

Global sensitivity analysis for complex ecological models: a case study of riparian cottonwood population dynamics

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Abstract. Mechanism-based ecological models are a valuable tool for understanding the drivers of complex ecological systems and for making informed resource-management decisions. However, inaccurate conclusions can be drawn from models with a large degree of uncertainty around multiple parameter estimates if uncertainty is ignored. This is especially true in nonlinear systems with multiple interacting variables. We addressed these issues for a mechanism-based, demographic model of *Populus fremontii* (Fremont cottonwood), the dominant riparian tree species along southwestern U.S. rivers. Many cottonwood populations have declined following widespread floodplain conversion and flow regulation. As a result, accurate predictive models are needed to analyze effects of future climate change and water management decisions. To quantify effects of parameter uncertainty, we developed an analytical approach that combines global sensitivity analysis (GSA) with classification and regression trees (CART) and Random Forest, a bootstrapping CART method. We used GSA to quantify the interacting effects of the full range of uncertainty around all parameter estimates, Random Forest to rank parameters according to their total effect on model predictions, and CART to identify higher-order interactions. GSA simulations yielded a wide range of predictions, including annual germination frequency of 10–100%, annual first-year survival frequency of 0–50%, and patch occupancy of 0–100%. This variance was explained primarily by complex interactions among abiotic parameters including capillary fringe height, stage–discharge relationship, and floodplain accretion rate, which interacted with biotic factors to affect survival. Model precision was primarily influenced by well-studied parameter estimates with minimal associated uncertainty and was virtually unaffected by parameter estimates for which there are no available empirical data and thus a large degree of uncertainty. Therefore, research to improve model predictions should not always focus on the least-studied parameters, but rather those to which model predictions are most sensitive. We advocate the combined use of global sensitivity analysis, CART, and Random Forest to: (1) prioritize research efforts by ranking variable importance; (2) efficiently improve models by focusing on the most important parameters; and (3) illuminate complex model properties including nonlinear interactions. We present an analytical framework that can be applied to any model with multiple uncertain parameter estimates.

Key words: CART; demographic model; global sensitivity analysis; model uncertainty; *Populus fremontii*; Random Forest; Sacramento River.

INTRODUCTION

Effective ecosystem conservation necessitates a mechanistic understanding of the complex interrelationships among multiple biotic and abiotic factors (Nelson 2005). This is especially true when management decisions must be made in the face of changing future conditions (Agardy et al. 2005), where factors such as climate change and invasive species can dramatically alter the trajectory of populations. Demographic modeling is a valuable tool in understanding complex ecological systems and directing conservation and land-use policies

(Morris and Doak 2002). These models are typically created using data gathered from existing data sets, published literature, and controlled experiments that were not necessarily conducted for the express purpose of parameterizing models. This approach inherently results in models with parameter estimates of varying accuracy due to the availability and quality of existing data sets (Beissinger and Westphal 1998). Furthermore, the parameters with the most available data are not necessarily the parameters that have the greatest effect on model predictions, and in some cases, empirical data may be lacking for parameters that can drastically alter model predictions (Biek et al. 2002, Beissinger et al. 2006). Therefore, before applying ecological models to address conservation problems, it is important to understand the sensitivity of model outcomes to the

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intrinsic uncertainty in parameter estimates (e.g., Nicholson and Possingham 2007, Naujokaitis-Lewis et al. 2009, Fullerton et al. 2010).

Sensitivity analyses offer a vital tool for quantifying the effects of input parameters on model predictions, thereby providing insight into which parameters may be most influential in an ecological system (e.g., Fieberg and Jenkins 2005, Cariboni et al. 2007). These analyses can also indicate which parameters require precise estimates for models to yield accurate predictions. Although sensitivity analyses are often used in applied ecological modeling, the majority of analyses hold all but one parameter in a model constant while quantifying the effect of altering a single parameter (reviewed in Naujokaitis-Lewis et al. 2009). These methods, known as local sensitivity analyses or one-at-a-time methods (Fieberg and Jenkins 2005, Cariboni et al. 2007), are useful in some contexts, but can be problematic in more complex models for two key reasons. First, if there is uncertainty in the other model parameters, then it is unclear at what constant values these parameters should be held while a single value is varied. This decision can have substantial effects on the outcome of the analysis (Wagner 1995). Secondly, in ecological systems there are often complex, nonlinear interactions among factors so that the effect of changing two or more variables simultaneously can have a far greater or lesser effect on model predictions than the total effect of varying those factors independently (e.g., Ciannelli et al. 2004).

