Predictability of cottonwood recruitment along a dynamic, regulated river

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RACHEL ERIN WRIGHT
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Approved:

Gregory B. Pasternack, Chair

Yufang Jin

Mary L. Cadenasso

Committee in Charge

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ABSTRACT

Riparian vegetation planting and management are vital to river engineering projects. To inform these activities, a better understanding of what influences riparian vegetation recruitment and identifying where vegetation will most likely establish and survive is needed. This study investigated whether the recruitment of *Populus fremontii* (Fremont cottonwoods), a dominant riparian species in the western USA, could be predicted at 0.91-m^2 resolution deterministically and statistically throughout a dynamic, alluvial regulated river. The testbed was a ~ 34-km stretch of the Yuba River in California, USA, mapped in 2017 after a large flood reset the terrain. Five years later from August through November 2022, a field campaign characterized juvenile cottonwoods recruitment. For the deterministic test, a riparian seedling recruitment model was used with expert-estimated parameters. Bioverification analysis, or comparison of model predictions to observed organism locations, found that the model did not accurately differentiate the predicted optimal locations from the lethal locations. Hydrophysical and topographic variables were then used as predictor rasters in a data-driven, supervised classification Random Forest (RF) model with cottonwood presence and absence data to statistically test whether recruitment locations could be predicted. The RF model performed well, having an overall accuracy of 87% and reached an AUC-ROC value of 94% with only a few predictors. When the statistical model was coupled with biophysical interpretations of model behavior, topographic variables were much more significant drivers for recruitment locations than hydrophysical variables. Further mechanistic developments to understand underlying governing equations and parameters are feasible drawing on the lessons from bioverification and the RF model. Both

deterministic and statistical methods are recommended to advise stakeholders about suitable locations for riparian vegetation restoration or topographic characteristics needed to promote restoration efforts, as each yield unique insights.

Keywords: Riparian seedling recruitment, ecohydraulics, modeling, machine learning, river revegetation, cottonwood

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1 INTRODUCTION

Riparian forests exist at the interface between terrestrial and aquatic environments, creating highly dynamic, diverse, and structurally complex habitats (Naiman et al., 1993). Within this zone, vegetation, hydrology, and topography all influence each other with varying degrees of magnitude and directionality (Swanson et al., 1982). Hydrogeomorphic processes provide plants with water and nutrients and regenerate new sites for colonization, while established vegetation influences the flow field, sediment transport, and deposition processes (Camporeale et al., 2013; Gurnell, 2014; Gurnell et al., 2012; Politti et al., 2018). This creates a biologically diverse and synergistic landscape dependent on disturbance regimes (Gregory et al., 1991; Stromberg, 2001).

A long history of human manipulation of rivers due to flow regulation, deforestation, intensive agriculture, urbanization, channelization, and mining has resulted in cumulative effects that transformed riverine landscapes (Downs & Piégay, 2019; Wohl & Merritts, 2007). In the Western United States, these anthropogenic processes have greatly reduced riparian forests to remnants of varying size and quality, and have severely impacted habitat-forming foundational species (Abell, 1989; Braatne et al., 1996; Patten, 1998). Despite the enormity of this problem, there has been limited and variable success with riparian revegetation efforts (González et al., 2015; Kondolf & Micheli, 1995; Stromberg, 2001), stressing the need to better understand what causes an effort to succeed or fail. This has led to an increased need of identifying the appropriate environmental criteria to support efforts attempting to establish new riparian forests and improve existing ones rooted in scientific theory (Thomson et al., 2001).

Identifying these ideal environmental conditions from a physical process viewpoint is complex, as the characteristics of a river system are a product of dynamic hydrogeomorphic processes. River bank and floodplain heterogeneity provide the physical template for the spatial pattern and development of varying riparian vegetation communities (Gregory et al., 1991). Topographic gradients impact the amount of energy and force of river flows, resulting in areas of erosion or deposition (Swanson et al., 1982). These sediment transport processes may impact vegetation through uprooting, burial, and erosion (Politti et al., 2018), and affect the substrate's ability to retain the moisture needed for root growth by influencing sediment composition and grain size (Camporeale et al., 2013). Microtopography, or the localized topographic variability in soil surface elevation and roughness, also impacts the immediate hydrologic conditions experienced by a seed or plant (Moser et al., 2007; Pollock et al., 1998). Environmental characteristics resulting from varying microtopographic patterns may influence the distribution of plants through the creation of differing habitats (Titus, 2016). These variations in soil conditions and topography result in a high diversity of riparian plant species that can coexist (Naiman et al., 1993).

To maintain this characteristic diversity, species need to successfully recruit into the riparian system. In semi-arid western North America, cottonwoods (*Populus*) are a foundational pioneer species. They are among the first to colonize disturbed or bare areas (Stromberg, 1993) and are a dominant tree species (Amlin & Rood, 2002; Braatne et al., 1996; Patten, 1998; Stella et al., 2010). They are important for stabilizing channel banks, providing rich wildlife habitats, maintaining biodiversity, creating shade and shelter, and serving as a source of streamwood (Naiman et al., 1993).

Successful natural recruitment of cottonwoods and other pioneer species is also crucial for the continuation of riparian forests. The ecophysiological requirements for cottonwood recruitment and survival are intricately linked to fluvial hydrologic and geomorphic processes. Recruitment of these pioneer species is largely dependent on large, infrequent flows, which provide the necessary physical disturbance to create open space for colonization, dispersal of seeds, and substrate moisture for early root growth and consequent seedling recruitment (Benjankar et al., 2020; Rood, Braatne, et al., 2003; Stella et al., 2010). After recruitment, seedling survival is then reliant on environmental factors such as access to sunlight and a root growth rate comparable to recession rate declines of the water table in order to maintain access to moisture (Amlin & Rood, 2002; Benjankar et al., 2020; Stella et al., 2010).

Numerous pressures on cottonwoods arise from human manipulation of riverine systems. Dams and flow regulation can change the natural flow and sediment regime (Poff et al., 1997), impacting hydrologic processes and environmental suitability for cottonwood seedling recruitment (Dixon et al., 2012; Mahoney & Rood, 1998). Livestock grazing, land clearing, and mining can reduce recruitment and seedling growth rate, resulting in habitat fragmentation and altered sediment processes (Patten, 1998; Stromberg, 1993). These influences threaten the hydrogeomorphic processes needed for cottonwood reproduction and survival, and also impact the ecological integrity of riparian forests and connected ecosystems (Braatne et al., 1996; Poff et al., 1997).

Degradation is particularly relevant in the arid and semiarid regions of western North America, where water resources are often intensely regulated for human needs by dams and diversions (Hauer & Lorang, 2004; Poff et al., 2003). Management of regulated rivers systems must be able to maximize ecological benefits from varying water years to encourage and determine existing natural recruitment opportunities for cottonwoods and other pioneer riparian species. However, identifying the best way to accurately predict cottonwood seedling recruitment in support of long-term river management is still a challenge.

To untangle impediments on riparian vegetation conservation, this study tested the ability of existing scientific theory and methods to accurately predict locations of cottonwood recruitment throughout a regulated, dynamic river corridor by implementing the state of knowledge in two different modeling approaches, one deterministic and one statistical. The physical processes and environmental conditions included in the two models were further explored to examine the conditions needed for both natural recruitment and for accurately predicting recruitment. Prediction accuracy was evaluated using cottonwood field observations, yet the novelty of this work lies in exploring outcomes of different prediction approaches and how that can inform riparian ecology and conservation.

1.1 Cottonwood Recruitment Background

Cottonwood recruitment occurs both sexually through seeds and asexually as clonal processes. Seedling recruitment for riparian regrowth is important to maintain in a river in addition to having clonal processes, as it supports genetic diversity, offsets losses due to mortality, and is the primary method of colonization on new or barren surfaces (Braatne et al., 1996; Dixon et al., 2012; Mahoney & Rood, 1998). These bare surfaces are created when flows high enough to induce sediment mobilization uproot existing vegetation, clear away ground cover and detritus, and/or bury young vegetation by depositing sediments. In non-cohesive soils, uprooting vegetation may occur through Type I or Type II uprooting mechanisms, which respectively reference early germinated or mature vegetation (Edmaier et al., 2011). Type I uprooting occurs when the drag force exceeds the root resistance of the plant, while Type II uprooting is when the scouring near the base of the plant exposes the root system and decreases the root anchoring resistance until turning into Type I (Edmaier et al., 2011). When high flows recede, cottonwoods may colonize the suitable areas of newly deposited sediment and moist open ground (Friedman et al., 1995). These barren surfaces are important to pioneer species like cottonwoods, which are shade intolerant and poor competitors, making access to full sunlight critical for seedling growth and development (Braatne et al., 1996; Johnson 1994).

In the semiarid western United States, rivers exhibit winter and spring flooding followed by flow recession in the late spring and summer (Lins, 1997). Cottonwoods have adapted to releasing seeds after the peak in seasonally high spring flows from mountain snowpack melting, with a limited dispersal time period and a seed viability that quickly declines (Braatne et al., 1996; Mahoney & Rood, 1998). An abundant number of seeds are produced every year by mature cottonwoods and are dispersed by the wind and water (Braatne et al., 1996; Stromberg, 1993). Annual variability in hydrogeomorphic processes result in episodic recruitment, with higher recruitment in some years or decades compared to others (Dixon et al., 2012; Scott et al., 1997; Stromberg, 1998).

Cottonwoods are dependent on the groundwater table and the associated capillary fringe in the substrate for moisture. For germination to successfully occur, substrate requires continual moisture for the first few weeks of establishment (Cooper et al., 1999; Fenner et al., 1984). After germination, surface moisture conditions and receding water table rates impact the success of seedling growth and development (Amlin & Rood, 2002; Stella et al., 2010). Seedlings must be able to grow sufficiently long roots to reach the receding water levels (Stromberg, 1993), with drought stress or mortality for seedlings where the water table recedes faster than their roots can grow (Amlin & Rood, 2002; Mahoney & Rood, 1991; Stella et al., 2010).

Areas where cottonwood seedlings colonized may then be vulnerable to high flows with sufficiently intense hydraulic forces that result in scouring or depositional processes, risking mortality (Politti et al., 2018). When these large flows result in areas flooded with slow moving or stationary water, erosional and sediment transport impacts are less (Amlin & Rood, 2001). Prolonged inundation over multiple weeks can also be stressful or lethal to seedlings as it can lead to oxygen depletion in the root zone (anoxic conditions), root growth suppression, reduce transpiration, and cause decay (Amlin & Rood, 2001; Auchincloss et al., 2012). Impacts to a seedling and the number of inundation days it can survive are dependent upon the age and size of the seedling, as well as the depth, clarity, and temperature of the water (Auchincloss et al., 2012; Friedman & Auble, 1999).

1.2 Riparian Vegetation Modeling

Numerical models serve to capture the details of scientific understanding about a natural phenomenon and provide specific quantitative predictions about it. Many scientific ideas cannot be codified into mathematics, or can only be done so partially, so models are necessarily simplifications. Nevertheless, the ways in which a given model is uncertain and its levels of accuracy and precision can serve as indicators of the state of understanding of a phenomenon.

Solari et al. (2016) and You et al. (2015) summarize mathematical models analyzing riparian vegetation within a disturbance regime, including effects of vegetation on hydro-morphodynamics by influencing flow resistance (Järvelä, 2004; Luhar & Nepf, 2013), sediment transport (Lopez & Garcia, 1998), or bank dynamics (Bertoldi et al., 2014; Zong & Nepf, 2011), and the reverse of hydro-morphodynamics on vegetation by impacting seed dispersal (Groves et al., 2009; Merritti & Wohl, 2016), recruitment (Mahoney & Rood, 1998), or mortality and woody debris inputs (Edmaier et al., 2011; Gregory et al., 2003; Haga et al., 2002; Villanueva et al., 2014). Mathematical models also vary in purpose to analyze systems at the individual (Mahoney & Rood, 1998; Scott et al., 1999), population (Clipperton et al., 2003; Phipps, 1979), or community level (Camporeale & Ridolfi, 2006). In addition, these mathematical model may differ by being deterministic, statistical-empirical, or statistical-stochastic, or a combination thereof (Jajarmizadeh et al., 2012).

This study used the novel Riparian Seedling Recruitment sub-module (RSRM) (Phillips & Pasternack, 2022) within a free, open-source software called River Architect (Schwindt et al., 2020; https://riverarchitect.github.io). The RSRM is a spatially distributed, deterministic numerical algorithm designed to determine the theoretical suitability of locations for Fremont cottonwood (*Populus fremontii*) seedling recruitment by predicting the potential success for a seedling to survive through its first year of life (Phillips & Pasternack, 2022). The scientific foundation for the RSRM is the recruitment box model (Mahoney & Rood, 1998), which relates the timing and inter-annual pattern of stream stage to the physiological needs for cottonwood seedling recruitment. The recruitment box model has been validated by successful instream flow restoration programs (Rood et al., 2005; Rood, Gourley, et al., 2003; Rood & Mahoney, 2000). It has also been used in the development of other spatially distributed models for cottonwood seedling recruitment (Benjankar et al., 2014, 2020; Stella, 2005). A more detailed description of the RSRM conceptualization and development can be found in Phillips & Pasternack, (2022).

