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A dynamic riparian forest structure model for predicting large wood inputs to meandering rivers

Running head: Dynamic forest structure modeling to predict riverine large wood loads

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Abstract

Fluvial processes strongly influence riparian forests through rapid and predictable shifts in dominant species, tree density and size that occur in the decades following large floods. Modeling riparian forest characteristics based on the age and evolution of floodplains is useful in predicting ecosystem functions that depend on the size and density of trees, including large wood delivered to river channels, forest biomass and habitat quality. We developed a dynamic model of riparian forest structure that predicts changes in tree size and density using floodplain age derived from air photos and historical maps. Using field data and a riparian forest chronosequence for the 160-km middle reach of the Sacramento River (California, USA), we fit Weibull diameter distributions with time-varying parameters to the empirical data. Species were stratified into early and late successional groups, each with time-varying functions of tree density and diameter distributions. From these, we modeled how the number and size of trees in a stand changed throughout forest succession, and evaluated the goodness-of-fit of model predictions.

Model outputs for the early successional group, composed primarily of cottonwoods and willows, accounted for most of the stand basal area and large trees >10 cm DBH for the first 50 years. Post-pioneer species with slower growth had initially low densities that increased slowly from the time of floodplain creation. Within the first 100 years, early successional trees contributed the most large wood that could influence fluvial processes, carbon storage, and instream habitat. We applied the model to evaluate the potential large wood inputs to the middle Sacramento River under a range of historical bank migration rates. Going forward, this modeling approach can be used to predict how riparian forest structure and other ecosystem benefits such as carbon sequestration and habitat respond to different river management and restoration actions.

Keywords: riparian stand structure, forest succession, ecological chronosequence, meandering alluvial river, large wood recruitment, carbon sequestration, river restoration, Weibull tree diameter distribution, riverine habitat

1. Introduction

Riparian forests provide many critical ecosystem functions and services in river corridors. These include carbon storage, terrestrial habitat, and inputs of nutrients and large wood (LW) to the stream network (Gregory et al., 1991; Fetherston et al., 1995; Naiman et al., 2005). Along dryland rivers, riparian woodland often comprise the only closed-canopy forest ecotype of any size throughout the landscape (Stella et al., 2013). These areas are critical habitat for many birds and other wildlife species (Manley and Davidson, 1993; DeSante and George, 1994), and are sources of instream large wood that enhance fluvial geomorphic processes and provide unique microhabitats for aquatic communities (Crook and Robertson, 1999; Wohl 2013). Quantifying these riparian ecosystem functions and services — and managing both their quantity and quality into the future — requires predictive models of how riparian forest structure changes over time.

On alluvial rivers, riparian trees interact with fluvial forces on short and long timescales, resulting in the co-evolution of both geomorphic landforms and ecological communities (Jeffries et al., 2003; O'Connor et al., 2003; Corenblit et al., 2007; Bendix and Stella, 2013; Kui et al., 2017). In many river systems, riparian forest development is tightly coupled with floodplain evolution, with stand initiation dating to large flood years (Scott et al., 1997; Friedman and Lee, 2002; Philipsen et al., 2021). Parameters such as maximum tree age, stand density, tree size distributions, and successional dynamics have all been shown to covary with the age of fluvial landforms (Lytle and Merritt, 2004; Van Pelt et al., 2006; Stella et al., 2011; Cline and McAllister, 2012; Janssen et al., 2020a). Projecting riparian forest development based on floodplain age is thus useful in numerous management contexts, including predicting rates of carbon storage, habitat distribution and change, and potential contributions of large wood based on rates of bank migration (Gurnell et al., 2002; Latterell and Naiman, 2007; Matzek et al., 2018). Floodplain age can often be derived readily from air photographs and other records, as opposed to forest stand age, which requires dendroecological methods or other intensive means (Shafroth et al., 2002; Greco et al., 2007).

The challenge for modeling riparian forest characteristics and ecological processes relevant for river corridor management embodies the classic bias-variance tradeoff (Hastie et al., 2009). This is to find an appropriate balance between simple models with reasonable accuracy but low resolution, versus complex models with

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better resolution but high variance (i.e., model test error) when applied in new ecological contexts (Monserud 2003; Cao 2014). Forest growth and yield models have been used in forestry applications for over a century, and modern variants project stand-level timber volumes as a function of tree size and density, stand age, and site quality (i.e., the maximum potential tree height achieved for a given site) (Titus and Morton, 1985; Weiskittel et al., 2011). These models typically produce robust predictions at the whole stand level, but suffer from low resolution and do not capture important dynamics of naturally regenerated stands (Cao 2014). At the other extreme are more complex and flexible models that simulate the growth of individual trees within a stand, and can incorporate complexities such as multiple species and tree ages, disturbance history, and competition (e.g., Pacala et al., 1993; Liu and Ashton, 1995). Some individual tree models also produce diverse outputs that include community dynamics, fire effects, biomass and carbon storage, and biogeochemical fluxes (Crookston and Dixon, 2005). Although valuable in some contexts, these models can accumulate errors due to their many individual predictions, and have other major drawbacks, including many variables to parameterize, large input data requirements, and built-in assumptions and species mixes that are not appropriate for riparian ecosystems (Liu and Ashton, 1995; Matzek et al., 2018).

In this context, diameter distribution models, which have been used in forestry since at least the 1970s (Bailey and Dell, 1973) provide a useful middle ground. In this approach, the forest stand is represented by a distribution of tree sizes (typically diameter at breast height, DBH), whose shape and variance can change over time as a function of stand age (Rennolls et al., 1985; Cao 2004; Weiskittel et al., 2011). The most common distribution used is the Weibull function, which is very adaptable and can describe diameter distributions that are exponentially decreasing (e.g., as in natural or uneven-aged stands), uniform, symmetrically humped, or skewed either left or right (Merganic et al., 2006; Nanos et al., 2017). The basic Weibull function has two parameters, *scale* and *shape*, which describe the degree of spread and the skewness of the data (e.g., tree diameter distributions for varied stand conditions including uneven ages (e.g., Zhang and Liu, 2006; Gove et al., 2008), different species mixtures (e.g., Liu et al., 2002; Lin et al., 2017). Weiskittel et al., 2011). This approach is appropriate for

modeling floodplain forests, which often contain riparian tree cohorts of greatly varying size and which are subject to strong shifts in environmental gradients over time.

In this study, we modeled how riparian forest structure shifts over the course of community succession on alluvial rivers, and projected how it would change under different scenarios of channel migration and bank erosion. We used an extensive riparian forest inventory derived from field surveys conducted along the Sacramento River (California, USA) to parameterize a family of Weibull distributions of tree diameters, whose sole predictor is floodplain age, as derived from planform change on aerial photos and historical maps. Many riparian forest characteristics such as tree density, size, and species distributions scale with floodplain age (Stella et al., 2012; Janssen et al., 2020a); as such, we can use it as a proxy variable for many correlated environmental and biotic variables. In contrast to single-species, even-aged forest growth and yield models, our model assumes that riparian forests are multi-aged and naturally recruiting, and it incorporates general shifts from pioneer to post-pioneer tree species. The model also produces estimates of uncertainty (e.g., in tree density predictions), which are especially important when it is used within an applied context.