The utility of sensitivity analyses for applied conservation can be maximized when the analysis considers the full range of uncertainties in parameter estimates by varying multiple parameter estimates simultaneously. This approach, referred to as global sensitivity analysis (GSA [Wagner 1995]), acknowledges a greater extent of model uncertainty, including potential interactions and nonadditive effects (Saltelli et al. 1999). However, the widespread application of GSA in ecological models has been hindered because the model output can be unwieldy and methods of analyzing these data can be computationally intensive (Saltelli et al. 1999, Fieberg and Jenkins 2005, Cariboni et al. 2007, Naujokaitis-Lewis et al. 2009). Consequently, while GSA techniques do exist, they are presented primarily in mathematical modeling journals (e.g., Saltelli et al. 1999) and are not commonly used in research with an applied conservation or resource management focus (but see, e.g., Ellner and Fieberg 2003, Pereira et al. 2004). For example, in addressing the issue of poaching, which threatens the one-horned rhinoceros in Nepal, Poudyal et al. (2009) did not employ a GSA, stating that “given the large number of variables in our models, a full, factorial sensitivity analysis would be impractical and difficult to interpret.” Similarly, in a review of 87 spatial population viability models published from 2000 to 2006, Naujokaitis-Lewis et al. (2009) found that although sensitivity analyses were conducted in 97% of the

studies, none used GSA and only one assessed interactions among input parameters.

The underutilization of global sensitivity analyses in ecological modeling is unfortunate, because GSA can elucidate important interactions among uncertain variables that heavily influence model predictions, illuminating important properties of a model's structure that are not immediately obvious (e.g., Ginot et al. 2006). These insights can be used to identify research priorities to allow crucial parameter estimates to be improved before models are applied (Curtis and Naujokaitis-Lewis 2008). However, the ability of GSA to identify research priorities requires an accessible analytical tool that can provide a straightforward index, ranking parameters based not only on their individual contributions to model uncertainties, but also on their higher-order interactions with all other uncertain parameters. The ability to analyze and present this information in a concise and logical format is crucial when presenting model results to policy makers, land managers, and potential funding sources.

Since GSAs were first employed, a variety of approaches have been taken to analyze the resulting output (reviewed in Archer et al. 1997, Saltelli et al. 1999, Fieberg and Jenkins 2005), but as yet none has become widely used in applied conservation (Naujokaitis-Lewis et al. 2009). Approaches to analyzing GSA output that are based on multiple linear regression are limited by the assumption of a linear relationship between input variables and model output metrics (Saltelli et al. 1999). Methods such as Sobol' indices (Archer et al. 1997, Sobol' 2001, Ellner and Fieberg 2003, Fieberg and Jenkins 2005), Fourier amplitude sensitivity test (FAST [Saltelli et al. 1999]), and traditional analysis of variance (ANOVA [Ginot et al. 2006]) partition the variance in model output metrics and can evaluate higher-order interactions among input parameters. However, these too assume linear responses and are limited in their ability to identify and illustrate complex interactions among specific input parameters (Saltelli et al. 1999).

To address these limitations we developed an alternative framework to analyze GSA output using a combination of classification and regression trees (CART) (Breiman et al. 1984) and Random Forest (Breiman 2001a). Random Forest is a nonparametric classification method that applies random subsets of the data to produce multiple classification and regression trees, which are then used to calculate classification error rates and to quantify parameter importance (in this case parameter effect on model predictions, i.e., sensitivity) (Breiman 2001a). This approach has several advantages: (1) Random Forest importance values include the effects of all higher-order interactions and do not assume linearity; (2) this method is accessible and easy to use, because CART and Random Forest packages are available in Program R and can be downloaded free; (3) robust GSA results for models with 10–20 param-

eters require a sample of ~2000 Monte Carlo simulations, rather than a fully factorial set of several million simulations (Wagner 1995); and finally (4) this method produces straightforward results that are easy to interpret because Random Forest ranks model input parameters based on their effect on model output metrics, and CART produces a regression tree that provides a visualization of the complex interactions that result in these rankings and are otherwise difficult to conceptualize.

We demonstrate the utility of this analytical technique using a demographic model of Fremont cottonwood (*Populus fremontii*). Fremont cottonwood offers a prime example of a complex ecological system in which a global sensitivity analysis can be particularly useful because of the multiple biotic and abiotic interactions that drive cottonwood demography (Stella et al. 2006, Stromberg 2007). The ability to prioritize research efforts and improve important parameter estimates in demographic models is especially valuable in these complex ecosystems where multiple factors increase the uncertainty of population projections. Cottonwood population dynamics are driven by interactions between biological factors and the physical drivers of river channel morphology (e.g., channel meandering and cutoff, flow variability, and sediment transport) that collectively create essential habitat and cause mortality through scour and sediment deposition (Karrenberg et al. 2002, Stella et al., *in press*).