Time, finances, site accessibility, and other such local constraints may prevent *in situ* collection of environmental variables or measurements necessary to calibrate a deterministic model. Alternatively, a small sample of data might be better used for training a statistical-empirical model, such as an artificial intelligence machine learning (AI/ML) model when there is an abundance of remote sensing data, especially environmental variables derived from airborne LiDAR (Diaz-Gomez & Pasternack, 2021; Guisan et al., 1999; Rew et al., 2005; Shoutis et al., 2010; Vogiatzakis & Griffiths, 2006). Like statistical-empirical models in general, AI/ML models are most useful and can be highly accurate for professional practice when tuned on and applied to a local setting, staying within the range of conditions for which tuning was done. Relationships between species and the environment are often complex and nonlinear, allowing classification ML procedures to provide more meaningful analysis of ecological data then traditional statistical methods may be able to (Cutler et al., 2007; De'Ath & Fabricius, 2000).

One such procedure is the Random Forest (RF), which uses classification trees to repeatedly split the input data into more homogenous groups using different combinations of explanatory variables (Breiman, 2001). RF's allow for the exploration of prediction patterns and processes through the use of both discrete and continuous explanatory variables, variable importance measures, and graphical representations. A previous study by Diaz-Gomez & Pasternack, (2021) used a RF with topographic metrics derived from airborne LiDAR to predict where vegetation had successfully established on the same testbed river as this study. Presence and absence points of naturally established vegetation were randomly selected from LiDAR-derived data and used with 17 topographic explanatory variables, ultimately achieving an accuracy metric (i.e., AUC) of 77% (Diaz-Gomez & Pasternack, 2021). The workflow created by Diaz-Gomez & Pasternack, (2021) was modified to be utilized in this study for predicting the presence and absence of juvenile cottonwoods.

1.3 Research Questions

The goal of this study was to evaluate the state of cottonwood recruitment predictability. The predictability of cottonwood seedling recruitment locations is both of interest as a basic science topic to evaluate how well the scientific community understands recruitment as a spatio-temporal biophysical mechanism and as an applied tool to improve the success of the cottonwood vegetation component of riparian revegetation projects, whether in terms of setting up the right conditions for natural recruitment or to guide manual planting. To achieve this goal, both a deterministic and a statistical-empirical model were used, which showcased the potential that each offers when addressing a real river in need of active conservation measures. The deterministic model implemented mathematical equations describing hydrogeomorphic processes and was coupled with empirically-derived biophysical cottonwood metrics. The statistical-empirical model explored relationships between environmental variables and cottonwood presence/absence. Each approach makes different assumptions and provides unique, valuable insights. Together they generate expert-based, physical interpretations of environmental processes and requirements needed for cottonwood seedling recruitment.

Three specific, tractable research questions were posed, each with an accompanying hypothesis (**Table S1**). These questions focus on juvenile cottonwoods of five years old or younger, which in this study are defined to be less than 5 m tall (Braatne et al., 1996; Nagler et al., 2005; Zamora-Arroyo et al., 2001). The first question explores how the predicted cottonwood seedling recruitment locations from a deterministic numerical model compare to field locations of juvenile cottonwoods. It was hypothesized that the field locations of juvenile cottonwoods would occur in the more favorable and optimal recruitment locations predicted by the RSRM, as it models the biophysical and hydrogeomorphic processes (i.e., shear stress during disturbance flows, peak flows during seed dispersal, stream stage recession rates, and inundation periods) important for cottonwood seedling recruitment.

The second question evaluates how field locations of juvenile cottonwoods compare to presence/absence classification predictions by the statistical RF machine learning model through several performance metrics. Due to the use of both the RSRM hydrophysical variables important for cottonwood seedling recruitment and topographic variables that capture the heterogeneity and small-scale variations in terrain needed for maintaining riparian vegetation diversity, enough spatial information should be available for successful model predictions. Therefore, it is hypothesized that satisfactory performance metrics will result when held to high modeling standards.

The third question uses results from the statistical machine learning model in an interpretive analysis to ascertain whether statistically important predictors are also biophysically explaining suitable conditions for recruitment and cottonwood presence and absence. Both topographic and hydrophysical variables were included as potential explanatory variables, with the distance from and elevation above the wetted channel hypothesized to be the most important drivers in juvenile cottonwood presence. This is based on terrain-hydrology-cottonwood relationships. Seeds are deposited in receding flood flows along the active channel margins to create recruitment bands (Braatne et al., 1996; Mahoney & Rood, 1998; Scott et al., 1997; Stromberg, 1993), while recruitment elevations are dependent on an access to moisture that does not result in scouring by high flows at lower elevations or drought stress at higher elevations (Mahoney & Rood, 1998; Scott et al., 1997).

2 STUDY SETTING

2.1 Hydrology and Geomorphology

The lower Yuba River (LYR) is a ~ 37.5-km-long, gravel-cobble regulated river in Northern California's Central Valley. It was selected to serve as the testbed for evaluating cottonwood seeding recruitment predictability with deterministic and ML models because extensive research has been done on the river's environmental history and current conditions. There are also detailed, abundant datasets to support model development and testing.

The Yuba catchment drains 3,480 km^2 of the western Sierra Nevada Mountains before reaching the confluence with the Feather River (**Figure 1**). This area has a dry summer subtropical climate, experiencing cool, wet winters and hot, dry summers. The LYR's hydrology is driven by winter rainstorms and spring snowmelt, with most of the annual precipitation occurring between November and March. Flow to the LYR is partially regulated by dams and diversions (YCWA, 2013), including 79-m-high Englebright Dam and 7.3-m-high Daguerre Point Dam (both mining sediment barrier dams), but to a less degree than for other rivers in the region (Escobar-Arias & Pasternack, 2011). In fact, large floods (> 25-yr recurrence interval) that produce sustained above-bankfull discharges driving among the most voluminous morphodynamics in North America for a river of its size (Gervasi et al., 2021) occur on an approximate decadal cycle for recorded history (Guinn, 1890). They are caused by atmospheric rivers and rain-on-snow events (Garvelmann et al., 2015).

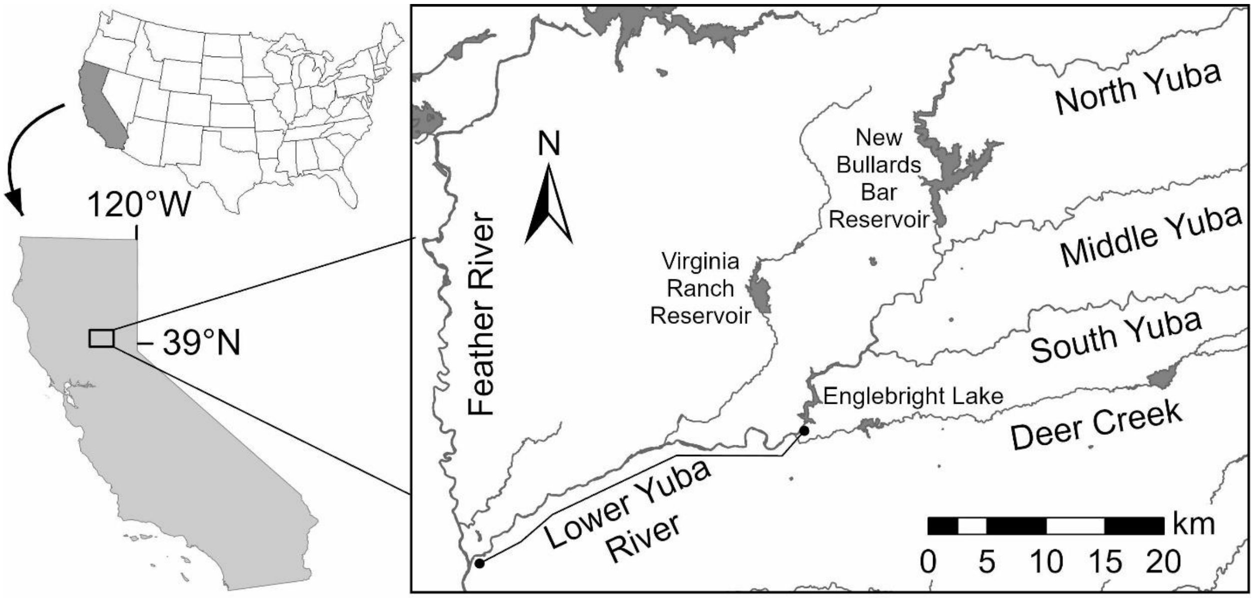

Figure 1. LYR map and location within Northern California.

An estimated 280,209,355 m^3 of hydraulic mining sediment was created within the Yuba's catchment during and after California's Gold Rush between 1852 and 1906 (James, 2005), with almost 90% of it remaining there by the 1980's (Adler, 1980). Sedimentation aggraded the LYR's natural channel by 8-26 m (Adler, 1980; Gilbert, 1917) and changed the channel pattern. Sediment reworking and export continue to influence aquatic and riparian habitats (YCWA, 2013; Carley et al., 2012).

The LYR corridor was also historically modified. Dredging of mine tailings during the 20th century to extract more gold was done in a way that created wide, tall training berms that line the LYR for several kilometers to focus flow in an active river corridor to keep it out of neighboring dredger mining areas (James, 2005). Flood-borne migration of mining sediment down the Yuba River valley led to the construction of Daguerre Point Dam (DPD) in 1906 to prevent mining sediment from being exported to the Feather and Sacramento Rivers. The sediment-barrier Englebright Dam (ED) was built in 1941 in the canyon defining the entrance to the LYR. The deposition of unconsolidated mining sediment buried pre-existing riparian vegetation and may have altered riparian conditions by reducing the extent and diversity of vegetation, covering the existing soil with debris, and may have altered the capillary fringe and impacted soil moisture availability for roots (YCWA, 2013).

While the historic river valley underwent dramatic changes, the containment of flow into a smaller corridor where it has been for many decades has by now yielded a remarkably dynamic river responding to a dynamic flow regime (Gervasi et al., 2021). For example, studies have found the LYR to have ecologically functional flows (Escobar-arias and Pasternack, 2011), diverse and self-sustainable landforms (Strom et al., 2016; J. R. Wyrick & Pasternack, 2014), and an abundance of high-quality anadromous fish habitat (Kammel et al., 2016; Moniz & Pasternack, 2021; Pasternack et al., 2014). New projects are underway to expand the area of the functional river corridor (e.g., Southall et al., 2022). Given the current dynamism in the river, the setting is a good testbed for this study.

2.2 Vegetation and Streamwood

The LYR supports many woody species, including in order from more abundant to least, varying willow species (*Salix* sp. and *Cepthalanthus occidentalis*), Fremont cottonwood (*Populus fremontii*), blue elderberry (*Sambucus nigra* ssp. *caerulea*), black walnut (*Juglans hindsii*), and more (YCWA, 2013). LiDAR analysis in 2008 found that within the floodprone inundation area (i.e., width for which mean depth is double mean bankfull depth), sections of the LYR downstream of DPD were more densely vegetated than those upstream (Burman & Pasternack, 2017). Further within the floodprone area, channel and floodplain landforms had lower density of vegetation compared to higher elevation fluvial landforms. By studying aerial photographs from 1947 to 2010, a 15%-80% increase in total vegetative cover by area was observed in most LYR reaches, which are distinct geomorphic sections delineated on the basis of tributary junctions, hydraulic structures, river bed slope, and valley width (Wyrick & Pasternack, 2012), while one of the upstream reaches had 10% less vegetative cover (YCWA, 2013). This is attributable to flow regulation, which is a common global phenomenon (Gordon & Meentemeyer, 2006).

The LYR receives an abundance of streamwood from its catchment. Wood flows over Englebright Dam's ogee crest, providing some potential for asexual recruitment and creating structural complexity where large wood accumulates. Vaughan (2013) estimated that the Yuba catchment stores 600,500 m^3 of large streamwood. Senter et al., (2017) estimated that the North Yuba River exports 1.8-2.2 m^3/year/km^2, so when applied to the whole Yuba catchment that could be 6264-7656 m^3/yr, with high interannual variability.

Even though riparian vegetation is increasing along the LYR both downstream and through time, the river has large expanses of unshaded terrain. Some stakeholders seek projects to promote even more expansion of riparian vegetation and its riverbank ecotone and floodplain habitats, both for the stakeholder's sake as well as to provide enhanced cover habitat for the rearing lifestage of federally threatened Chinook salmon and steelhead trout. Riparian vegetation that is more structurally and biologically diverse provides shade and a food supply, regulates light and temperature (SYRCL 2013), and creates in-stream habitat and shelter through large woody debris (Naiman et al., 2002).

Due to these needs, there are multiple ongoing or planned aquatic, riparian, and floodplain restoration projects along the LYR.

3 METHODOLOGY

3.1 Experimental Design

The primary scientific novelty of this study is in exploring how the outcomes of different prediction approaches inform the science of riparian ecology and the practice of riparian conservation, not necessarily in producing accurate predictions. To answer the questions posed in section 1.3, an experimental design was developed using available data and data to be collected during a field campaign (**Figure 2**). This section presents the overall approach; major subroutines in the design are detailed in subsequent sections.