To illustrate the value that the succession model can have in addressing questions related to riverine ecosystem function, and the services that floodplains provide to people and nature, we used it to estimate the inputs of large wood to the Sacramento River based on a range of channel migration rates experienced during various historical periods. Because of its critical role in riverine geomorphic function and feedbacks, and providing habitat for many wildlife and fish species (Crook and Robertson, 1999; Collins et al. 2012; Wohl 2013), increasing the supply of instream large wood has been identified as an important restoration objective for the Sacramento and other human-modified rivers (Florsheim et al., 2008; Golet et al. 2013).

2. Methods

2.1 Site description and riparian forest dataset

The Sacramento River catchment is the largest in California, draining 68,000 km² from the Cascade, Sierra Nevada, Klamath and Coast Range Mountains through the northern Central Valley to the San Francisco Bay-Delta (Figure 1). The middle reach of the river has a gravel-bedded, partially meandering channel that extends for 160 river kilometers between a major diversion dam in Red Bluff downstream to Colusa, where

the river becomes constrained between narrow levees. The mainstem is regulated at Shasta Dam which was built in 1942 to capture peak flows for irrigation supply and hydropower generation during the summer dry season (Buer et al., 1989). Despite significant flow regulation that truncates peak discharges, reduces sediment supply, and elevates base flows, geomorphically significant events still occur and result in active, albeit more limited, channel migration as well as cutoffs (Singer 2007; Micheli and Larsen 2011). Riparian forest area has decreased by an estimated 90% throughout the Central Valley since European settlement (Katibah 1984), yet the middle Sacramento River corridor has the largest extant stands remaining in California (Buer et al., 1989). The dominant riparian tree species include Goodding's willow (Salix gooddingii), Fremont cottonwood (Populus fremontii), box elder (Acer negundo), California walnut (Juglans californica), Oregon ash (Fraxinus latifolia) and valley oak (Quercus lobata). The dominant genera, forest structure, and community dynamics are typical of large rivers in semi-arid regions such as the Missouri River in the northwestern U.S. and the Rhône in southeastern France (Johnson, 1992; Johnson et al., 2012; Janssen et al., 2020a, 2020b). Besides forest cover, riparian areas also support herbaceous, grassland and mixed scrub communities (Figure 2).

The riparian inventory was conducted from 2010–2012 on 19 large point bars within the middle reach Sacramento River (Supporting Information S1) and comprises a chronosequence of forest composition and structure over a century long (Table 1; Stella et al., 2012). The sampling design was based on a plot stratification scheme derived from GIS maps of vegetation type and floodplain age (Figure 2). The vegetation map was developed from a 2007 aerial photo series produced by the Geographic Information Center of California State University Chico in conjunction with The Nature Conservancy and the University of California, Davis (Nelson et al., 2008; Viers et al., 2010). The inventory plots were concentrated within riparian forest areas, which were defined as all mapped floodplain assemblages dominated by trees. The riparian forest area was further stratified by floodplain age (FPA) using an existing map of 11 landform age classes spanning 4–107 years old derived from digitizing channel boundaries on sequential aerial photographs and historical maps (Greco et al., 2007). Dendrochronological analysis of these stands confirms that forest stand age closely follows floodplain age (Stella et al., 2011; Irons 2016). At all point bar sites, we established fixed-area (500 m²) circular plots at randomly-located plot centers within

each of the floodplain age classes present, for a total of 441 plots (Table 1). Within each plot we sampled all woody stems >10 cm diameter, and recorded species and DBH. We also measured stems 2–10 cm dbh and counted all smaller stems within a 50 m² subplot; these data were not used in the forest development model.

2.2 Modeling approach and rationale

To predict how tree density and size shift over the chronosequence of floodplain age, we used a Weibull function with time-varying parameters for shape and scale in conjunction with a function describing how tree density varies with floodplain age. The approach was adapted from distribution-based growth and yield models used in forestry and silviculture (Hyink and Moser, 1983; Rennolls et al., 1985; Qin et al., 2007; Weiskittel et al., 2011). However, the compositional complexity of naturally-recruiting, non-commercial forest stands necessitated some key innovations to represent more realistic ecological processes. Specifically, these include accounting within the community for species with very different life history strategies, diameter distributions, and relative dominance within the riparian forest over time (Liu et al., 2002; Zhang and Liu, 2006; Lin et al., 2016).

Even though demographic processes such as recruitment, growth and mortality can vary greatly among species within natural forests, those with similar suites of traits can be grouped into general life history guilds or seral groups (Wilson 1999; Merritt et al., 2010). In most riparian forests, though some species have generalist life history strategies, there is usually a dichotomy between early-successional, pioneer tree species (e.g., willows, poplars and alders) that establish quickly on new geomorphic surfaces and dominate young stands, versus post-pioneers that establish later and dominate older floodplain communities (Supporting Information S2). The pioneers' effective dispersal by wind and water, fast growth and acquisitive resource strategy typically results in many large trees, primarily cottonwood and tree-form willow species, establishing early during stand development (Karrenberg et al., 2002). Over time, they decrease in density, as they cannot regenerate under shade, and absent any newer stochastic disturbance events, are replaced with slower-growing and initially smaller late-successional species that increase in proportional density and biomass over the course of several decades (Fierke and Kauffman, 2005; Dybala et al., 2019a). Because successional shifts can occur rapidly (i.e., within several decades) in dryland riparian

communities (Fierke and Kauffman, 2005; Greco et al., 2007; Janssen et al., 2020a, 2020b), we distinguished between pioneer and post-pioneer seral groups in the diameter distribution modeling, fitting Weibull and tree density functions for each group separately (Figure 3). In the modeling, we included only tree species that had densities greater than 2 trees ha⁻¹; rarer species were excluded, as they represented a negligible proportion of stand density and basal area.

Assignment of species to seral group followed regional descriptions of vegetation associations (Vaghti and Greco, 2007), and life history traits such as dispersal mechanism, seed size, growth rates, and shade tolerance (Baldwin and Goldman, 2012). This approach of stratifying species along ecological strategies is consistent with our general understanding of the unique life histories of pioneer riparian trees (Karrenberg et al., 2002; Rood et al., 2003), as well as recent trait-based approaches to defining riparian plant guilds for predictive modeling (Merritt et al., 2010; Janssen et al., 2020a). Other researchers have proposed similar approaches, using fusions of several Weibull distributions, to represent different species and/or multiple age classes within a stand (Liu et al., 2002; Zhang and Liu, 2006; Lin et al., 2016).

2.3 Model structure

For each of the two seral groups, early- and late-successional species, we generated two submodels: (1) a Weibull function with a size parameter to account for the minimum diameter recorded, and scale and shape parameters modeled as power functions of floodplain age; and (2) a separate function that predicts tree density from floodplain age. Both equations were modeled empirically from the riparian inventory data. We expected the density of early successional species to decrease over time (assuming that the initial years when DBH <10 cm are not captured by the function), and density of late successional species to increase during the first few decades before leveling off later in the forest community trajectory (Figure 3; Supporting Information S2).

