain et al. 2014) and where trees are precisely located to the datum (± 10 cm to ± 1 m). This level of spatial accuracy requires survey-grade Global Positioning Equipment and accurate, slope-corrected ground measurements of

distances within sampling plots. Some processes such as treefall (Figure 1) or cumulative effects of multi-year drought (Figure 2) may be defining processes for western forests, and these processes that play out over long periods of time need to be studied over large spatial extents in order to provide enough power to reveal statistically meaningful patterns. Larger data sets with accurate tree positions provide the ability to characterize spatial autocorrelation (e.g., Lutz et al. 2012; Figure 6), and those results can be applied to smaller study areas to potentially disentangle niche effects versus priority effects.

Practicality and Sustainability

The temporal reach of long-term research plots is inherently different than research funding cycles. However, data collection continuity is a requirement of longitudinal research. With a few exceptions (e.g., USDA Forest Service FIA and National Science Foundation LTER), funding is generally not available for monitoring, except when tied to specific short-term research questions. However, most forest measurement techniques can be easily taught to undergraduate students, and much work can be done with volunteers working in conjunction with experienced staff. Contributed labor, whether through volunteers or students, can increase the sustainability of the long-term observational research. There is also a question of sustaining research over decadal scales. If multiple investigators work together, there is more potential to defray long-term sampling costs through related, but shorter-term research that is more congruent with granting agencies' expectations. In addition, if the investigators are of different career positions, those more junior can learn from the more senior members, and be ready to step into leadership roles. Age-diversity, increasing in ecological sciences (i.e., Lutz et al. 2008), is likely to improve experience in logistics to these large, long-term projects. Practicality and sustainability can also synergistically be improved through project definition and outreach. Involving the broader community with an easily understood research goal and one that is perceived as worthy can improve project sustainability. When it is possible to do the bulk of measurements in a

short period of time, a ‘research pulse’ can bring participants together for the short period of time necessary for an annual mortality and recruitment check.

Empirical Support

Recent comparative studies in western North America (e.g., Gilbert et al. 2010, Wang et al. 2011, Swenson et al. 2012, Chisholm et al. 2013, Wang et al. 2013, Michel et al. 2014) show the value of large (25.6 ha) and medium-sized (1 ha) plots, but this scientific value is maximized when data are directly comparable. With collaborators, I established two 25.6 ha plots (the Yosemite Forest Dynamics Plot in Yosemite National Park, California, and the Wind River Forest Dynamics Plot in the Gifford Pinchot National Forest, Washington [Lutz et al. 2012, 2013]) affiliated with both the Smithsonian network of forest observation plots and the USGS Sierra Nevada monitoring network. These Pacific Slope forest plots are characterized by large, persistent woody structures, with emergent trees 150 cm to 200 cm in diameter, and canopy heights from 55 m to 65 m. Snag densities are high (e.g., 77 snags ha⁻¹ in Wind River [Lutz et al. 2013] and 105 snags ha⁻¹ in Yosemite [Lutz et al. 2012]), with considerable coarse woody debris (e.g., 221 Mg ha⁻¹ in Wind River [Harmon et al. 2004] and 53 Mg ha⁻¹ in Yosemite [Lutz et al. 2012]). The distribution of large-diameter trees is very heterogeneous, and tree local neighborhoods are very diverse. Average tree densities are approximately 1,100 trees ha⁻¹ to 1,300 trees ha⁻¹. Using a 400 m² grain size, these forests exhibit 95th percentiles of density and basal area that are about twice the mean values, with maxima approximately three times the mean (Lutz et al. 2012, 2013).

Using these two large plots, we have been able to investigate spatial patterns of large-diameter trees and the correlations of factors associated with death. The spatially explicit effects of large-diameter individuals is apparent at intertree distances on the order of 10 m (Lutz et al. 2014a), and clustering is apparent on the order of 50 m (Lutz et al. 2013), an intertree distance not testable in smaller plots. Large permanent plots will

be important as managers emphasize restoration of composition and structure, especially in drier *Pinus ponderosa* and mixed-conifer forest types of the West. Understanding pre-fire suppression patterns may be important to restoring fire resilience to these landscapes, research that requires large, contiguous plots (Larson and Churchill 2012) where restoration prescriptions will need to be monitored for effectiveness (Churchill et al. 2013, Larson et al. 2013).

The large number of mortalities (~ 500 per plot per year) and detailed pathology exams of newly dead trees allow the multiple factors associated with tree death to be examined by species and diameter class. Although annual mortality rates (considered by individual) have been relatively stable, the causes have varied, leading to variation in mortality expressed in biomass. In Yosemite, there was a large wind event in 2012 (a “Mono Wind”, once every two to three decades) that disproportionately affected the large-diameter trees. Every large-diameter tree that fell during this event had extensive structural root rot or extensive heart rot (see also Holzwarth et al. 2013). Similarly, two trees were killed by a combination of lightning strikes followed by an attack by turpentine bark beetles (*Dendroctonus valens*), not usually considered a mortality agent in unburned forests. The data support long-understood notions that trees die from multiple contributing factors (e.g., Manion 1981) and provide important parameterization for modeling rare but important mortality events.