To answer the first question investigating how predicted recruitment locations compared to field locations of juvenile cottonwoods, the Riparian Seedling Recruitment sub-Module (RSRM; section 3.2) was used to predict seedling recruitment potential along the LYR for the years 2017-2021 and test results against cottonwood locations collected in the field. A set of spatial data inputs and the mean daily flow record was used in RSRM modeling (section 3.2.1), which produced outputs consisting of recruitment potential predictions and hydrophysical variables (section 3.2.2 & section 3.2.3). Predictions were treated as hypotheses to be tested with observations in 2022. As it was not feasible to look at every location within a ~ 10^7 m^2 area, an equal-effort, randomly stratified sampling scheme (section 3.3) was constructed for the field campaign. Sites were surveyed with a consistent observation protocol (section 3.4).

Model predictions were tested against field observations of cottonwood presence locations (section 3.5) using a previously published bioverification methodology (Kammel et al., 2016).

To answer the second question evaluating a Random Forest (RF) machine learning model's prediction accuracy for cottonwood presence/absence, a RF model was used with topographic variables and the hydrophysical outputs from the RSRM as predictor variables (section 3.6.1). Surveyed cottonwood locations from the field campaign were used as presence points, while absence points were randomly generated within the surveyed field sites (section 3.6.2). The predictor variables and presence/absence points were then used in a repeated k-fold cross-validation, which was the chosen resampling method used for RF implementation (section 3.6.3). A model performance assessment was then carried out through investigating several metrics to determine whether the RF could accurately predict juvenile cottonwood presence or absence (section 3.6.4).

For the third question, a ranking of variable importance generated by the RF was used to investigate the top ranked predictor variables and their biophysical sensibility for cottonwood recruitment (section 3.6.5). How these variables influenced the probability of predicting cottonwood presence, and how they compared between presence and absence locations was explored and analyzed.

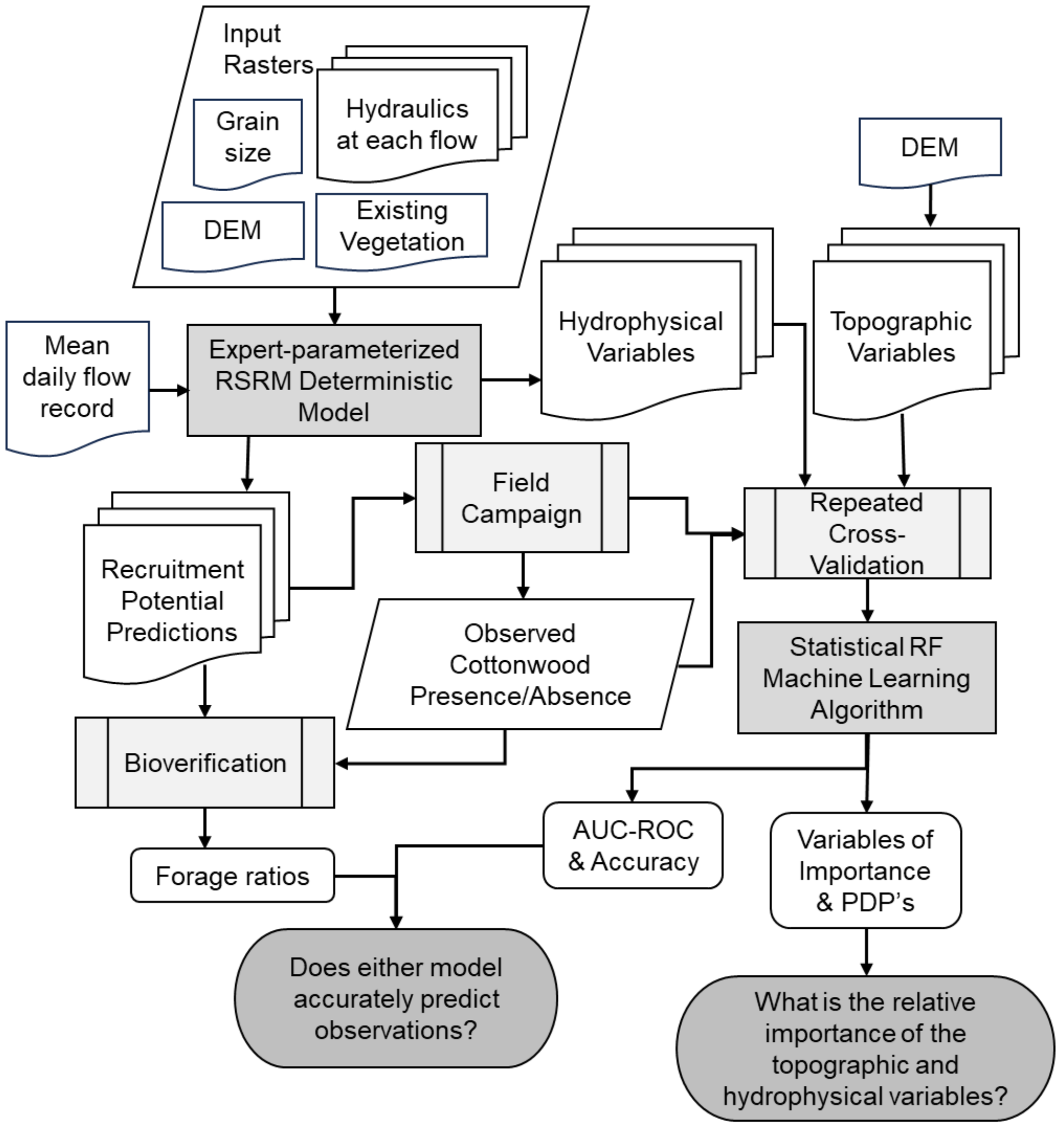

Figure 2. Experimental design and structure for the use of a deterministic and statistical model.

Most spatial analyses were performed in ArcGIS Pro (ESRI, Redlands, CA), while machine learning modeling was performed in R. Most of the data in this study was collected in American customary units and then converted to SI units, leading to non-integer values being reported in some instances where one might expect the selection of integer values, such as raster cell size.

3.2 Riparian Seedling Recruitment Sub-Module

This study used the Riparian Seedling Recruitment sub-module (RSRM) to generate testable hypotheses about locations where cottonwoods would be likely to recruit and survive the first year of life on the LYR. As this was the first application of a novel model, there were no pre-existing model parameter value sets from past calibrated models to use as a starting point to parameterize this model and inform the field campaign. Further, in the absence of any seedling observational data, model parameter sets could not be calibrated in advance. This component of the study did not seek to implement a *post hoc* framework in which the answers would be used to tune the test. Instead, the approach was consistent with how this type of model might be implemented in conservation practice for project planning and design in the absence of pre-existing data. Thus, physically realistic values were chosen on an expert basis with reference to the literature on Fremont cottonwoods and then newly collected observational data was used to test how well the model performed with the expert-based values. Commonly, models do not perform well without calibration, even when they are supposed to be physically realistic, but it is important to do that testing at the outset with a new model to help evaluate whether the scientific understanding underlying model structure and model parameterization is literally true and accurate enough for prediction.

Four hydrophysical processes were used in the RSRM to evaluate whether suitable site conditions for recruitment were met:

(1) Preparation of the bed through higher flows generating a large enough dimensionless bed shear stress to create new bare surfaces before seed dispersal,
(2) Desiccation or drought survival from stream stage and groundwater recession,
(3) Survival during prolonged inundation periods,
(4) Scour survival from flows with a high enough dimensionless bed shear stress for scouring affects after germination.

The extent of the peak modeled flows during seed dispersal was used to define areas of recruitment analysis. As an expert-based parameter selection, each of the four processes was equally weighted and given a numerical value indicating favorable (1.0), stressful (0.5), or lethal (0.0) conditions for a given cell defined by the threshold values for each process. A metric describing recruitment potential was then solved for and provided recruitment potential predictions at a 0.46-m^2 resolution.

3.2.1 Data inputs

The mean daily flow record was collected at different points along the LYR (**Table 1**). Due to the physical processes in RSRM, flow records must start two years prior to the year of interest, using May 2nd as the beginning of seed dispersal. For example, Predictions for 2017 require daily flow records from May 2, 2015 to May 2, 2018. The years analyzed in this study were 2017 to 2021, requiring the mean daily flow record for the years of 2015 to 2022.

Spatial data inputs used in RSRM modeling included topography, hydraulics, sediment grain size, and vegetation data. Topographic data and derivative variables were available from a 0.91-m resolution 2017 digital elevation model (DEM) (**Table S2**). The DEM came from a point cloud integrating airborne LiDAR, boat-based multi-beam echosounder, and ground-based RTK GPS surveys (Silva & Pasternack, 2018; Gervasi et al., 2021). Steady-state hydraulic rasters for velocity, depth, and water surface elevation (WSE) were available from TUFLOW HPC, a validated two-dimensional (2D) hydrodynamic model with outstanding performance (Pasternack, 2023; **Table S3 & Table S4**). A total of 45 flows from 8.5-2,464 m^3/s were used, covering the range of discharges that occurred on the LYR for the years of interest. Grain size data for the LYR was available from a previous study that used a machine learning algorithm based on LiDAR data and grain size samples from the field to create a sediment facies map (Díaz Gómez et al., 2022). The average grain size was approximated for regions not included within the mapped area. An existing 2017 vegetation map created from LiDAR data was used to identify areas of established vegetation (i.e., taller than 0.6 m).

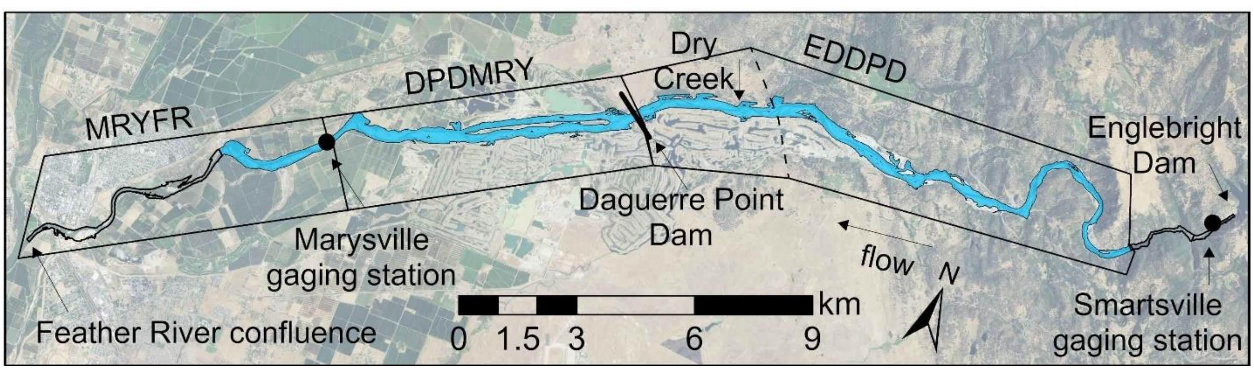

Figure 3. The LYR with the three domains MRYFR, DPDMRY, and EDDPD, gaging stations, and dams. The blue region of the river represents the section that was used for field data collection. The dashed line within EDDPD represents where this domain was split into two hydrological sections.

The study area (**Figure 3**, blue) was split into three different RSRM modeling domains for computational and analysis efficiencies. Further, the Dry Creek tributary inflow and an irrigation diversion at Daguerre Point Dam (**Figure 3**) required use of three different discharge data sources. The inflow from Dry Creek required the upstream modeling domain to be split into two hydrological sections (**Table 1**).

Table 1. Hydrologic data sources for each modeling domain.

Domain	Domain Description	Flow Data
1) MRYFR	Reach extends from just upstream of the confluence with the Feather River to 3.4-km downstream of the Marysville gaging station.	USGS Marysville gage (11421000)
2) DPDMRY	Reach extends from 3.4-km below the Marysville gaging station to just downstream of Daguerre Point Dam.	USGS Marysville gage (11421000)
3A) EDDPD (downstream)	Reach extends from to just upstream of Daguerre Point Dam to confluence with Dry Creek	The Yuba Water Agency has projected flows through 2017 for both above and below the Dry Creek tributary. A linear regression comparing the flows above and below Dry Creek was used to find the slope for flows <1,000 cfs, 1,000-10,000 cfs, and > 10,000 cfs. USGS Deer Creek gage (11418500) and Englebright near Smartsville gage (11418000) were added together. Flows were respectively multiplied by the slope for each category above.
3B) EDDPD (upstream)	Extends from just upstream of Dry Creek to Englebright Dam	USGS Deer Creek gage (11418500) and Englebright near Smartsville gage (11418000) were added together

3.2.2 Hydrophysical variables

Threshold values were set in the RSRM to evaluate whether hydrophysical processes created suitable conditions needed for seedling recruitment and survival (**Table 2**). The RSRM uses the wetted area extents for the maximum and minimum flows during the seed dispersal period to create the spatial domain for areas of possible germination. An existing vegetation map can be included to remove areas with established vegetation from analysis, as these are areas with competition for sunlight and moisture.