For a given floodplain age class, the cumulative distribution function (CDF) of diameters for each seral group was calculated using the Weibull function:

$$F(x) = 1 - \exp\left[-\left(\frac{x}{b}\right)^{c}\right]; \ x \ge 0; b, c > 0$$
 Eqn. (1)

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Where *x* is DBH (cm) and *b* and *c* are the scale and shape of the distribution function, respectively. The minimum DBH for *x* was 10 cm, corresponding to the lower limit of the inventory data, and also for standard definitions of large wood (Ruiz-Villanueva et al., 2016; Wohl 2013). The scale and shape parameter values for each floodplain age Weibull CDF were empirically derived via maximum likelihood estimation using data from the relevant subset of plots of equivalent age (Cao 2004; Gove et al., 2008). We quantified uncertainty in these estimates as 95% confidence intervals (2.5% and 97.5% quantiles) computed using a bootstrap resampling method (R functions *fitdist* and *bootdist* in library *fitdistrplus*; Supporting Information S3).

Once the Weibull parameter values were solved for each of the floodplain ages, we used them in regression equations for each of the seral groups to predict the scale and shape parameter estimates as a continuous power function of floodplain age (FPA):

parameter (scale *b* or shape
$$c$$
) = $\beta_0 \times \text{FPA}^{\beta_1}$ Eqn. (2)

where β_0 and β_1 are the parameter estimates in linearized models using ordinary least squares regression from the inventory data. Because the parameter estimates for both scale and shape varied non-linearly, floodplain age was log-transformed in both equations. The response parameter for shape was also log-transformed to satisfy residual assumptions of the linear model. Thus, for any riparian forest stand on a floodplain surface of given age *j*, we can predict the scale (*b_j*) and shape (*c_j*) parameter values of the modeled Weibull CDF for tree diameters, $\hat{F}(x)_i$.

In order to convert the tree diameter CDF to number of trees, the size class probabilities must be multiplied by the density of trees in the stand. As with the Weibull parameters, tree density varied with floodplain age, and this relationship differed for early and late successional trees. We modeled the tree density for each seral group from the inventory data, with density as a power function of floodplain age:

$$N = \beta_2 \times \text{FPA}^{\beta_3} \qquad \qquad \text{Eqn. (3)}$$

where *N* is the number trees for a seral group (in trees ha⁻¹), and β_2 and β_3 are estimated parameters for the linearized function. The density of early-successional trees was logtransformed to satisfy residual assumptions, and late-successional tree density was modeled on the original non-log scale. Estimates of average tree density were backtransformation into the original scale (tree ha⁻¹) prior to combining with the corresponding diameter CDFs. The number of trees in a given DBH size class was computed from the fitted values for the tree diameter CDF (Eqn. 1 and 2) and stand density function (Eqn. 3). For a given floodplain age *j* and DBH size class *k*, the predicted number of trees $\hat{N}_{j,k}$ was calculated as the product of the modeled estimate for tree density, N_j and the probability p_k of the presence of trees in the *k*-th DBH class. This probability is determined by the difference in CDF between the upper and lower DBH limits:

$$\widehat{N_{j,k}} = N_j \times p_{j,k},$$
Eqn. (4)
$$p_{j,k} = \widehat{F}(upper d_{j,k}) - \widehat{F}(lower d_{j,k})$$
Eqn. (5)

This process is done for all size classes within the early and late-successional groups separately, and the results pooled by size class to generate the whole-stand estimates (Figure 3). All analyses were done in R, version 3.6 (R Core Team 2019).

2.4 Assessing model goodness-of-fit

The goodness-of-fit of model parameters to empirical data was evaluated using the adjusted coefficient of determination (R^{2}_{adj}) and the significance levels of the regression models (*F*-test). These included the general linear models of tree density and the Weibull scale and shape parameter to floodplain age (Figure 3).

We assessed the goodness-of-fit of the final model predictions, which comprised the expected number of trees in each DBH size class per seral group and per floodplain age, against the empirical field data. Root mean square error (RMSE) and residuals were computed between the predicted and observed tree densities for each seral group separately, grouped by 10-cm diameter classes (i.e., 10–20cm, 20–30cm, etc.), and for each of the 11 floodplain age classes recorded (Liu et al., 2002; Pogoda et al., 2019). Because the scale of the residuals is in number of trees, this approach allowed us to assess the potential for over- versus underestimating the number of trees in a stand, and whether the precision of the estimate varied by tree size class or by floodplain age.

2.5 Modeling diameter distribution change during ecological succession

We used these models to illustrate change in riparian tree density and diameter distributions over time, simulated for floodplain surfaces of various ages. We generated CDFs of these diameter distributions separately for early and late successional groups and projected the number of stems distributed among size classes for six floodplain

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ages ranging from a decade after landform development to 250 years, which is the approximate mean turnover time estimated from historical rates of channel migration and which matches estimates of stand replacement time in other riparian systems (Bragg, 2000; Van Pelt et al., 2006; Stout et al., 2018).

2.6 Model applications to a range of river erosion scenarios

To illustrate the application of this model and approach to river management, we projected the number and size distribution of trees contributing to instream large wood that would be dislodged by bank erosion along a meandering river. We used the middle reach Sacramento River as the case study, where large wood inputs have been reduced from historical levels downstream of Shasta Dam due to peak flow reduction, widespread bank revetment, and loss of riparian forest habitat (Micheli et al., 2004; Greco et al., 2007; Michalková et al., 2010). Large wood is important for creating instream habitat for numerous native taxa in this system, including macroinvertebrates, fish (including salmonids), reptiles and amphibians (Miller et al., 2010). In the Sacramento and other regulated rivers, increasing the supply of instream large wood to reverse losses due to river management and improve critical habitat for fish and wildlife is an important restoration objective (Golet et al., 2013; Fremier et al., 2014).

We analyzed a range of scenarios for the Sacramento River, using historical rates of channel migration in the post-dam period (1946–2004) as a proxy for bank erosion. Pre-dam erosion rates were not analyzed because the time period of comprehensive aerial photos available constituted only 11 years prior to 1946, a period too short to be representative of the channel migration regime during the pre-dam period (Greco et al., 2007). First, we quantified channel migration throughout the reach in GIS using channel boundaries digitized from aerial photos (Greco et al., 2007). Of the 11 channel boundary maps available, we chose five years — 1946, 1960, 1976, 1991, and 2004 — that spanned the post-dam period. The channel boundary dates chosen were spaced relatively evenly in time (13 to 16 year periods) in order to standardize the degree of negative bias that may occur in estimating migration rates due to the channel eroding back into prior locations between map dates (lelpi and Lapôtre, 2020). For each sequential pair of channel boundaries, we superimposed 140 transects at a perpendicular orientation to the channel throughout the reach, calculated the distance between centerlines at each transect, and divided these distances by the intervening

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number of years to calculate an annual rate of bank migration. We then summarized these local rates as density distributions for each period in order to interpolate specific erosion rate quantiles.

We generated a range of scenarios of potential large wood inputs based on the aggregated post-dam era (1946–2004). We interpolated the 5th, 25th, 50th, 75th and 95th quantiles of this distribution, representing the range of channel migration (and thus bank erosion) expected at any one location during each period. We applied these rates of land area loss to floodplain surfaces adjacent to the river that were mapped as riparian forest, excluding the portion of the floodplain areas mapped as non-forest cover types (e.g., crop fields and grasslands; Nelson et al., 2008). The predicted tree counts were weighted by the proportions of riparian forest cover currently within each floodplain age class; t

he oldest surfaces (\geq 107 years) represented >40% of floodplain area (Table 1; Greco et al., 2007). The results of these calculations, computed separately for early and late seral groups and then combined by DBH class, comprised the final tree frequencies by size class expected to be recruited annually as instream large wood to the channel. The outputs are scaled per kilometer of river bank, and can be applied to the entire 160km reach or alternatively to individual riverbank locations.