The ultimate goal of our model is to estimate the effects of altered river flow regimes, changes in climate, and restoration options on cottonwood occurrence, germination rates, first-year survival frequency, and age structure. However, making these predictions will require an accurate model based on empirical data and quantification of parameter estimate uncertainty. We applied the GSA and Random Forest approach to the cottonwood model to identify which areas of research would be most productive in improving model predictions and ensuring that future applications of the model yield robust results. We used this approach to: (1) quantify and rank the effect of uncertain input parameters on model predictions; (2) determine if different output metrics are equally sensitive to the uncertainty in each input parameter; and (3) identify important interactions among uncertain input parameters in determining model outcomes.

METHODS

The global sensitivity analysis framework

Mechanism-based models comprise multiple interacting parameters, each estimated with its own associated degree of uncertainty. In our model of cottonwood population dynamics, these parameters included both the physical characteristics of dynamic fluvial environments as well as biological parameters, all of which are determinates of cottonwood establishment, growth, and survival (Table 1). The model was parameterized using

published data from cottonwood studies and experiments carried out in field and laboratory settings in the Sacramento River valley and other semi-arid basins (Table 1; Appendix A). To understand the effect of the uncertainty surrounding these parameter estimates on model predictions, we ran 2000 Monte Carlo simulations (Sobol' 2001) that randomly sampled a parameter space consisting of three estimates for each of the 14 different model parameters, which collectively represented 4 782 969 possible parameter estimate combinations. Wagner (1995) demonstrated that a sample of 2000 parameter combinations is adequate for GSA of models with 10–20 parameters; and that additional samples do not significantly improve accuracy. The three estimates used in our GSA simulations represented a low, moderate, and high estimate for each parameter based on available data (Table 1, Appendix A). Parameter estimate ranges reflect uncertainty from multiple sources, including lack of empirical data, measurement error, and spatial and temporal variation.

At the beginning of each 175-year simulation, a random estimate was drawn for each of the 14 different parameters from the three possible values for each parameter, resulting in the simultaneous perturbation of all 14 parameters rather than the manipulation of a single parameter with all other values held constant, as in local sensitivity analyses. Because the model is deterministic, the variations in output metrics (i.e., number of patches occupied, proportion of patches occupied by adults, frequency of successful germination years, and frequency of years with successful first-year survival) are the direct result of the variation in the combinations of parameter estimates used in each model run.

While many of these randomly chosen parameter combinations may not be ecologically realistic, this process allowed us to quantify the range of model predictions that can result from interactions among uncertain parameter estimates across their range of possible values. This approach focuses on parameter uncertainty rather than model uncertainty due to model structure, environmental or demographic stochasticity, or uncertain future conditions (Fieberg and Jenkins 2005). We applied this GSA approach to our mechanism-based population model of Fremont cottonwood; however, the technique could be applied to any model with multiple uncertain parameters.

Populus fremontii life history

Fremont cottonwood is the dominant canopy tree species in semi-arid riparian ecosystems in the western United States (Braatne et al. 1996), and is considered a foundational species for riparian plant and animal communities because of its size, the structural complexity it provides, and its widespread distribution (Ellison et al. 2005). Our model was developed for cottonwood populations on the middle Sacramento River, which drains the largest river basin in California (70 000 km²).

In many of the river systems where Fremont cottonwood occurs, flow regulation and altered sediment transport patterns have changed the natural rates and patterns of flooding and river channel migration, which in turn limit the creation of suitable habitat for seedling establishment (Cooper et al. 2003, Stromberg 2007, Stella et al. 2010). Simultaneously, increased drought frequency due to climate change and increases in agriculture and population density have led to a heightened demand for water in western North America (Gleick and Chalecki 1999); this has resulted in significant changes in the amount and timing of water availability for all cottonwood life history stages. On the Sacramento River, these changes have resulted in a reduction in riparian forest area and population declines for cottonwood and other species that depend on the trees for food, nesting habitat, and cover (Katibah et al. 1984).