The preparation of the bed before seed dispersal and the scouring flows after dispersal are both analyzed through the dimensionless bed shear stress ($\tau *$) with the equation from Schwindt et al., (2019):

$$\tau *= \frac{1}{D_{84}g(s-1)}\left[\frac{u}{5.75log_{10}(12.2h/2D_{84})}\right]^2 \quad (2)$$

where D_{84} is the grain diameter approximated as D_{84}=2.2D_{50} (Rickenmann & Recking, 2011), g is the gravitational acceleration (9.81 m/s^2), s is sediment grain and water density ratio (2.68 g/cm^3), u is the water velocity (m/s), and h is the water depth (m). The dimensionless bed shear stress is calculated for each provided discharge and compared against the thresholds for partially and fully mobilized sediment transport in every cell. The flows during the 2 years prior to seed dispersal are analyzed to determine the bed preparation, while the flows after germination during the seed dispersal period through the following May are used for the scouring survival analysis.

Inverse distance weighted (IDW) interpolation is used in River Architect to spatially extrapolate the WSE raster for the river's wetted area at a given discharge to estimate the water level elevation (WLE) beyond the wetted area (Larrieu et al., 2021). When WLE < DEM, then WLE is the groundwater level. When WLE > DEM, then it is the WSE of disconnected ponds, swales, and floodplain channels. Inundation duration is tracked for every cell when the WLE has a greater value than the DEM. Consecutive days of inundation are counted throughout the inundation survival period during the seed dispersal period after germination through the following May.

Desiccation stress may occur if seedling roots cannot maintain contact with the soil moisture as WLE recedes. A recession rate of 1 cm/day was considered stressful and 2.5 cm/day was considered lethal (Amlin & Rood, 2002; Mahoney & Rood, 1998; Phillips & Pasternack, 2022; Stella et al., 2010). The mortality coefficient is used to quantify the recession rate and is calculated using a 3-day moving average for each cell, as this accounts for a time lag associated with the capillary fringe and the rate at which seedlings can grow roots (Braatne et al., 2007; Burke et al., 2009). The desiccation survival period begins during the seed dispersal period when germination begins and ends when baseflow starts.

Table 2. Criteria set for the physical processes in the RSRM by Phillips & Pasternack, 2022. The metric code was given depending on where a cell fell within the criteria for each condition. Bed shear stress was divided into the bed preparation phase and the scour survival phase.

Process	Criteria	Condition	Metric
Seed Dispersal Period	May 2 - July 4		
Bed Shear Stress (Bed preparation / scour survival)	0.047	Fully prepared / Fully disturbed	1 / 0
	0.030	Partially prepared / Partially disturbed	0.5 / 0.5
	0.000	Unprepared / Undisturbed	0 / 1
Mortality Coefficient (Desiccation survival)	< 20 days	Favorable	1
	20-30 days	Stressful	0.5
	>30 days	Lethal	0
Inundation	< 14 days	Favorable	1
	14	Stressful	0.5
	28	Lethal	0

3.2.3 Recruitment potential predictions

After applying constraints to the hydrophysical processes, the recruitment potential for a given cell is determined. The metric for each hydrophysical process is weighted by a coefficient and then the product of those terms is computed to create recruitment predictions at a 0.46-m^2 resolution (**Table 3**). For example, a cell with physical process performing at the lethal metric will result in the cell being classified as lethal for potential seedling recruitment, while a cell with every physical process performing as favorable results in being classified as optimal. This method is a common approach in environmental science and management (Leclerc et al., 1995; Renard et al., 1997). In the absence of any prior knowledge, all coefficients were given the same value of 1.0. Each hydrophysical process was weighted equally when computing the recruitment potential classes. Using the Random Forest model to determine the ranking of importance for each hydrophysical variable can provide insights for adjusting the weighting of each process for future use.

Table 3. Final recruitment potential classes from Phillips & Pasternack, 2022.

Combined Value	Stressful Parameters	Description
1	0	optimal
0.5	1	favorable
0.25	2	stressful
0.125	3	tolerable
0.0625	4	likely lethal
0	-	lethal

3.3 Field Site Selection

Random sampling is often beneficial, but it is problematic when the relative availability of different conditions is highly unequal. It will oversample abundant conditions and under-sample or entirely miss rare conditions. A solution is a stratified, random equal-effort sampling scheme (Legendre & Legendre, 1998; Zhang et al., 2020). Locations were stratified based on their RSRM-predicted recruitment potential class, and an equal number of randomly selected locations from within each class were surveyed (**Figure 4**). As a goal, ≥ 10 sites per class across the whole LYR were to be sampled, with 3-4 sites per class in each domain. Sites that were inaccessible were not considered. The study area was truncated upstream of the LYR's terminus because intense unauthorized land use and residency in the flood prone area yielded unnatural vegetation presence/absence and made field work potentially unsafe.

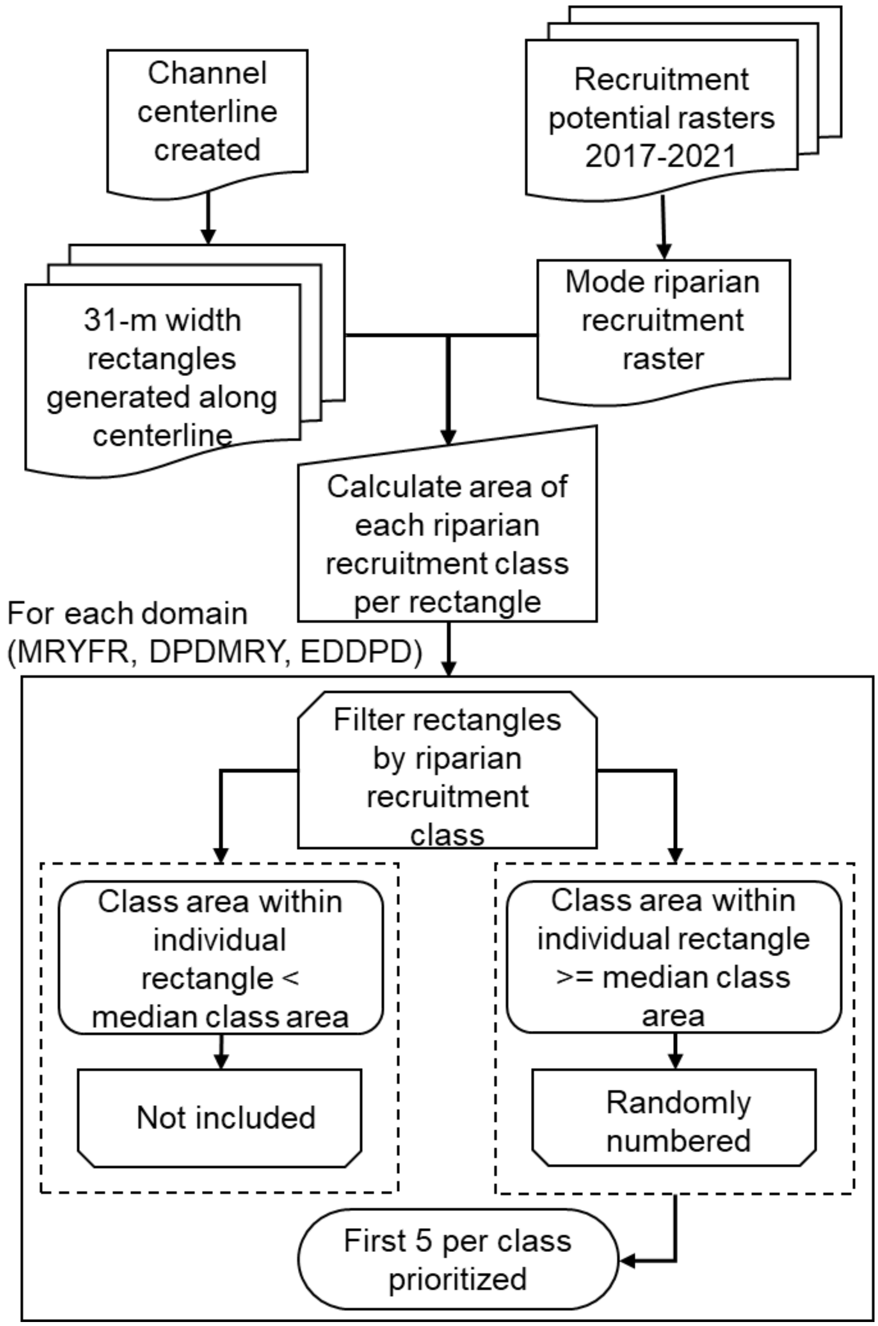

Figure 4. Workflow for field site selection. MRYFR, DPDMRY, and EDPDP model domains illustrated in **Figure 3**.

Following the method of Wyrick and Pasternack (2014), the LYR's centerline was stationed and sectioned every 31 m, laterally spanning the wetted area of the highest discharge of 2,384-m^3 in the 2015-2022 flow record. Cross-sections were then buffered out 15.5 m upstream and downstream to yield rectangles. Rectangles were split with the centerline. Due to meandering and topographic nonuniformity, rectangle lateral extents and areas varied.

The mode (i.e., most commonly occurring values) of annual recruitment potential values was calculated for each modeled grid cell along the LYR for the RSRM outputs of years 2017-2021. The area was then calculated for each mode riparian recruitment class within every rectangle. For each domain, the rectangles were filtered and grouped by the riparian recruitment class that occurred within it, with the potential for a rectangle to be grouped multiple times if more than one class occurred within it. The median area for each class within each domain was calculated and used as a baseline value for consideration of a rectangle as a potential sample site. Any rectangle with a class area below the respective median value was not included in site selection to avoid intense, costly labor to find and survey tiny areas, while rectangles with a class area above the median were randomly numbered. Rectangles randomly numbered one through five were prioritized as potential sample sites, with safety and accessibility also being considered.

3.4 LYR Field Data Collection

Field sites were mapped August through November 2022 (**Figure 5**). For rectangle sites that had cottonwoods, data was collected from every individual present. A hand-held Trimble GeoXH mapping-grade GPS was used to navigate to and mark the boundaries of each site to be surveyed. A survey-grade Trimble R8 RTK GPS receiving real-time corrections from a commercial regional benchmark network was used to record geographic coordinates (horizontal accuracy of ~ ± 3 cm) of every cottonwood observed within the site. If a slope, boundary, or other obstacle prevented close contact to the base of a tree, the GPS point was collected at the closest possible location along with the distance and compass direction to the tree; coordinates were adjusted later in ArcGIS Pro.

Observation methods differed by plant height class. For cottonwoods < 2-m tall, a tape measure and caliper were used to measure height and stem diameters, respectively (**Figure 6**). Diameters were measured above the root collar and at 50% of the height. If the tree was > 2-m tall, diameter at breast height (DBH) was recorded using a diameter tape, while height was measured using Pythagorean relationships between a set distance to the base of the tree and the angle to both the top of the canopy and the base of the tree. The angle was collected using a clinometer, while a measured distance from the base of the tree was collected using a long tape measure.

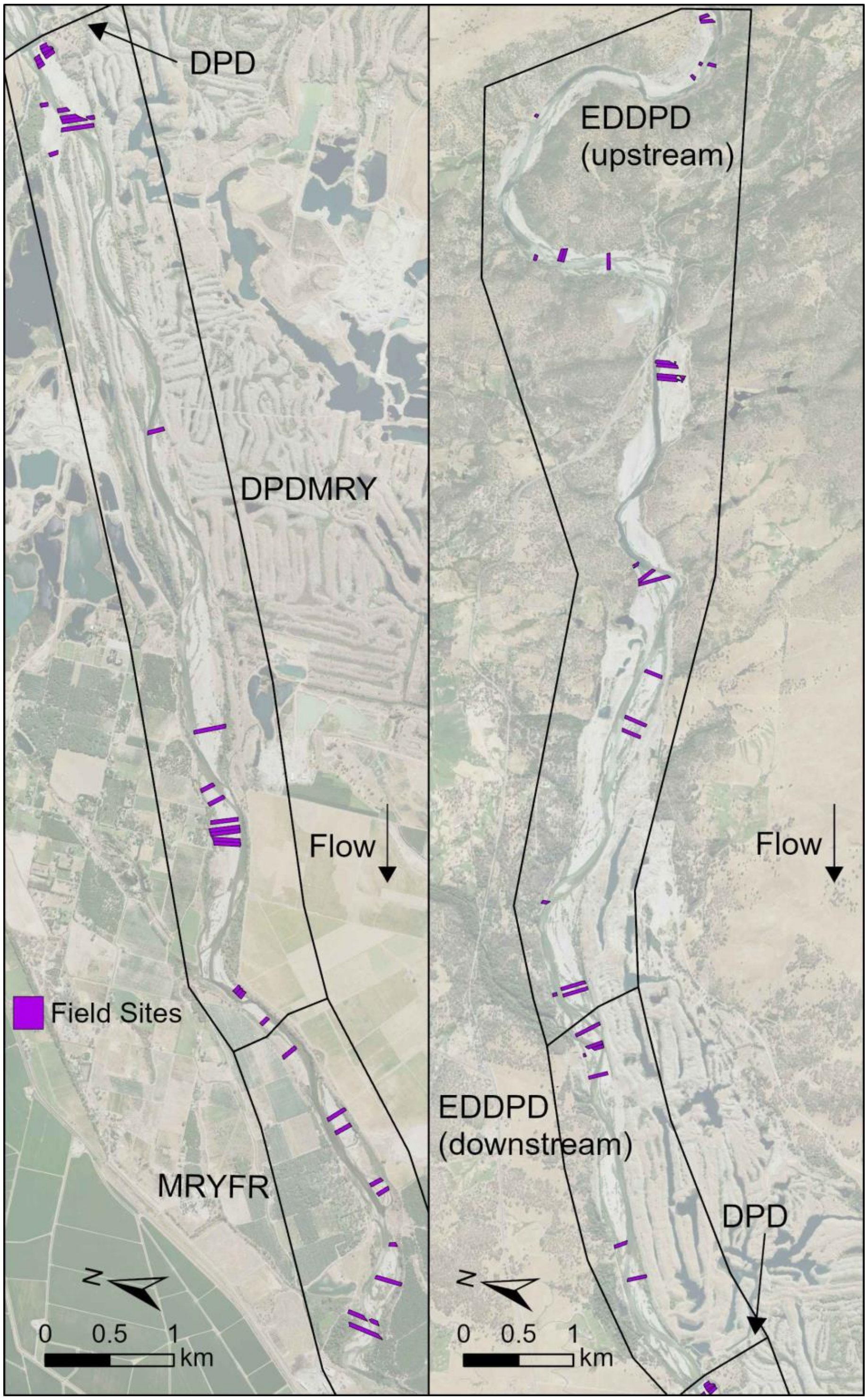

Figure 5. LYR field site locations within the modeling domains. The map is split at Daguerre Point Dam (DPD). Downstream of DPD is the left image and upstream of DPD is the right.