3. Results

3.1 Riparian forest composition

There were 25 woody species recorded in the Sacramento River forest inventory, for a total of 7855 stems >10 cm DBH (Stella et al., 2012). After excluding rare species (mean density < 2 trees ha⁻¹), 7756 trees total from twelve woody species were included in the diameter distribution models. The early successional species group was comprised of *P. fremontii, Salix exigua, S. gooddingii, S. lasiolepis, and S. lucida ssp. Lasiandra.* Late successional species included *A. negundo, Ficus carica, F. latifolia, J. californica ssp. hindsii (syn. J. hindsii), Platanus racemosa, Q. lobata,* and *Sambucus nigra (syn. S. mexicana)* (Vaghti and Greco, 2007). The early successional species had diameter distributions that increased in size and spread with age, as indicated by the rightward shift of the cumulative size distribution (Figure 4A). This is consistent with their lifehistory strategy of effective dispersal, early colonization of new floodplain surfaces, and fast growth (Karrenberg et al., 2002). Late-successional, shade-tolerant species that can regenerate in a closed canopy were virtually absent in floodplains < 8 years old and had more narrow diameter distributions over the chronosequence of stand age (Figure 4B). As these species are typically slower-growing and, except for *P. racemosa* and *Q. lobata*, reach smaller maximum sizes (Table 2), the late-successional tree diameter distributions typically had <10% of their trees greater than 30 cm DBH, and were only represented in the oldest floodplain age classes (Figure 4B)

3.2 Model parameters

The analysis of stand density with floodplain age using the plot inventory data produced distinctly different trends for the early and late seral groups (Figure 5A). The density of early successional trees >10 cm dbh decreased sharply from a peak of >800 trees ha⁻¹ within the first two decades to <200 by age 50. Densities continue to decrease at 100 years and beyond, which is reinforced by empirical tree age data for the main cottonwood and willow species in the community, whose lifespans are generally <100 years (Irons, 2016). In contrast, the density of >10 cm late-successional trees was negligible for floodplain surfaces <15 years old and grew steadily for the following 60–70 years to a stable range of 200–300 trees ha⁻¹ past the end of the chronosequence. The general linear models derived from the inventory data yielded adjusted R² values of 0.88 for both the early and late seral groups.

The Weibull parameter optimization produced a range of values for both scale (Figure 5B) and shape (Figure 5C). As floodplain age increases, the scale parameter, which affects the distribution's overall spread and maximum height, increased non-linearly from 14.8 to 29.5 for the early-successional seral group and from 16.3 to 22.7 for the late-successional group over the first 100 years. The shape parameter, which determines the overall form (e.g., monotonic or modal) of the distribution, decreased non-linearly over that period, from 5.8 to 1.3 for the early seral group and 3.5 to 1.8 for the late seral group (Supporting Information S3). Monotonically increasing or decreasing relationships for the shape and scape parameters indicate that the diameter distribution changes substantially and consistently from young to old floodplain ages (Figure 5B and C). The parameter values shifted more for the early successional group, corresponding to rapid growth of pioneer trees early in succession and their decline during later seral stages. When these estimates were used to model the parameters as a function of floodplain age, the resulting general linear models were significant for all

parameters and had goodness-of-fit adjusted R² values ranging from 0.74–0.90 (Table 3).

The CDF plots from the modeled Weibull functions (Figure 6) matched the empirical data over the same century-long time period (Figure 4) in both shape and spread of the distributions over time. The modeled CDFs and PDFs for tree diameters shifted to the right (i.e., included proportionally more large trees) with increasing floodplain age, which indicated that with time, floodplain forest stands contained an increasing proportion of large individuals. As with the empirical data, early seral tree diameters (Figure 6A and C) changed more than for late seral trees (Figure 6B and D), with a greater spread in the distribution over time.

In addition to the projections of diameter distributions within the century-long period represented by the field data chronosequence, we extrapolated the distribution to an age corresponding to the expected floodplain residence time under steady-state conditions (Merigliano et al., 2013). Using the historical rates of channel migration (Section 2.6), we multiplied the median erosion rate for the post-dam period (Table 4) by the length of the reach (160 km) to estimate 0.389 km² of floodplain land eroded annually. Dividing these into the total area of floodplain (104.89 km²; Table 1), we estimated an expected residence time of 270 years; this corresponds to a turnover rate of 187 years for 50% of the floodplain area (Everitt, 1968; Merigliano et al., 2013). In Figure 6, we projected the CDF of tree diameters at 250 years, the approximate expected floodplain residence time.

Note that these calculations make the simplifying assumptions that the current (i.e., post-dam) erosion rate represents the long-term rate of floodplain creation, that channel movement is uniformly or randomly distributed across the floodplain, and consequently that floodplain area decreases exponentially with age (Everitt, 1968). Merigliano and colleagues (2013) have shown that this is often not the case, especially in aridland river systems where stochastic large floods strongly influence the age distribution of the floodplain area.

3.3 Model projections and goodness-of-fit

The modeled densities of trees on floodplains of different ages show two different predictions for early versus late successional trees (Figure 7). The early successional group, including Fremont cottonwood and Goodding's willow, have high densities of small (10–30 cm) trees on young floodplains <30 years old, and a greater range of tree sizes more evenly distributed on older floodplains. This pattern reflects their fast growth rates and dominance of stand basal area during the early and middle phases of community succession, but also a rapid self-thinning process to low densities after 50 years. In contrast, the late successional species have a relatively narrower range of tree diameters, predominantly between 10–30 cm, and very few trees >50 cm within the first century (Figure 7). Low frequencies on young floodplains and their distribution patterns reflect their slower recruitment rates relative to pioneer species, as well as slower radial growth over time.

The overall model goodness-of-fit was examined via residual plots of observed minus predicted final tree densities (Figure 8) and calculations of root mean square error (Table 5). The RMSE across all size and FPA classes was 45.04, with the largest errors in the smallest diameter classes, especially for early successional trees on younger floodplains (Figure 8A). This is consistent with the large stochasticity in flood history, floodplain development and recruitment success of pioneer trees on young geomorphic surfaces. The model's goodness-of-fit improved with increasing tree sizes greater than 20 cm DBH. Compared to the early seral group, predictions for the late successional trees were more accurate (Figure 8B). Model fits were very high for large trees (>60 cm DBH), though the number of trees in these diameter classes was generally low (\leq 10 trees ha⁻¹).

3.4 Bank erosion and large wood recruitment projections

During the post-dam period from 1946 to 2004, the median local rate of channel migration was 2.43 m yr⁻¹, with the 5th and 95th quantiles ranging from 0.03 to 18.75 m yr⁻¹ (Table 4). Among the four subperiods (Figure 9), channel migration was slightly lower immediately after the dam closure (1946–1960) compared to the later periods (1960–1976, 1976–1991, 1991-2004). The earlier low migration period followed the large reduction in peak flows with the onset of flow regulation.