Model Systems and Transcending the Ecology of Place

Longitudinal data require a huge investment in data collection and maintenance. Sampling density is high, but replication in the local landscape is very low. Selection of ecosystems for this extensive study must consider generality and the ability to extrapolate over the landscape. Appropriate study areas function as model ecosystems, analogous to model organisms used for studying plant biology. Our use of model ecosystems, like our use of model organisms, also requires that we limit questions to those appropriate to the model. Two important model ecosystems for western forests

include Douglas-fir/western hemlock (*Pseudotsuga menziesii*/*Tsuga heterophylla*) and Sierra Nevada lower montane mixed conifer (*Pinus lambertiana*/*Abies concolor*). Other model systems in western North America would include ponderosa pine (*Pinus ponderosa*) forests and woodlands, Colorado Plateau high elevation mixed-conifer forests and Rocky Mountain mixed-conifer forests, among others. Whether the model ecosystem construct has utility in an era of non-stationarity is unclear, but these model systems are also broadly distributed throughout western North America, and therefore are useful to developing management responses as well. Another potential problem with the selection of model systems, and indeed the entire ‘big plot’ concept is the lack of replication, which could allow plot selection biases to influence results. For this reason, large plots should be used in conjunction with smaller, distributed plots where possible (although the unique spatial analyses permitted by using large plots cannot be done with smaller ones).

The study of model ecosystems is facilitated by uniform field collection procedures, data structures, and data management designed for comparison (Dengler et al. 2011). The Smithsonian Forest Global Earth Observatory (ForestGEO) maintains and publishes field methods designed for the tropics (Condit 1998), but usable in western forests with minor alterations (e.g., Lutz et al. 2012, 2013). Additions to the standardized Smithsonian protocol that may be important in temperate forests include mapping of species of lower stature (e.g., shrubs and ferns, to the extent that they may influence the tree community; Lutz et al. 2014b) and fuels (e.g., to the extent that subsequent fire may structure the tree community; Gabrielson et al. 2012). The large plot network coordinated by the Smithsonian (ForestGEO), because of its uniform protocols, has the potential to uniformly compare and contrast demography, growth, mortality, and succession around the world (see also Anderson-Teixeira et al. 2015).

There has been considerable research into the conditions and causes contributing to tree mortality leading to methods and classifications for “factors associated with death.” As much of this

longitudinal work has been done in the Pacific Northwest and the Sierra Nevada, it is broadly applicable across the West. When uniform field methods in pathology exams are combined with existing technical infrastructure (e.g., Franklin et al. 1990, Condit 1998, Condit et al. 2014), direct comparison of mortality dynamics across ecosystems becomes practical. It also becomes practical to acquire and merge other data sets, such as micrometeorology data and remote sensing layers. Although many field methods and data structures, if managed consistently, could yield equivalent results, adherence to reasonable standards increases the applicability of an individual data set to questions of theory. Using recognized (albeit *de facto*) standards allows longitudinal research from one study to transcend the “ecology of place” and become useful in questions of global significance such as forest pattern (Wang et al. 2011), forest change (Anderson-Teixeira et al. 2014), remote sensing of global carbon stocks (Réjou-Méchain et al. 2014), and how scale affects forest function (e.g., Chisholm et al. 2013).

The period of observation necessary to consider infrequent disturbances such as fire or wind storms is at odds with the timing of graduate students working on a two to five year schedule, or the grants supporting same. These processes are common in the 500-year history of the oldest trees in a forest. Similarly, climate-mediated forest change may be concentrated in brief periods of extreme climate that may occur once or twice a decade. In short, extremes matter, and data need to be collected when they occur. The development of longitudinal data relevant that will become valuable when these infrequent events arise falls on individuals and organizations with longer time horizons, principally governmental agencies, research programs, and individual university researchers (Larson et al. 2013). However, the systematic problem of low funding levels and lack of leadership in funding long-term research continue to make research programs of this nature difficult to perpetrate.

It has often been the case that longitudinal studies are at odds with the philosophy that science proceeds only by controlled experimenta-

tion. However, the unintended, uncontrolled, but real-world experiment of anthropogenic change is ongoing. Longitudinal data sets allow us to monitor, model, and project forest changes. One common query I receive about longitudinal research from graduate students, is, “What’s your question?” That there are many questions, both short- and long-term, that cannot be satisfactorily answered by traditional short term studies is a novel concept for them. However, most forest ecologists evolve beyond this “tyranny of the question” to add a program of longitudinal data to augment their experimental, modeling, and short-term research. As an illustration of this phenomenon, there was once a biological technician just starting his Ph.D. studies in the early 1980s who joined the establishment team for the initial plots in the Sierra Nevada network. He recalls that he “thought it was likely a huge waste of time; after all, no specific hypothesis was being tested.” Thirty years afterwards, this ecologist is the principal investigator for the USGS Sierra Nevada longitudinal network, and has seen data from the plots used to test a multitude of specific hypotheses and published results in the highest quality scientific journals (e.g., van Mantgem et al. 2009, Stephenson et al. 2014). Without existing longitudinal data, ecological questions that potentially explain events in the recent past cannot be examined.

Conclusion

In this time of great forest change, research methods and tools that have yielded excellent results for over a century need to be extended. We can no longer assume that forests that start today are the same as, or develop along the same trajectory as forests that started centuries ago (e.g., Davis and Shaw 2001, Freund et al. 2015). Forest ecology will have to emphasize tracking large numbers of individuals for mechanistic understanding of

scales and patterns of forest development (Levin 1992). Research into specialized aspects of forest function and development, whether it be related to soil nutrients and fungi, drought ecophysiology, forest microclimate, biomass accumulation, or canopy architecture, will increasingly need to simultaneously consider the spatial and temporal context of forest plants. In particular, understanding the context of tree death and recruitment, those most rapid contributors to forest change, requires large spatial extent, spatial accuracy, and annual sampling. Large permanent plots with extensive, layered data sets can provide this context, serving as a template for investigations into the multiple, interrelated factors that contribute to forest change.

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