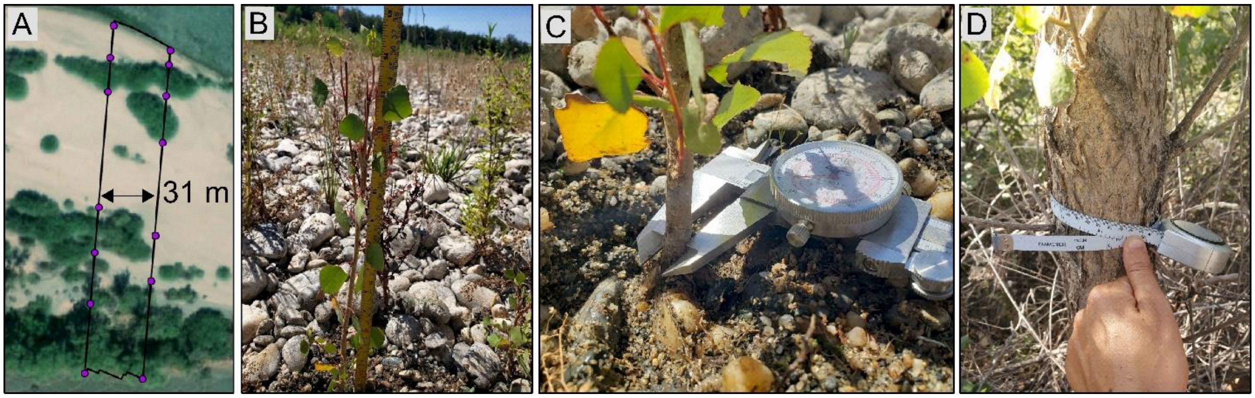

Figure 6. An example field site (A) and methods for data collection: B) measuring height with a tape measure, C) diameter above the root collar with a caliper, and D) DBH with a diameter tape.

A total of 2,957 juvenile cottonwood locations were recorded within the boundaries of 70 sampled sites. Recruitment class 0.0625 had less sampled classes due to the way the RSRM calculates recruitment classes (**Table 4**). Most sites in DPDMRY were at the upstream and downstream ends, as the middle could only be reached by kayak. EDDPD was fully accessible.

Table 4. Number of recruitment classes sampled per domain.

	Recruitment Class						
Domain	0	0.0625	0.125	0.25	0.5	1	Total # Sites
MRYFR	4	0	4	2	0	0	10
DPDMRY	5	0	7	4	6	5	27
EDDPD	6	4	6	6	6	5	33
Total # Sites	15	4	17	12	12	10	70

3.5 Bioverification

An evaluation of RSRM prediction accuracy was performed through a method termed bioverification, comparing the number of recorded locations of juvenile cottonwoods within each area of recruitment potential classes modeled (Kammel et al., 2016; Moniz et al., 2020; Pasternack et al., 2014). Bioverification uses an electivity index to evaluate two criteria. First, there must be at least one recruitment potential class exhibiting preference and at least one exhibiting avoidance to demonstrate that the model can differentiate conditions. Second, the electivity index must increase as recruitment potential increases from class to class (Kammel et al., 2016). A large number of electivity indices exist, but given the abundance and simplicity of this data, the classic forage ratio (FR) was used. It was calculated as the ratio of the percent of cottonwood observations in a recruitment potential class (i.e., percent occurrence, aka utilization) to the percent area of that class (i.e., percent availability). A FR > 1 indicates an organism's preference for a habitat, while a FR < 1 indicates an avoidance. The further from 1.0 a FR value is, the more a habitat is preferred or avoided by the designated organism. A FR ≈ 1 for a class indicates behavior indistinguishable from random and cannot be attributed to a species showing preference or avoidance for that class in the model.

When performed with other statistical tests, such as Mann-Whitney U test and statistical bootstrapping with random points, the FR has been found to be an acceptable metric for bioverification (Kammel et al., 2016; Pasternack et al., 2014). Statistical bootstrapping is a method used for determining a measure of accuracy for sample estimates, with random sets of the same sample size created and used with the test metrics to quantify the statistical confidence limits and evaluate whether the observations behave like a random variable or not. This study did not require the additional steps with statistical bootstrapping, because the results were so extreme that they could not be random, given the sample sizes.

To compute FR values, the percent utilization and percent availability were needed. The percent utilization for each class was determined by dividing the total number of juvenile cottonwoods across the sampled sites in each recruitment potential class by the total number of juvenile cottonwoods found in the whole dataset. The total area for each riparian recruitment potential class was calculated by summing the area of all sampled sites for a given class, using the 2017-2021 mode recruitment potential class values from field site selection. Total class areas were then summed to compute total model-prediction area. The percent area for each riparian recruitment potential class was then calculated by dividing each individual class area by the overall total area of predicted classes. A second set of FR values were also computed using the 2017-2021 maximum recruitment potential class values for a given cell (**Table S7; Figure S2**).

3.6 Random Forest Model

A RF supervised classification algorithm was used to address the second scientific question (**Figure 7**), modifying the RF model previously used to predict and analyze all riparian vegetation on the LYR (Diaz-Gomez & Pasternack, 2021). Two-step pre-processing was undertaken to prepare predictors (section 3.6.1) and a binary response variable of presence or absence (section 3.6.2). The values of each predictor were then extracted at each binary response variable location and used in the caret package in R (Kuhn, 2008) to perform the RF and generate hypothesis-testing metrics (section 3.6.4).

RF's are a machine learning technique that use an ensemble of decision trees that are aggregated to make a more accurate classification decision (Breiman, 2001), and have been observed to have a high classification accuracy when compared to other classification methods (Cutler et al., 2007). The number of trees used was 500 as the conservative default value needed to stabilize the prediction accuracy (Maxwell et al., 2018; Diaz-Gomez and Pasternack, 2021). The number of explanatory variables sampled at every node was between 1 and the number of variables (20), defined on a grid with a resolution of 1 (Probst et al., 2018, Zhang et al., 2020, Diaz-Gomez and Pasternack, 2021).

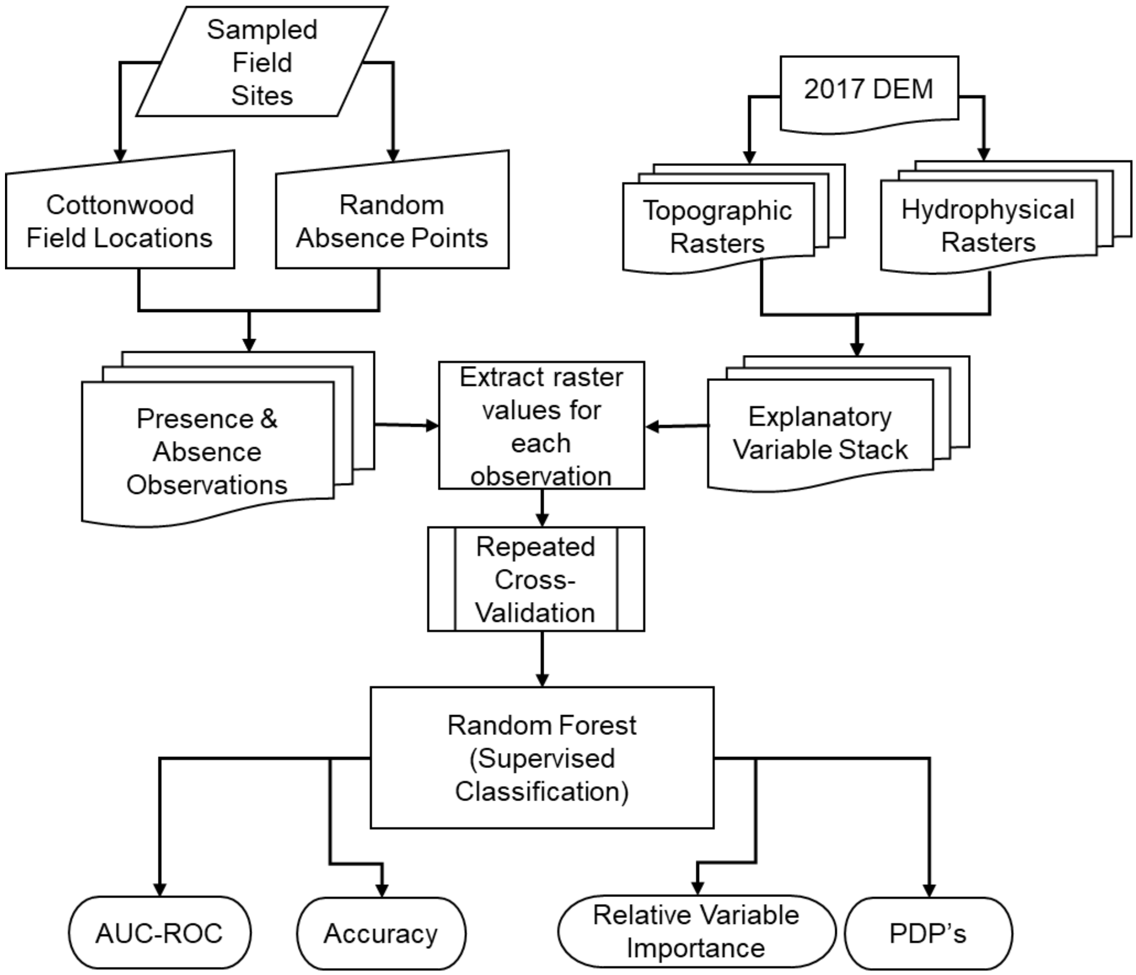

Figure 7. Processing and workflow for the RF machine learning model

3.6.1 Predictors

A total of 20 predictor variables were chosen for the classification of juvenile cottonwood presence or absence, using the four hydrophysical variables from the RSRM and 16 DEM-derived topographic features characterizing the terrain in 2017 (**Table S5**). The RSRM creates 0.46-m resolution rasters for the four 2017 hydrophysical rasters, which were later resampled to the same 0.91-m resolution as the DEM and the subsequent topographic variables. Topographic variables were numerically continuous, while hydrophysical variables had three discrete values (**Table S5**)

3.6.2 Binary class variable

For the supervised classification, cottonwood presence and absence was used as the binary class variable. Field locations of juvenile cottonwoods were used to indicate presence cells at 0.91-m resolution. Cells that fell within cottonwood clusters were classified as presence, with no differentiation made between cells containing one or more cottonwoods. As a result, the 2,957 observed juvenile cottonwood locations were reduced to 1,349 presence cells. An equal number of absence cells were randomly created without duplication in any one cell within surveyed sites after excluding presence cells, resulting in a total of 2,698 samples for model training and testing.

3.6.3 Implementation

The repeated k-fold cross-validation resampling method was used for RF implementation, where k indicates the number of groups the dataset is split into (10 herein). The observations at 0.91-m resolution were divided into 10 subsets (or folds) of equal size, each with 269 samples. One group is taken as a holdout for model validation while the remaining nine are used to train the model. This process is then repeated 10 times until every fold has both trained and validated the model. The repeated k-fold cross validation effectively captures the generalization performance of the RF model, by ensuring that the predictive model's skill report does not depend on the way that training and testing data are chosen, which in this case is the difference between the model estimated and true values (Kuhn & Johnson, 2013).