In the scenarios of large wood recruitment to the Sacramento River, the model predicted a rate of 66 trees ≥ 10 cm DBH recruited annually per river kilometer as instream large wood at the post-dam median annual bank erosion rate, 2.43 m yr⁻¹ (Table 4; Figure 10). Of these, 47% are early seral trees. Between the 5th and 95th quantiles of local erosion rates, the number of trees recruited varies from 1 to 508

stems per km of river bank. Of the trees >30 DBH that are considered the most functional large wood fraction, the median erosion rate would yield approximately 19 trees km⁻¹ yr⁻¹, or 29% of all of those modeled (>10 cm DBH), with the 5th and 95th erosion quantiles yielding <1–145 large trees km⁻¹ yr⁻¹.

4. Discussion

In this study, we developed a quantitative model to predict shifts in riparian forest structure with landform age, focusing on tree diameter distributions, and applied it to project potential recruitment of instream large wood at a range of bank erosion scenarios along a large meandering river. The numerical model is based on the Weibull distribution that is commonly used in forest biometrics, with the added feature of a hierarchical structure in which the Weibull function parameters themselves are functions of floodplain age. We incorporated several salient features of riparian communities into the model, including their strong reliance on floodplain formation processes for stand establishment and development, and the divergent trajectories of early versus late seral trees in terms of tree size, density and stand dominance. Both the component parameters and predictions from the model had high goodness-of-fit with empirical data. With the model, we generated predictions of potential instream large wood inputs to the middle reach Sacramento River based on a range of historical channel migration rates. In similar fashion, river managers can generate a range of predictions under different flow and streambank restoration scenarios, which would provide valuable information for deciding how to maximize riverine aquatic habitat, including that of threatened and endangered salmonid species that occur in this system (Crook and Robertson, 1999). Importantly, this same succession model could be applied to address other critical questions related to management and restoration of forested floodplain systems, including the change in biomass and carbon storage due to both autogenic stand development processes and disturbance from bank erosion (Matzek et al., 2018; Dybala et al., 2019a).

4.1 Modeling riparian forest structural shifts over time

Floodplain plant communities are difficult to model for a number of reasons. Riparian forests and woodlands are particularly complex because of their dependence on flood disturbance, large environmental gradients that change quickly both seasonally and interannually, and because of the large ranges in traits, growth rates and life history strategies of their component species (Friedman and Lee, 2002; Stella and Battles, 2010). As a disturbance-dependent ecosystem, riparian forests are highly patchy and have high heterogeneity in species composition, tree size, stand biomass, and abiotic factors (Balian and Naiman, 2005; Keeton et al., 2007). As a result, most traditional forest biometric models are not adequate for modeling this rapid change and complexity.

The forest structure model using Weibull diameter distributions that we developed captured the major features of naturally-recruiting riparian stands along a dynamic alluvial river. As in real life, the modeled density and distribution of trees changed non-linearly with time, with distinct differences between pioneer species and those that replaced them as the community developed. As is common during forest development in many biomes, the density of early successional trees dropped significantly within the first three decades of stand initiation whereas the late successional trees increased slowly and steadily. As floodplains and forest stands aged, the CDF curves shifted to the right, indicating a greater relative proportion of larger trees, particularly on stands ranging from 100 to 250 years, our estimated average stand residence time. However, trends in tree density, maximum tree size, and the distributions' rates of change differed greatly between seral groups. Mature pioneer trees were much larger and more numerous earlier in the chronosequence, reflecting the fast growth, early dominance, and short lifespans of cottonwoods and large treeform willows such as *S. gooddingii* in this system (Friedman and Lee, 2002; Johnson et al., 2012; Irons, 2016). In modeling parameter space, these dynamics were quantified as greater change in the Weibull shape and scale parameters with time in the early seral group compared to the late seral group.

In all these respects, the model simulated well the salient structural features of riparian forests and the rapid shifts that occur early in their development (Fierke and Kauffman, 2005; Balian and Naiman, 2005; Van Pelt et al., 2006; Janssen et al., 2020a). Thus the model can be applied and parameterized for other rivers where floodplain formation processes are dynamic and where riparian inventory data are available. Because species turnover and successional shifts are rapid in the Sacramento River and similar semi-arid regions (e.g., Friedman and Lee, 2002; Johnson et al., 2012; Janssen et al., 2020a, 2020b) compared to colder and more temperate regions (e.g., Bragg, 2000; Van Pelt et al., 2006), model parameterization in other biomes will require local riparian forest data collected across a representative range of stand ages. Though not spatiallyexplicit, the model can be combined with vegetation maps and floodplain surfaces of known age to simulate riparian forest dynamics throughout a river corridor (e.g., Latterell et al., 2006; Kui et al., 2017; Philipsen et al., 2021).

4.2 Linking stand structure to floodplain age using time-varying parameters

The approach we took in adding a dynamic, time-dependent component to the Weibull distribution function is a novel adaptation of diameter distribution models. As such, it has several advantages. First, the time-varying parameters allow for the distribution of a given species or group (e.g., seral stage) to change continuously over time. In this way, it can be used in a predictive capacity to both infer the forest stand structure on floodplains of known age (e.g., derived from aerial photography and/or historical maps) and to project how tree size distributions will change in the future. The approach is different from most diameter distribution models used in forestry research that simulate the size structure of a stand of a given age; this is even the case with finite mixture models that simulate multiple species and tree ages within a stand (Liu et al., 2002; Gove et al., 2008; Lin et al., 2016). More complex, process-based forest models with an explicit time component usually simulate individual trees which are then aggregated to the stand level. Though more realistic than diameter-distribution models, individual-based models are parameter- and data-intensive, and questions remain in how best to deal with the cumulative uncertainty that arises when combining their many individual predictions (Pacala et al., 1993; Liu and Ashton, 1995; Bugmann 2001; Crookston and Dixon, 2005).

Another advantage to our model is that we use floodplain age, which can be readily determined from aerial photos and maps, as the sole predictor of stand dynamics. This replaces the common requirement in forest models to determine stand age from field data and tree-ring analysis, which can be cumbersome (Weiskittel 2011). Floodplain age is a good proxy for stand age because studies on alluvial rivers in various biomes show that pioneer riparian trees, including willows, cottonwoods and alders, colonize new alluvial surfaces rapidly after floods, often within the first 5–10 years (Scott et al., 1996; Stella et al., 2011). However, lag rates can vary due to the suitability of establishment conditions in the post-flood years and to tree dating inaccuracy

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introduced by subsequent sedimentation on the original establishment surface (Miller and Friedman, 2009; Merigliano et al., 2013; Irons 2016). Therefore, floodplain age is not only useful in predicting stand age, but it is also a singular driver that influences tree density, characteristics of the tree size distribution, and species composition. These relationships vastly simplify the inputs for a riparian forest model, though uncertainties in dating floodplain surfaces and unknown forest establishment lags may introduce error in model parameter estimates.

Our approach in modeling the parameters of a tree size distribution as functions of stand age differs from process-based riparian ecosystem models that simulate community change over time. In process-based models, shifts in riparian community composition and properties are usually driven by interactions with environmental factors such as river flow regimes, drought intensity and duration, and groundwater dynamics on population demographic rates. These models can simulate long-term trends for particular riparian species' populations (Lytle and Merritt, 2004; Dixon and Turner, 2006) and communities (Lytle et al., 2017). However, these models typically require a large number of species-specific parameters and data, which may not be available for many riparian systems. The many parameters can lead to equifinality in model predictions, which confounds validation attempts, and may require complex sensitivity analyses to assess their relative influence on modeled response variables (Harper et al., 2011). Our distribution-based approach does not include the influence of environmental drivers such as flood-dependent recruitment and stand establishment, which is a critical demographic process for pioneer trees. This is borne out in our model validation results, which had the lowest goodness-of-fit and highest RMSE for early successional trees on young floodplains, which would be the most sensitive to stochastic antecedent floods (Figure 8; Table 5).