Fremont cottonwood life history, like that of other pioneer riparian species, is driven largely by the physical processes that shape river channel morphology, determine sediment dynamics, and allow rivers to meander over time (Karrenberg et al. 2002). These processes create suitable habitat patches for cottonwood germination and simultaneously cause some of the major sources of cottonwood mortality, including scour and sediment burial (Fig. 1). The timing of seed release typically coincides with spring snowmelt floods that provide the moisture necessary for germination (Stella et al. 2006). Seeds are released in a short pulse in spring and are extremely abundant during this period, with long-distance dispersal occurring by both wind and water (Braatne et al. 1996). Seeds are only viable for a few weeks (Horton et al. 1960, Stella et al. 2006), and there is no seed bank. Seedling root growth is rapid and must keep pace with the gradual recession of the spring snowmelt flood to avoid desiccation (Mahoney and Rood 1998, Stella et al. 2010). Seedlings establishing at low elevations are prone to mortality from scour, sediment burial, and inundation (Fig. 1 [Dixon et al. 2002]), while those establishing at higher elevations risk desiccation through physiological limitations of root growth rate (Stromberg et al. 1997, Mahoney and Rood 1998, Shafroth et al. 1998). Although germination typically occurs annually, seedling mortality rates are extremely high (Cooper et al. 1999). After establishment, growth is rapid, with trees reaching maturity at heights of 10–15 m in 5–10 years, after which survival rates are typically very high (vanHaverbeke 1990).

Cottonwood model structure

Because of the dependence of pioneer riparian species on river hydrology and geomorphology, population models for these species need to incorporate physical factors as major determinants of survival (Bendix and Hupp 2000). For Fremont cottonwood and other species within this functional group, a patch-based model is most appropriate for modeling population dynamics at

the scale of a river corridor or region (Lytle and Merritt 2004). Discrete patches of suitable habitat for cottonwood germination are created when: (1) river channels migrate laterally, depositing sediment on the inside of river bends; (2) when channels move abruptly across a floodplain, creating abandoned channels; and (3) when overbank flows erode and deposit sediment on existing floodplain surfaces, creating new patches of uncolonized floodplains (Huggenberger et al. 1998). These events typically occur with annual-to-decadal frequency (Benda et al. 2004). The scoured patches of bare substrate occur within a matrix of habitat that is unsuitable due to previous colonization by other species; cottonwood seedlings are shade intolerant and are poor competitors (Braatne et al. 1996, Karrenberg et al. 2002). Patches colonized by cottonwood are typically dominated by a single cohort because recruitment is pulsed and new patches only remain suitable for a short time after initial deposition.

We developed our mechanism-based population model in MATLAB (R2009b) for Fremont cottonwood stands along a 60-km reach of California's Sacramento River between Hamilton City and Butte City (Fig. 2). We ran simulations for 175 years, approximately twice the life span of Fremont cottonwood trees in California (Stella 2005) and a tractable period for considering decadal variation in flow regimes. The model predicts patch occupancy and age structure at the end of each 175-year model run as well as germination and first-year survival frequency over 175 years. The model begins with a physical-based model of river channel migration that simulates suitable cottonwood habitat patch creation and predicts the location and size of newly created sites resulting from high-flow events that initiate bank channel erosion, deposition, and chute cutoff (Larsen et al. 2006a, b). The channel meander migration model is based on the equations of Johansson and Parker (1985) and is enhanced by including empirical data on channel position, floodplain configuration, bank erodibility, and variable stream hydrology. Building on previous work, the physical model parameters were calibrated for the Sacramento River using historical aerial photography and historical flow data (Larsen et al. 2006a). Prior to running the demographic model, we ran the meander model with a fixed 175-year hydrology series to produce a distribution of patches of varying ages and sizes. The model is deterministic and, for the conditions specified, produced 10 550 patches, with the majority of patches ranging in size from 12 to 500 m². The hydrology series was based on the actual regulated flow record from the Sacramento River (1945–2008) with the series repeated until 175 years was reached (Larsen et al. 2006a). The model assumes that mature stands of riparian vegetation delineated from historical data reduce erosion by 50% (Micheli et al. 2004); however, it does not include erosion reduction (i.e., increased bank stability effects) due to vegetation patches created during the modeling process.

TABLE 1. Parameter estimates used in simulations of Fremont cottonwood patch occupancy along a 60-km reach of the Sacramento River.