3.6.4 Model performance analysis

Just as the bioverification framework used to test the RSRM had two criteria - one to demonstrate predictability in terms of differentiation of locations and another to demonstrate that the directionality of how variables worked matched biophysical mechanistic sensibility - RF performance testing must also achieve both of those outcomes. The performance analysis of the RF model serves the first need and was assessed through several performance tests. The first few metrics were through an averaged confusion matrix to visualize the accuracy and relative error among presence and absence classes using the hold out testing data, for each of the 10-folds from the 10 repetitions. The matrix portrays the number of correct and incorrect predictions by the RF and relates the overall accuracy, producer's and user's error, and omission and commission errors (Fawcett, 2006; Sokolova & Lapalme, 2009). The accuracy is calculated as the number of correct predictions to the overall number of predictions, relaying the effectiveness of the model. The producer's accuracy portrays the sensitivity, the ratio of correctly classified presence points, and the specificity, the ratio of correctly classified absence points. The best sensitivity or specificity is 1.0, meaning all the predictions were correct, while 0.0 would be the worst. Omission and commission errors respectively represent the reference or classified cells omitted from the correct class, with a balance between these errors as the ideal. These metrics provide a deeper understanding of the performance of the model beyond the accuracy, portraying how well it classified both presence and absence, which may not result in the same ratio value.

The next assessment used the area under the curve (AUC) for the receiver operator characteristic (ROC). The ROC plots the proportion of true positives (i.e. proportion of presence points correctly identified as presence) on the y-axis against the proportion of false positives on the x-axis (i.e. proportion of absence points classified as presence) (Fawcett, 2006). The ROC space is conceptually simple, with the point (0, 0) representing no positive classifications, the point (0, 1) representing unconditional positive classifications, and the point (1, 0) representing a perfect classification. The AUC indicates the area between the ROC curve and the diagonal from (0, 0) to (1, 1) and represents the probability that a randomly chosen positive instance will rank higher than a randomly chosen negative instance (Fawcett, 2006). It ranges from 0 to 1, with 0.5 indicating random predictions, equaling the diagonal line the area is calculated between, and 1.0 indicating a perfect classification, with no realistic classification model having an AUC<0.5 (Fawcett, 2006).

3.6.5 Predictor variable importance

A strength of the RF algorithm is the ability to generate a ranking of variable importance. The permutation based feature importance was used, which is measured by the decrease in the model's prediction accuracy when a variable is permuted (Breiman, 2001). Partial dependence plots (PDP) were also used to further examine the marginal effect a variable has on the predicted outcome of the model when all other explanatory variables are held constant at their mean values (Friedman, 2001). In this study, it would be the effect a predictor has on the probability of the RF model predicting cottonwood presence, allowing a visual to examine how the probability of predicting presence increases or decreases as the variable value changes. These metrics help interpret the contribution of individual predictors to the overall performance of the Random Forest model, and by inference perhaps to explain how the natural phenomenon works mechanistically.

To further evaluate biophysical mechanistic sensibility, the median value (i.e., middle value within a dataset) for the more important predictors was inspected to evaluate differences in presence and absence locations. Then, directionality of the predictor-cottonwood relationship and the predictor extent of presence and absence conditions were vetted against biophysical reasoning and evaluated. For example, if the model were to predict that presence points were at a detrended elevation corresponding to the bottom of pools in the river, then there might be high statistical predictability in the model but it is biophysically wrong, as cottonwoods cannot recruit at that type of permanently inundated location. To be considered an accurate and useful model, important variables were not only considered statistically important for prediction but also biophysically realistic and meaningful to understand the natural phenomenon of cottonwood recruitment.

4 RESULTS

4.1 Cottonwood Recruitment Patterns

A higher density of cottonwoods was located downstream of DPD than upstream of it (**Figure 8**). Downstream of DPD recruitment for seedlings that germinated in the

2022 summer was observed to be in sporadic dense patches, located mostly on lateral and point bars, islands, or along backwater and abandoned channels. Newly formed and dynamic islands were also found to have dense clustering of seedlings. Juvenile cottonwoods that were not in their first growing season were found in scattered stands among other riparian species, such as willows, or by themselves. There were dense and robust stands of mature cottonwoods observed in these regions.

Upstream of DPD, a dense seedling cluster was found on an active point bar. However, juvenile cottonwood locations were more scattered and individual in this section. Moving upstream, the surfaces became barer and had less vegetation present. A smaller number of mature cottonwoods was observed in this segment.

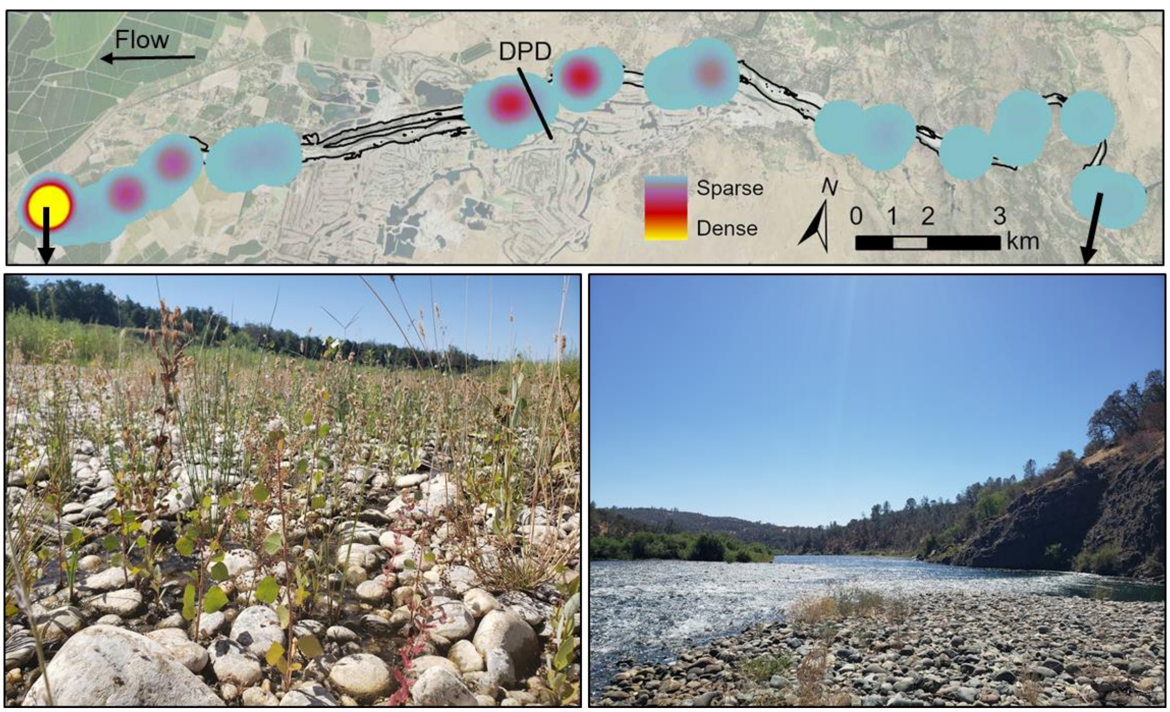

Figure 8. Heat map of surveyed cottonwoods along the LYR with two perspectives, one downstream of DPD and one above.

4.2 Question 1: Does the RSRM Bioverify?

Among the total of 2,957 young cottonwood presence locations used in the forage ratio (FR) calculations, 1,408 presence points were located within RSRM modeled results and 1,550 presence points were outside modeled areas (because the RSRM considers this area beyond the modeled wetted area during seed dispersal). Four recruitment potential classes had FR values indicating avoidance, while one ("tolerable") had a value indicating preference (**Table S6; Figure 9**). These results meet bioverification criteria one but fail criteria two. Criteria one requires the occurrence of both preference and avoidance to be exhibited by separate classes, which can be seen in **Figure 9**. Criteria 2 requires that the FR, the percent of cottonwood occurrence to the percent area available for each recruitment class, increase as the recruitment potential increases, which did not occur. The FR calculated using the 2017-2021 maximum recruitment potential class values did not change overall results (**Table S7; Figure S2**).

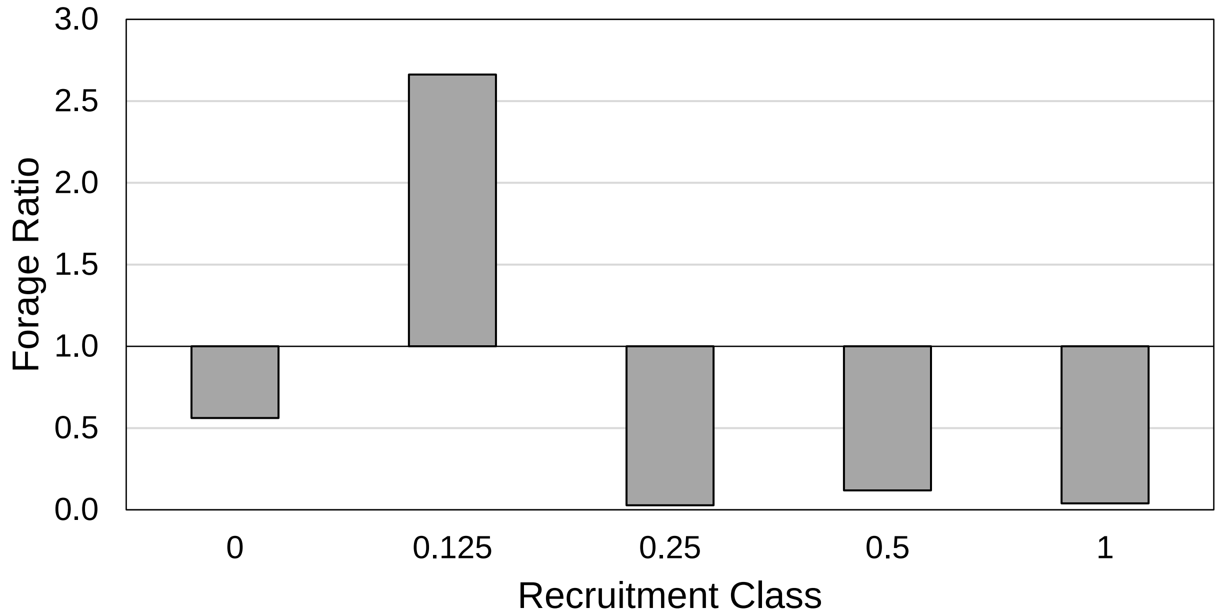

Figure 9. Forage ratio test results using the 2017-2021 mode recruitment class values for the expert-parameterized implementation of the RSRM. The class that represented “tolerable” recruitment potential was the only one that resulted in a FR indicating preference.

4.3 Question 2: Does the RF Model Accurately Predict Presence and Absence?

When compared with the testing data, the averaged confusion matrix of the Random Forest prediction portrayed an overall accuracy of 87% of correctly predicting either an absence or presence point with a p-value < 2e-16 (**Table 5**). For cottonwood presence the producer’s accuracy (sensitivity) was 89% (omission error of 11%) and the user’s accuracy was 86% (commission error of 14%). For cottonwood absence the producer’s accuracy (specificity) was 85% (omission error of 15%) and the user’s accuracy was 88% (commission error of 12%). In other words, 89% of cottonwood presence cells were predicted to be presence cells, while 14% of absence cells were predicted to be presence cells. On the other side, 85% of cottonwood absence cells were predicted as absence, while 12% of presence cells were predicted to be absence.

The RF model had a higher accuracy for predicting presence, while still obtaining the goal of having a good balance between the producer and user accuracies for presence and absence. The model performed well with an AUC-ROC of 94% (**Figure 10**), reaching this value with 8 variables available at each tree node (**Figure 11**). Remarkably, even a single variable produces an AUC-ROC > 90% and adding just three more variables increases the result to 93%.

Table 5. The averaged confusion matrix for the RF repeated cross-validation scheme. The bolded values represent the correctly classified observations.