Another assumption of our model is the reliance on a riparian forest chronosequence to parameterize the model components (Stella et al., 2012). In using the floodplain age-stratified inventory data, we made assumptions common to all spacefor-time substitutions. Chronosequences assume that all sites differ only in age and that each site has traced the same history since floodplain creation in its abiotic and biotic components (Johnson and Miyanishi, 2008; Walker et al., 2010). In other words, the system is in equilibrium with regard to long-term environmental conditions, disturbance frequency and magnitude, and regional species pools. Riparian forests that

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retain many natural functioning elements are generally appropriate for chronosequence studies (Walker et al., 2010), which have been used effectively to investigate succession patterns in a number of biomes (Scott et al., 1997; Fierke and Kauffman, 2005; Balian and Naiman, 2005; González et al., 2010; Cline and McAllister, 2011). In rivers heavily modified by flow regulation and channelization, these assumptions do not always hold, and riparian community dynamics often diverge from more natural systems (Janssen et al., 2020b).

Though the middle reach Sacramento river corridor has undergone high rates of land conversion and forest loss since the 19th Century (Katibah 1984), and hydrologic change since the 1940s (Singer 2007), the remnant riparian woody vegetation community is surprisingly intact and resilient to biotic invasion (Vaghti and Greco 2007), with several notable exceptions. Despite local installations of bank revetment throughout the reach and a post-dam reduction in channel migration, bank erosion and cutoff events still occur with some regularity (Micheli et al., 2004; Constantine et al., 2010; Michalková et al., 2011), driving the formation and evolution of new forest stands (Greco et al., 2007; Stella et al., 2011). In the riparian inventory site selection and study design, we chose actively migrating point bars with large expanses of naturallyrecruited forest, while excluding cultivated, restored, or otherwise heavily modified floodplain areas (Figure 1; Supporting Information S1). Extensive dendrochronological analysis (N = >1000 tree cores) of these stands confirms that forest stand age closely follows floodplain age (Irons 2016), and successional patterns are coherent and convergent (Stella et al., 2012).

4.3 Representing community composition using seral groups

Our model simplified assumptions about the stand species composition by dividing it into only two fractions, early and late seral trees. Finite mixture models that incorporate two or more diameter distributions have been used to simulate multi-age stands or those with multiple species, where each age cohort and/or species has a distinct size distribution (Liu et al., 2002; Gove et al., 2008). Lin and others (2016) took this approach in modeling a multi-age Mongolian riparian forest stand as a fusion of two species-specific Weibull distributions for spruce and larch. They modeled multiple-aged trees within a stand for each species based on dendrochronology and age-diameter models. Our study improved on this approach by modeling both seral groups as

continually shifting distributions through time using parameter values that were themselves continuous functions of stand age.

Our approach of dividing riparian stands into two finite distributions based on seral class would not be appropriate for a detailed riparian community analysis. However, it is effective and parsimonious for analyzing stand structure, specifically how the density and size distribution of the trees change over time (O'Hara 2014). Many riparian communities have distinct pioneer species with vastly different trait characteristics from post-pioneer species that dominate the stand after many decades (Karrenberg et al., 2002; Merritt 2013). Therefore, this is an effective approach that can be replicated on multiple rivers with different species mixes and environmental conditions (Stromberg and Merritt, 2016). Quantifying life history traits to group species into guilds is increasingly useful in modeling riparian communities' responses to environmental drivers such as hydrology, climate change, and human stressors (Merritt et al., 2010; Diehl et al., in press). This approach also mirrors the growing trend of analyzing plant assemblages through the lens of functional traits (Loreau 2010; Reich 2014), and shifts in community-weighted trait values (Shipley et al., 2006). Recent work has extended this approach to riparian communities (Aguiar et al., 2013; Lytle et al., 2017; Janssen et al., 2020a).

4.4 Quantifying bank erosion and large wood input rates

In the large wood recruitment scenarios we modeled for Sacramento River, the cumulative, area-weighted prediction of large wood (Figure 10) approximates a classic "inverse-J" shaped distribution common to forest stands (O'Hara 2014). The fraction of large trees, which are the most important as functional large wood (Gurnell et al. 2002; Collins et al., 2012), is dominated in the first 50 years by early successional species, particularly Fremont cottonwood in this system. The fraction of late seral trees increased with floodplain and stand age, until they comprise almost all trees at the average stand-replacing interval of 250 years (Figure 7). Large trees are critical components within the fluvial geomorphic and riparian forest feedback cycle. As downed wood, large trees act as key members within actively meandering rivers with short floodplain turnover time to stabilize geomorphic surfaces and create old forest patches that further contribute large trees to the system (Collins and Montgomery, 2002; Collins et al., 2012). In our scenarios of large wood production at a range of bank

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erosion rates, which were not spatially explicit, we made the simplifying assumption that the river erodes the forest in proportion to the areal distribution of stand ages on the floodplain. In reality, rivers in dryland regions such as the Sacramento usually erode young surfaces preferentially, and many in the southwestern U.S. are adjusting to lower peak flows due to dam construction and climate change; therefore the proportion and size distribution of young trees, especially pioneer species, may be overestimated in the large wood projections (Miller and Friedman, 2009; Bradley and Tucker, 2013; Merigliano et al., 2013).

Because erosion rates vary longitudinally and some areas are reworked repeatedly (Figure 9), actual floodplain residence times locally may be shorter and the contributions of large trees from older patches may be overestimated. However, this bias may be countered by the overrepresentation of large trees in persistent mature forest stands on old floodplain patches stabilized by large wood key members (Collins et al., 2012). A more mechanistic study of floodplain wood processes on the Sacramento, which is beyond the scope of this study, could elucidate the specific relationships and feedbacks between the growth rate of large trees relative to large wood mediated floodplain creation and persistence.

In estimating bank erosion rates from historical channel planform maps, we assumed that migration of the channel centerline is a good proxy for bank erosion. Because the channel also narrowed somewhat with flow regulation, these proxy estimates of bank erosion may be somewhat inflated; however other studies confirm that the general sequence and relative magnitude of bank erosion in post-dam subperiods match our analysis (Michalková et al., 2011). Additionally, the median rates of channel migration we measured were conservative and somewhat lower than the mean values reported in other studies for the Sacramento River (Brice, 1977; Micheli et al., 2004). Distributions of local erosion rates were right-skewed, with large local erosion events inflating the average relative to the median, which is the maximum annual erosion rate expected at any one location in 50% of years. An additional factor is the potential influence of the time period between air photos on the calculation of net erosion rates, and the potential negative bias with longer intervals (O'Connor et al., 2003). Though a recent global study of river migration rates found no influence of measurement interval (lelpi and Lapôtre, 2020), we nevertheless addressed this issue

by choosing planform data series with equivalent time intervals between photo dates for calculating annual erosion rates.

A long-term supply of large wood to the channel depends on both bank erosion that dislodges mature trees and regeneration of pioneer species that can attain large sizes relatively quickly. On alluvial rivers, large riparian forest stands establish on new fluvial surfaces that develop as a result of point bar migration and channel cutoff and abandonment (Everitt 1968; Scott et al., 1996; Stella et al., 2011). Both of these processes, bank erosion and regeneration on young floodplains, require active channel migration, which is driven by excess stream power during peak flows (Magilligan 1992; Larsen et al., 2006). Therefore maintaining a sustainable rate of large wood depends strongly on maintaining active channel migration processes (Friedman and Lee, 2002; Florsheim et al., 2008; Stout et al., 2018).

On regulated rivers that have experienced reduced bank erosion and channel migration, the rate of large wood recruitment is diminished relative to historical conditions. This is the case with the middle Sacramento River, where from 1999 to 2007 a 48% reduction in the number of large wood aggregations in the river was observed (Golet et al., 2013). This recent era follows a century-long period of land-use change that resulted in the loss of 90% of forest cover and presumably, a substantial proportion of pre-settlement wood supply for in-channel recruitment (Thompson, 1961). Therefore, restoring this ecosystem function and the many ecological benefits of large wood may include some combination of increasing peak flow releases, removing bank revetment where possible, and acquiring riparian easements to allow for forest development and bank erosion (Givertz, 2010; Fremier et al., 2014). Assessing how comprehensive and how long such measures would be necessary to restore large wood recruitment and transport function to the river would require further study, but the rapid rate of stand development and tree growth in this and other riparian systems would favor the success of targeted restoration actions (Golet et al., 2013; Dybala et al. 2019b; Janssen et al 2020a).

Our model can be used to evaluate the potential effects of these actions, by simulating scenarios with differing rates of bank erosion, both river-wide, as in the case of whole-system approaches such as increasing peak flows, or site-specific applications, such as removing bank revetment locally (Alexander et al. 2018). The modeled range of potential large wood inputs based on post-dam rates, including the large variation in

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erosion rate throughout the reach, will allow river managers to constrain estimates and expectations of what may be possible at any one location, and to calculate wood budgets under different scenarios of bank erosion and river management (Benda and Sias, 2003). An important caveat is that the model does not include a component for large wood already down on the floodplain, which can be considered a transient storage pool (O'Connor et al. 2003; Collins et al. 2012; Wohl 2020), nor does it incorporate differences in wood decay rates between early successional species such as cottonwood and willow, which tend to be fast, with the typically longer ones of later-successional species such as oak and walnut. Though standing snags were included in the forest inventories, downed wood was not quantified. Thus stem counts may be somewhat underestimates of the total large wood that is available to be recruited.

4.5 Additional Applications

When combined with other data and analyses, the model we developed and its predictive capacity can be applied to other important questions related to management and restoration of riparian floodplain systems. By characterizing rates of change of forest structure and shifts in the balance of early and late seral species as it relates to floodplain age, the model could be used to quantify the dynamics of habitat suitability for different species of wildlife (Seavy et al., 2009a). For example, Nur et al. (2008) found that on Central Valley rivers, structural variables including tree height and trunk diameter were often important in predicting songbird abundance, as was the composition of particular species, especially Fremont cottonwood and valley oak.

As an alternative or complement to habitat quality, the diameter distribution model can be used with allometric equations to estimate forest biomass stocks and their change over time (Crookston and Dixon, 2005). Predicting biomass and its rate of change as a function of floodplain age has direct relevance for estimating carbon capture and storage and hence the extent to which riparian systems can mitigate the effects of climate change (Seavy et al. 2009b; Sutfin et al., 2016; Daigneault et al., 2017). For example, Matzek et al. (2018) developed a carbon calculator for various riparian forest types based on tree inventory data (including that used in this study) and allometry for use in carbon trading markets in California. In the most comprehensive analysis of riparian ecosystems' potential for carbon storage, Dybala et al. (2019a) conducted a global synthesis and meta-analysis to identify general patterns of carbon

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sequestration in riparian forests. Their modeling projected large increases in soil carbon stocks as a result of riparian forest contributions over the first 50–100 years of stand development, and identified carbon storage as a key co-benefit of riparian habitat restoration (Dybala et al., 2019b).

More generally, information on the structure, composition and dynamics of floodplain forests is also fundamental for assessing how changes in river management affect riparian ecosystems (Johnson et al., 2012; Janssen et al., 2020b). Management actions that are relevant in this context include horticultural restoration, constraints on meander migration from installation of revetment, modifications of river hydraulics from levee construction, and flow regime changes caused by dams, diversions, and groundwater pumping. For all these reasons, new tools such as the dynamic forest structure model developed in this study are useful for modeling the status and benefits of riparian ecosystems now and into the future.

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Data Availability Statement

The data sets that support the findings of this study are available from the corresponding author upon reasonable request.

Conflict of Interest Declaration

The authors declare that there are no conflicts of interest, financial or otherwise.

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Table 1. Floodplain area and riparian forest cover distribution among floodplain age classes on the middle Sacramento River. Floodplain age is relative to the timing of the forest inventory (2011–2012) and was derived from aerial photos and historical maps; thus it represents a minimum surface age since channel migration. The intervals between photo/map series ranges from 2 to 18 years. The 107+ year age class includes all current forest stands on surfaces that were formed prior to 1904 and thus represents a substantially wider range of forest ages compared to the other age classes. The total riparian area, including the forest and non-forest land is 10,489 ha, and the total forested area is 7,535 ha.

Minimum floodplain age (years)	Year created	Floodplain Area (ha)	Riparian forest area (ha)	No. of plots sampled
4	2007	223	16	2
7	2004	437	116	17
12	1999	352	147	8
14	1997	541	296	28
24	1987	682	440	49
32	1979	722	543	47
47	1964	506	395	51
59	1952	478	339	43
73	1938	695	537	37
91	1920	485	361	26
107+	1904	5,370	4,344	74

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Table 2. Woody species used in the diameter distribution modeling. Species were included if their overall density of trees ≥ 10 cm DBH comprised ≥ 2 trees ha⁻¹ across all of the plots sampled. Summary statistics include tree counts and diameters sampled; the 95th quantile DBH represents the largest size classes observed for each species. The category "Seral group" distinguishes between early and late successional species groupings used in the diameter distribution modeling, and is based on life history data for riparian species in the Central Valley of California (Greco et al., 2007; Vaghti and Greco, 2007).

Species	Seral group	No. trees sampled	Proportion of all trees sampled	Mean DBH (cm)	Median DBH (cm)	95 th Quantile DBH (cm)
Acer negundo	late	1087	0.138	16.1	14.5	28.6
Ficus carica	late	429	0.055	14.8	13.4	25.6
Fraxinus latifolia	late	117	0.015	24.2	22	43.1
Juglans californica ssp. hindsii	late	958	0.122	22.0	19.3	43.5
Platanus racemosa	late	41	0.005	29.7	16.7	108.7
Populus fremontii	early	1620	0.206	35.6	29.1	80.5
Quercus lobata	late	117	0.015	26.3	20.6	62.8
Salix exigua	early	1150	0.146	14.3	13	23.1
Salix gooddingii	early	1081	0.138	21.1	17	45.0
Salix lasiolepis	early	265	0.034	13.3	12.2	19.2
Salix lucida ssp. Lasiandra	early	694	0.088	15.3	13.8	25.9
Sambucus nigra	late	197	0.025	15.3	13.8	26.0

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Table 3. Formulas and goodness-of-fit for general linear models of tree density and the Weibull parameters scale and shape as a function of floodplain age. Weibull parameter values were derived from the empirical field data using means of all plots within each age class. See Figure 5 for graphical representation of the models.