Prediction	Reference			
	Absence	Presence	Total	User Accuracy
Absence	**1147**	151	1299	88%
Presence	202	**1198**	1400	86%
Total	1349	1349	2698	
Producer Accuracy	85%	89%		

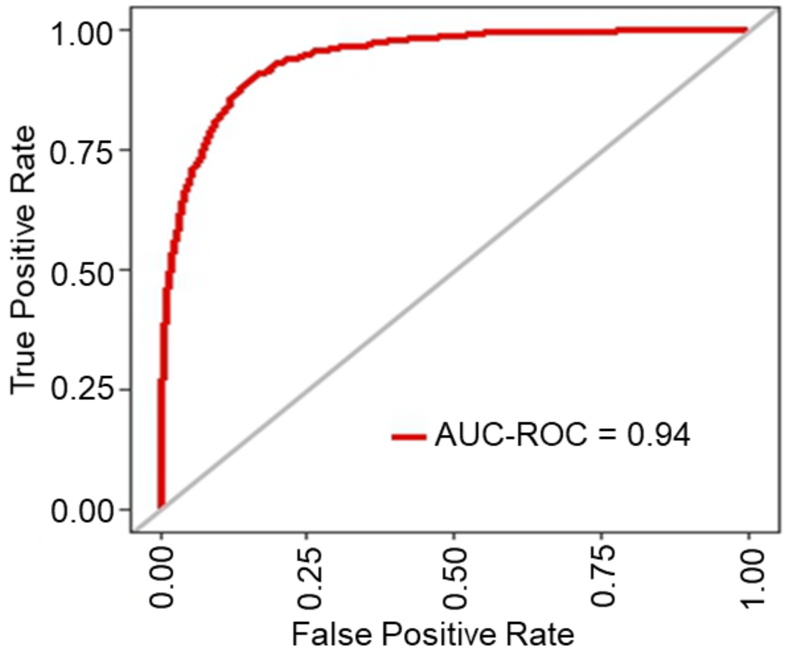

Figure 10. The AUC-ROC curve for the RF model

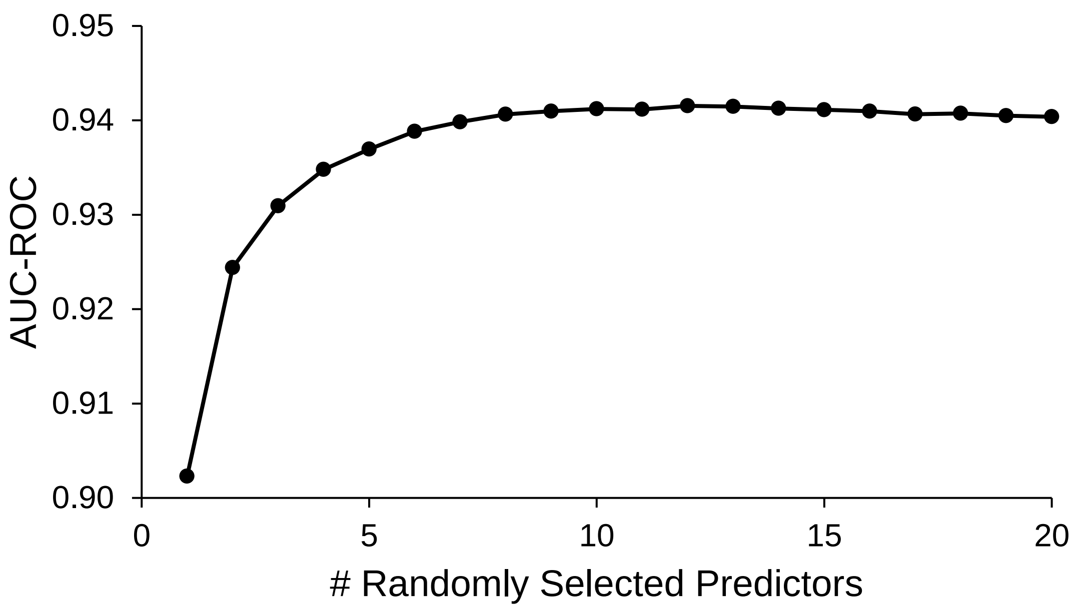

Figure 11. AUC-ROC value by number of randomly selected predictors.

4.4 Question 3: Drivers for Cottonwood Presence and Absence?

For predicting the presence/absence of young cottonwoods, the top four most important variables include detrended DEM, channel proximity, inundation survival, lateral relative aspect, and the vector ruggedness measure (VRM), based on the RF-generated variable importance ranking (**Figure 12**). Inundation survival was the only hydrophysical variable in the top five, with the other most important being topographic variables. The biophysical realism of these variables was further investigated with PDPs.

The detrended elevation, which was found to be the most important predictor variable, was a representation of the land surface when the down valley slope is removed while still preserving local topographic variations. It was assigned a relative importance of 100%, with all the following variables' relative importance compared against it. The probability of cottonwood presence increased from detrended elevations of 0 to 2 m before a sharp peak, then decreased as the elevation increased further (**Figure 13**), which is consistent with the logic of cottonwood recruitment. Channel proximity was the 2nd ranked variable with relative importance of 71% (**Figure 12**). The predicted outcome of cottonwood presence decreased as the distance to the channel increased (**Figure 13**), which is also realistic. Inundation survival was 3rd at 43% in terms of predictive power, however, PDP showed a negative relationship between presence probability and more favorable inundation metrics (i.e., the probability of presence predictions decreased as inundation become more favorable), which is not initially biophysically sensible (**Figure 13**). Lateral relative aspect was 4th at 21% (**Figure 12**). The presence probability initially decreased as lateral relative aspect increased from -1.0 (facing towards the river) to -0.75, before stabilizing until the probability decreased again at around 0.75 (facing away from the river) (**Figure 13**), which is realistic. Vector ruggedness measure (VRM) was close behind the lateral relative aspect, with a relative importance of 20% (**Figure 12**). The probability of cottonwood presence being predicted increased rapidly following a VRM of 0.0, before decreasing after a sharp peak and then stabilizing after a value of 0.02 (**Figure 13**). Based on these results, inundation survival was then removed from the predictors and the RF model was applied again to compare model performance and the ranked variables of importance (**Figure S4**). The accuracy was similar and the detrended elevation and channel proximity remained the two most important variables.

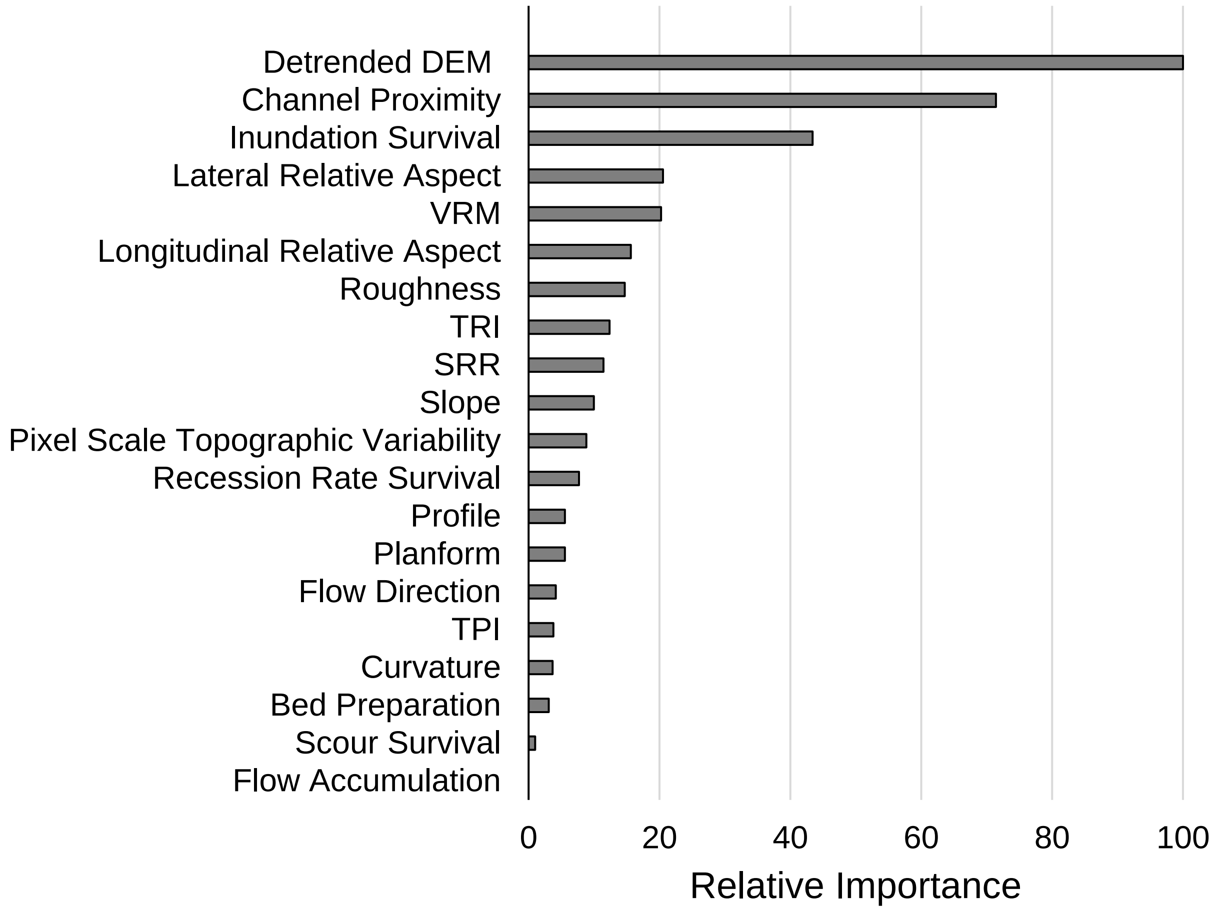

Figure 12. Relative contribution of variable importance for the RF model's predictions of cottonwood pres ence and absence. The most important variable is identified and assigned an importance of 100%, with the other variables ranked relative to it.

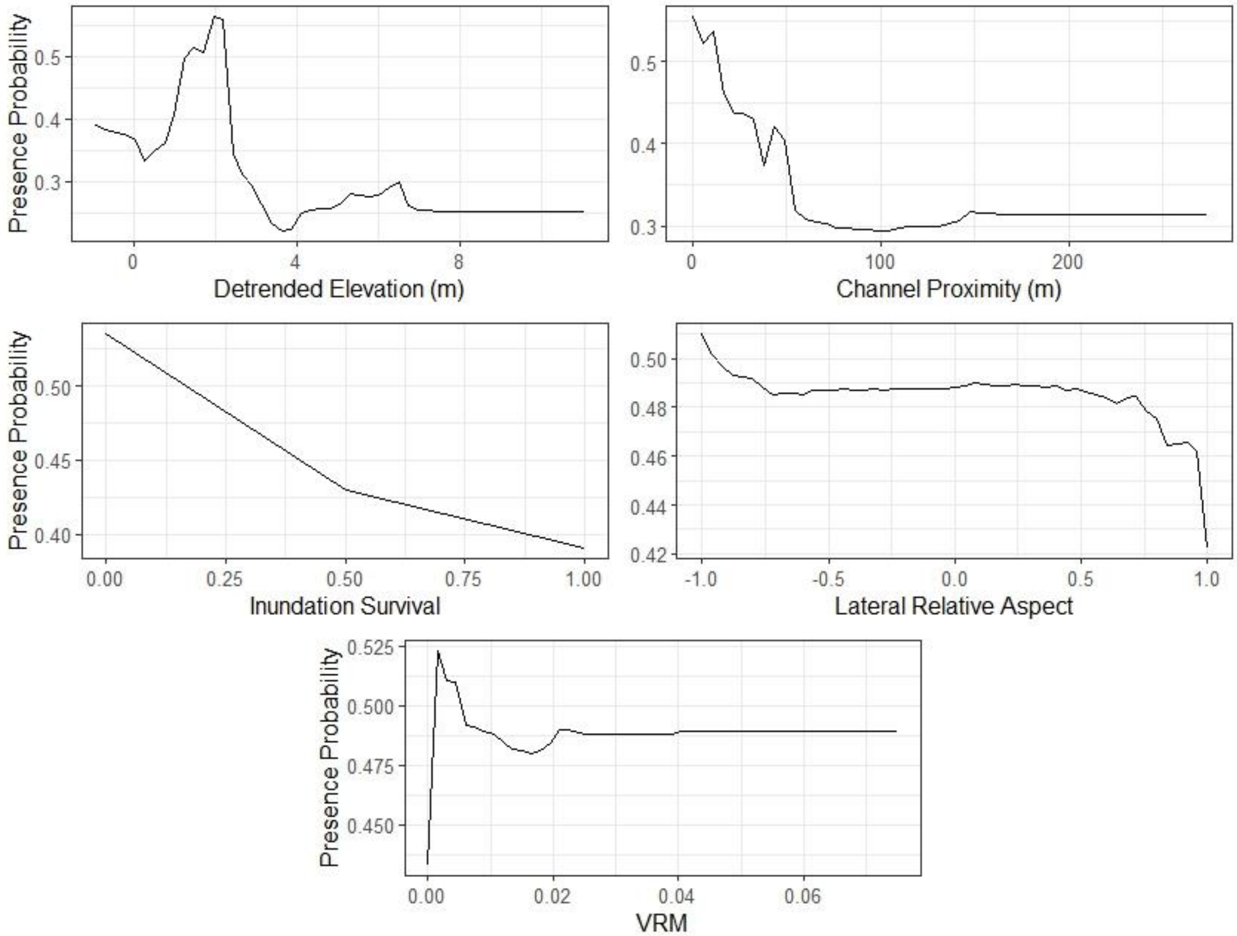

Figure 13. Partial dependence presence probability for the top four explanatory variables: detrended elevation (m), channel proximity (m), inundation survival, lateral relative aspect, and vector ruggedness measure (VRM). The black line represents the mean marginal response when the other explanatory variables were kept constant.

The median and lower/upper quantile values for the top five explanatory variables was further examined to interpret biophysical realism (**Table 6**). For the detrended elevation, presence cells were found at a lower elevation than the absence points. The upper quantile value for presence was equivalent to the lower quantile value for the absence cells. Presence cells also occurred closer to the wetted baseflow channel than the absence points. For the inundation survival, presence cells occurred at a lethal inundation and the absence cells at a favorable inundation. The median lateral relative aspect for presence was negative, indicating pixels facing towards the river while the absence points faced away. The VRM was similarly very small for both presence and absence, with an average presence VRM of 0.0018 and absence VRM of 0.0016.

Table 6. Median, lower quantile (LQ), and upper quantile (UQ) values of the presence and absence points for the top five most important explanatory variables.