Relationship	Models	R ² adj	F-statistic	p-value
Tree density (early) ~ FPA	$Y = \exp^{8.037} \times x^{-1.711} - 1$	0.88	73.22	< 0.001
Tree density (late) ~ FPA	$Y = -168.173 + 86.775 \times \ln x$	0.88	73.65	< 0.001
Scale(early)~FPA	$Y = 4.985 + 6.495 \times \ln x$	0.74	28.89	< 0.001
Scale(late)~FPA	$Y = 6.113 + 3.687 \times \ln x$	0.79	26.96	0.002
Shape(early)~FPA	$Y = \exp 2.022 \times x^{-0.406}$	0.90	87.28	< 0.001
Shape(late)~FPA	$Y = \exp 1.937 \times x^{-0.2792}$	0.78	25.25	0.002

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Table 4. Predictions of potential large wood pieces generated under various erosion rates corresponding to historical channel movement along the Sacramento River in the post-dam period, 1946–2004. Using these rates in the riparian forest model generates distributions of potential large wood. We summarize the pieces that are >10 cm dbh and >30 cm dbh for both early and late seral species groups. See Figure 10 for the full distributions predicted.

Local erosion quantile	Erosion rate (m km ⁻¹ year ⁻¹)	# early seral trees >10cm (# km ⁻¹ year ⁻¹)	# late seral trees >10cm (# km ⁻¹ year ⁻¹)	# early seral trees >30cm (# km ⁻¹ year ⁻¹)	# late seral trees >30cm (# km ⁻¹ year ⁻¹)
5 th	0.03	0.42	0.47	0.16	0.1
25 th	0.62	8.03	8.89	2.99	1.84
50 th /median	2.43	31.26	34.61	11.65	7.17
75 th	6.72	86.4	95.65	32.21	19.83
95 th	18.75	241.15	266.98	89.89	55.34

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Mid-point DBH (cm)	RMSE, Early successional trees	RMSE, Late successional trees	
15	208.89	68.78	
25	32.95	32.44	
35	23.85	16.79	
45	19.96	22.10	
55	24.31	28.91	
65	22.38	10.28	
75	21.24	10.02	
85	20.65	6.03	
95	19.19	8.53	
105	18.01	6.03	
115	11.94	8.53	
125	14.83	6.03	
135	14.61	0.00	
145	5.91	0.00	

Table 5. Root Mean Square Error (RMSE, in trees ha⁻¹) for early and late successional trees among all DBH ranges. The DBH classes are from 10–150 cm, in 10-cm intervals.



Figure 1. Map of the middle reach Sacramento River, which extends 160-km from Red Bluff downstream to Colusa, CA. Colored areas indicate remnant and restored riparian forest, with the historical, pre-settlement riparian zone shown in light grey. Map courtesy of The Nature Conservancy (Chico, CA).

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Figure 2. An example of a point bar along the middle Sacramento River at River Kilometer 277 (River Mile 172), showing (A) the floodplain age developed from historical maps and aerial photo series (Greco et al., 2008), and (B) vegetation cover categories (modified from Nelson et al., 2008). Areas designed as "Non-forest" were excluded from the stand structure modeling and predictions of large wood recruitment.

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Figure 3. Top box: flow chart diagram of empirical field data inputs (green boxes) and sequence of equations used to predict riparian forest tree size distributions and densities as a function of floodplain age. Bottom box: graphical illustration of the Weibull tree diameter distribution function and tree density model applied to predictions of instream large wood (LW) inputs based on rates of channel bank erosion. Annual inputs shown are based on a timescale matched to the period of record.



Figure 4. Riparian forest tree size distributions. The empirical cumulative distribution functions (CDFs) derived from riparian forest inventory plots of early (A) and late (B) successional tree groups. Colors and legend indicate groups of plots stratified by minimum floodplain age (FPA) and the corresponding years of aerial photos or historical maps. The oldest age class includes all remnant stands older than 107 years old. Distributions are shown only for FPA series with more than one sample point. The distributions shift down and to the right as FPA increases (from red to blue data series), indicating a greater proportion of larger trees on older surfaces.

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Figure 5. Relationship between floodplain age and tree density calculated from field inventory data (A), as well as Weibull parameters for scale (B) and shape (C) for early successional trees and late successional trees. Dashed and solid lines indicate power functions generated for the early and late successional seral groups, respectively. Panel (A), shows the mean density and standard deviation across all plots for a given FPA class, separated by seral class. In panels B and C, points and error bars indicate Weibull parameter values derived from the empirical field data using means of all plots within each age class. Error bars represent 95% confidence intervals for each floodplain age class, calculated using a bootstrap simulation approach. Estimates for floodplain age are derived from air photo and map analysis and are thus approximate depending on the intervals between photo series, which range from 2–18 years.



Figure 6. Predicted riparian forest tree size distributions. Top row: predicted cumulative distribution function (CDF) curves of tree diameter at breast height (cm) generated using the Weibull functions of early (A) and late (B) successional tree groups. Bottom row: predicted probability density function (PDF) curves of tree diameter at breast height (cm) generated using the CDF curves of early (C) and late (D) successional tree groups. Colors from red to blue indicate floodplain age from 10 to 100 years, within the span of the model calibration data, and the dashed grey line indicates an extrapolation to 250 years, which is the approximate mean turnover time calculated based on historical channel migration rates (see Figure 9 below).



Figure 7. Predicted change over time in the density and size distribution of riparian trees >10 cm dbh, simulated for floodplain surfaces ranging from 10 to 250 years old. Each bar represents the number of trees in a 10-cm diameter class.

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Figure 8. Residual plot of tree density predictions, grouped by diameter class and floodplain age. Each point represents the difference in tree density between observed and predicted values for each 10-cm dbh size class, for early successional (panel A) and late successional (panel B) tree groups. Separate colors indicate floodplain surfaces of different age, with youngest surfaces in red and oldest in blue.

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Figure 9. Annual channel migration rate along the entire middle reach Sacramento River for four sequential intervals of roughly equivalent length (13–16 years) during the post-dam period, 1946–2004. In each case, channel centerlines from the beginning and ending time series were differenced along 140 transects perpendicular to the channel, and the centerline shift annualized by dividing by the interval length. Left column: longitudinal variation in annual migration rate (m yr⁻¹). Right panel: density distributions of annual migration rates for each period, shown on a log distance scale.



Figure 10. Predictions of average annual distributions of large wood inputs (in stems per river kilometer) based on riparian forest model results and historical rates of channel migration for the aggregated post-dam period, 1946–2004. Large wood predictions were generated at the 25th, 50th (median), 75th, and 95th quantiles of bank erosion activity documented from aerial photographs. These predictions reflect the area-weighted age distribution of floodplain land occupied by riparian forest, which has greater representation on surfaces >100 years old (Table 1).

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Graphical Table of Contents

A dynamic riparian forest structure model for predicting large wood inputs to meandering rivers

We developed a riparian forest structure model that predicts shifts in tree size and density as a function of floodplain age on dynamic alluvial rivers. The model uses a Weibull distribution with time-dependent parameters and was calibrated with field inventory data from the middle Sacramento River (CA, USA). We generated predictions of large wood inputs based on historical bank retreat rates. Other applications include modeling the response of riparian forest biomass and habitat to different river management and restoration actions.