	Presence			Absence		
Predictor	LQ	Median	UQ	LQ	Median	UQ
Detrended Elevation (m)	1.3	1.6	2.4	2.4	3.3	4.1
Channel Proximity (m)	0.0	5.4	19.9	14.1	36.4	65.5
Inundation Survival	0	0	1	1	1	1
Lateral Relative Aspect	-0.96	-0.09	0.97	-0.78	0.53	0.95
VRM	6E-05	2E-04	1E-03	8E-05	3E-04	1E-03

5 DISCUSSION

5.1 Understanding RSRM Results

After comparing the RSRM results with locations of juvenile cottonwoods throughout the LYR, the uncalibrated, expert-based model was found to not bioverify. The test seemed to result in random results that did not necessarily indicate habitat preference or avoidance. This could be a reflection or culmination of many factors including: 1) a time lag between the years analyzed with the RSRM, cottonwood mortality and morphological disturbances that occurred during that time, and when field surveys occurred; 2) parameters used and the importance of local environmental factors and initial conditions; 3) unrecognized differential sensitivities of the parameter criteria used.

While the RSRM produces recruitment predictions for a seedling after its first year of life, it does not account for mortality that may have occurred after. Site selection for field data collection was based on the mode RSRM results for 2017-2021, so it is difficult to determine model accuracy if most seedlings died in earlier years. In addition, during the five years between the collection of data to create the 2017 DEM and the 2022 field season for this study, a few floods occurred and caused local geomorphic changes, potentially degrading model accuracy- though the same issue faced the RF model and it still yielded excellent performance. Many locations had minor to no changes, but particularly some depositional locations were highly prone to dynamism wherein the channel completely migrated and left behind abandoned or remnant channels. This resulted in the RSRM not being able to make predictions that reflected the current streambank or in areas with newly formed islands or land features. As erosional and depositional processes are important for the creation or disappearance of new or bare surfaces and the location of the wetted channel for access to water are important for seedling recruitment, morphological changes need to be acknowledged. Without the monitoring of sites for each of these years the RSRM was used, a complete evaluation is difficult.

While the criteria and thresholds set for the hydrophysical processes in the RSRM (**Table 2**) was chosen based on existing scientific literature, site specific decisions based on local factors need to be considered (Stella et al., 2010). It is also difficult to compare criteria and results from differing studies due to variations in experimental designs and environmental conditions (Politti et al., 2018). An uncertainty exists in the criteria set for the RSRM, as chosen values may not apply well to the LYR or using the same threshold values for the entire extent of the LYR may have been too general.

The sensitivity for one or more parameters could be high, impacting the success of results even if the values chosen were close to being suitable for the LYR. Smaller sections that were carefully selected and studied may have been necessary for a more successful validation of the RSRM. A propagation of error from the 2D modeled hydraulic inputs, interpolation of the WLE, and the modeling of the RSRM itself may have also impacted results. The RF relative importance analysis suggests that different variables have unequal roles, and so the choice of equal weighting of hydrophysical variables in the RSRM may require re-assessment.

There could also be other factors or processes that were not considered in the development of the RSRM. Variables relating to the climate or location and number of mature cottonwoods that may release seeds relative to model predictions were not included. The RSRM considers seeds dispersed by water but does not account for seeds dispersed by wind and deposited in areas not expected by the model. While seeds are typically dispersed by water, seeds dispersed by wind may be deposited within a few hundred meters or several kilometers through convective wind currents from the seed-dispersing tree (Braatne et al., 1996). A larger density of juvenile cottonwoods was in the sampled sites located below Daguerre Point Dam when compared to the upstream sites. One factor that may be contributing to this is that more robust and expansive riparian forests with mature cottonwoods were observed in this area, potentially producing a larger number of seeds to recruit on suitable surfaces. There could also be a role for the generally erosional setting upstream of DPD and depositional setting downstream of it (Carley et al., 2012), though that can change through time (Gervasi et al., 2021).

5.2 Cottonwood Presence and Absence

Despite some floods and morphodynamic changes from 2017 to 2022, the Random Forest (RF) model was able to accurately predict juvenile cottonwood presence and absence in 2022 based on conditions in 2017, as indicated by performance assessment metrics. An accuracy of 87% was achieved for correctly predicting cottonwood presence or absence. Sensitivity was larger than the specificity, indicating the model was better at correctly predicting presence locations versus absence. AUC-ROC was high, reflecting optimal performance by the RF (Fawcett, 2006). The RF had a strong performance, similar to other binary RF classification models (Cutler et al., 2007; Maxwell et al., 2018), suggesting that the predictor variables provided enough useful environmental information to identify characteristics of cottonwood recruitment locations.

The two most important variables from the RF were detrended elevation and channel proximity, which are indicators for depth to the water table and flood inundation depth. The directionality of the statistical relations aligned with observations in the field and expectations from cottonwood literature and is observed in a visual representation of predicted cottonwood presence or absence along a small section of the LYR (**Figure 14**). Juvenile cottonwoods were found to be at lower elevations and closer to the baseflow channel when compared to the absence points, likely having been deposited on the moist substrate during receding flows. Seedlings that had recruited along the active margin of the channel were mostly located in dense clusters on the edges of point and lateral bars, which have the geomorphic surfaces and sediment processes needed to create suitable bare surfaces for cottonwood seedling recruitment (Braatne et al., 1996, 2007; Mahoney & Rood, 1998). In one location of dense clustering, the migration of the active channel had created large extents of new bare surfaces, allowing a large band of new recruitment.

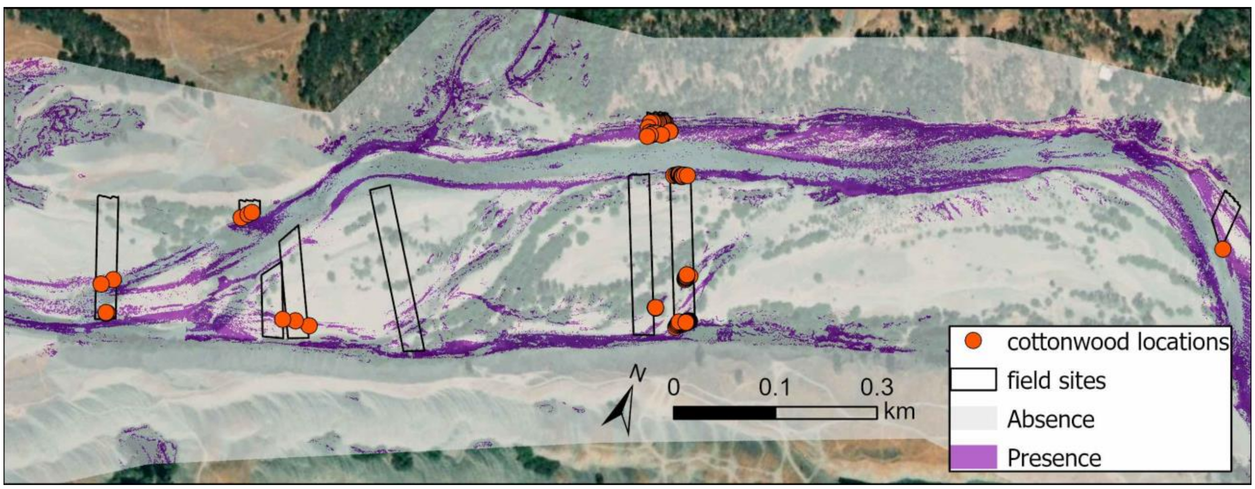

Figure 14. An example of the RF's predicted cottonwood presence (purple) or absence (grey), with surveyed juvenile cottonwood locations within the sampled field sites.

Inundation survival was ranked as the 3rd most important variable, with presence points having a median value of lethal inundation and absence having favorable inundation value. This is opposite to what was initially hypothesized yet was analyzed for biophysical sensibility. Seedlings that recruited on new or bare surfaces close to the baseflow wetted area would experience longer durations of inundation when compared to those that recruited at higher elevations. New recruits in risky locations may have been modeled in the lethal inundation zones by the RSRM. Changes that have occurred in active areas of the channel margin since 2017 may also have an influence. Recruitment since 2017 has occurred on newly created surfaces close to the channel that did not exist in 2017, which may have been modeled as inundated by the RSRM. The absence points were located further away from the active channel and may have experienced short or no periods of inundation. The ideal conditions of abandoned or remnant channels may have also been captured. Many abandoned channels below Daguerre Point Dam had been extensively colonized by juvenile cottonwoods, as the process of fine sediment deposition as the abandoned channel dewaters creates ideal moist surfaces and conditions for rapid colonization by pioneer species (Stella et al., 2011). Colonized abandoned channels above Daguerre Point Dam were not observed.

Long term survival for many of these recruited seedlings is not probable due to their location relative to the river water surface level during higher flow events, as they are likely to be scoured when sediment is mobilized. Cottonwood seedlings that had survived beyond their first few growing seasons and large cottonwood trees were observed in backwater areas or within willow and cottonwood bands on point bars and high on the riverbank far from the late summer stage position when the field sampling occurred.

Presence points were also more likely to face towards the river then away, as shown by the 4th most important variable being lateral relative aspect. The lateral relative aspect is linked to hydraulic and sediment processes (Díaz Gómez et al., 2022), and may also be associated with the deposition of seeds that were transported by water. While the vector ruggedness measure (VRM) ranked 5th in this study, it was the most important influencer in another study on the 2017 riparian vegetation of the LYR (Diaz-Gomez & Pasternack, 2021). The median VRM for presence and absence points were similar, but the presence points had a larger average VRM than the absence points. VRM expresses heterogeneity in the surface by representing both aspect and slope, indicating that micro-variability in the terrain is needed for cottonwoods to recruit and establish.

5.3 Management Implications

The ability to accurately predict cottonwood seedling recruitment locations along a dynamic, regulated river is useful for informing riparian revegetation efforts and planting projects. Areas where seedlings naturally recruit indicate desirable locations and environmental characteristics that could be used to maximize recruitment opportunities for cottonwoods when managing river flows during varying water years. The identification of recruitment areas and their environmental characteristics can also help to inform manual plantings, which are used as a common cottonwood revegetation method (González et al., 2018). Plantings have the benefit of human site selection in areas determined to be favorable and may not be as vulnerable as a newly germinated seedling. The success of a planting does not first depend on disturbance flows to create new, bare surfaces, and larger plantings with already present roots may not be as at risk to receding water table levels or scouring flows. Yet a revegetation effort may fail due to unaddressed underlying factors (Briggs et al., 1994; Stromberg, 2001) and if a chosen site was suitable at one point in time, fluvial morphodynamics can cause site suitability to change on a frequency set by the disturbance regime. While many planting projects may report high mortality rates, is this necessarily a sign of failure? Natural mortality occurs in seedling recruitment, so mortality should be expected with plantings too. A realistic planting mortality threshold for “success” should be defined to achieve the desired result for a revegetation effort.

Although the RSRM was not calibrated, it was used in a way that is common in management practice, so study results have consequences for professional practice. Commonly, projects are done at sites lacking long-term monitoring data or the breadth of scientific investigations done over the last two decades on the LYR. As a result, practitioners rely on literature and their expert judgment for whatever models they are applying. The results of this study suggest that the underlying science to make a mechanistic predictive model is still missing key factors. It is particularly puzzling when the RF model yielded remarkably accurate results from just two very simple topographic inputs. Thus, how topography asserts itself through a “mechanistic chain” of cause and effect is highly nontrivial and still elusive to simulate, necessitating further work. It may also be that the RSRM would be successful in a different setting than the LYR.

The LYR is a dynamic river, and so are many others around the world, so it is important to have tools that can be effective as rivers change. Full morphodynamic modeling is plausible but still experimental (Camporeale et al., 2013) and highly computationally expensive for long river segments at meter resolution. The DEM and hydraulic spatial data from 2017 were used in this study to model recruitment through 2021, which meant that the morphological changes to the LYR since 2017 were not accounted for. This is a realistic constraint as agencies or organizations involved in river management efforts may be limited by money, making infeasible yearly monitoring and the frequent updating of large river datasets (i.e., high resolution DEM, vegetation, substrate, etc.). The ability to accurately model cottonwood seedling recruitment, or the recruitment of other pioneer species, using datasets that are not updated on a frequent basis is a valuable tool for the planning and implementation of river revegetation projects. At this time, machine-learning modeling outperforms mechanistic modeling in this context.

6 CONCLUSIONS

This study found that the novel Riparian Seedling Recruitment sub-module did not bioverify, which could be due to time lags between the years modeled and when field work occurred, uncertainty in the parameter’s due to local conditions, or sensitivity in the chosen criteria. While the RSRM did not bioverify, the RF model was successful in predicting the presence or absence of juvenile cottonwoods. This indicates that there is enough useful information available about the environmental characteristics of juvenile cottonwood locations needed to predict recruitment. Detrended elevation and channel proximity were ranked as the two most important predictor variables by the RF. The methods described in this study could be used to help inform revegetation efforts through natural recruitment or manual plantings, potentially resulting in more cost-effective and successful projects. Care should be taken to study the characteristics of a given site to make sure model criteria are suitable.

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