| Parameter | Data source | Low estimate | Moderate estimate | High estimate |
|---|-------------|---|--|--|
| Stage–discharge relationship: $y = a(x - b)^{c\dagger}$ | 1 | $a = 11.59$ $b = 877.18$ $c = 0.1342$ | $a = 19.03$ $b = 1221.77$ $c = 0.1014$ | $a = 7.21$ $b = 488.66$ $c = 0.1665$ |
| Floodplain accretion rate function: $y = a(1 - [\exp(-bx)]) + c$ (determines change in patch elevation over time) \ddagger | 2, 3 | $a = 2.6$ $b = 0.02$ | $a = 3.6$ $b = 0.05$ | $a = 5.02$ $b = 0.08$ |
| Cumulative degree days predicting initiation of seed release (degree-days) | 4 | 182 | 234 | 280 |
| Seed availability window (number of days seeds are available for germination) | 4 | 20 | 40 | 80 |
| Height of capillary fringe (cm) | 5 | 5 | 30 | 100 |
| Seedling root growth rate (mm/d) | 6, 7 | 2 | 6 | 12 |
| Sapling and adult root growth rate (cm/yr) | 8 | 70 | 100 | 165 |
| Maximum rooting depth (m) | 6 | 3 | 4 | 5 |
| Seedling inundation threshold \S | 6, 9¶ | 15 | 30 | 60 |
| Sapling inundation threshold \S | 6, 9¶ | 30 | 60 | 90 |
| Adult inundation threshold \S | 6, 9¶ | 60 | 90 | 120 |
| Seedling scour threshold | 10, 11, 12¶ | 0.5 | 1.0 | 1.5 |
| Tolerated by saplings | 10, 11, 12¶ | 1 | 2 | 3 |
| Tolerated by adult trees | 10, 11, 12¶ | 2 | 3 | 5 |

Notes: Three estimates of each parameter, a low, moderate, and high value, were used to represent the range of uncertainty around each parameter estimate. One value for each parameter was randomly selected in each of 2000 model runs, and the variation in model predictions was used to determine the sensitivity of the model to each parameter and its associated uncertainty.

Data Sources: 1, three years of data from three USGS gages (Hamilton City [A02630], Ord Ferry [A02570], and Butte City [A02500]; (cdec.water.ca.gov)); 2, lidar data for the Sacramento River between Princeton and Colusa; 3, TerraPoint (2006); 4, Stella et al. (2006); 5, reviewed in Mahoney and Rood (1998); 6, Braatne et al. (1996); 7, Mahoney and Rood (1998); 8, Fenner et al. (1984); 9, Freidman and Auble (1999); 10, Bradley and Smith (1986); 11, Rood and Mahoney (1990); 12, J. C. Stella (*personal observation*).

\dagger Where x = discharge (cm) and y = stage (m).

\ddagger Where x is patch age (in years), y is patch elevation (in meters), and c is a constant representing the elevation of flow on the day the lidar data were collected.

\S Maximum number of days that trees can survive with their roots submerged under water.

|| Maximum depth of water (m) a tree can survive without being scoured out or uprooted (proxy for threshold tolerance of scour and sediment burial).

¶ Sources provided broad generalizations but did not provide quantitative estimates for the parameter, or provided data for species similar to Fremont cottonwood.

We applied the population model upon the physical template of patches created by the channel migration simulation. The population model begins by estimating the initiation of seed release (Stella et al. 2006) and moisture availability to predict germination success among patches created in each year (Fig. 3). Following germination, the model predicts survival and mortality of seedlings (<1 yr old), saplings (1–4 yr old) and adult trees (≥ 5 yr old) on each patch (Fig. 3). Seedlings that establish at low elevations near the river's edge are prone to scour, inundation, and burial by sediment (Mahoney and Rood 1998, Bendix 1999), whereas those that establish at higher elevations are prone to drought mortality as their root systems become disconnected from the water table (Fig. 1 [Dixon et al. 2002]). Saplings and adults, which have established root systems, are primarily vulnerable to sediment burial, scour, and flooding that creates prolonged anoxia in the root zone.

Germination and survival of Fremont cottonwood depend largely on the relationship between flow regime (flood magnitude, timing, and duration) and the relative elevation of the habitat patch above the river's water surface (Fig. 1). This relationship

determines the availability of moisture for germination as well as the ability of seedlings, saplings, and trees to withstand multiple sources of mortality including drought, scour, and inundation. The mean daily river discharge data that initially drove the river meander migration model were also used in the biological patch model to predict the elevation of the river's water surface, and thus the depth to water table on the floodplain and depth of flooding during high flows (Auble et al. 1994). To predict the water surface elevation from the river discharge data, we developed stage–discharge relationships based on data from three gages along the Sacramento River (Table 1; Appendix A) and estimated mean daily flow elevation for each day of every year of the simulations. To estimate the ground surface elevation of each patch in each year of the model, we developed a functional relationship between patch age and patch elevation by calculating a floodplain accretion rate using lidar data and data on historic channel migration patterns (Table 1; Appendix A). The floodplain accretion function represents the expected average rate over time, rather than discrete sedimentation events that occur with large floods.

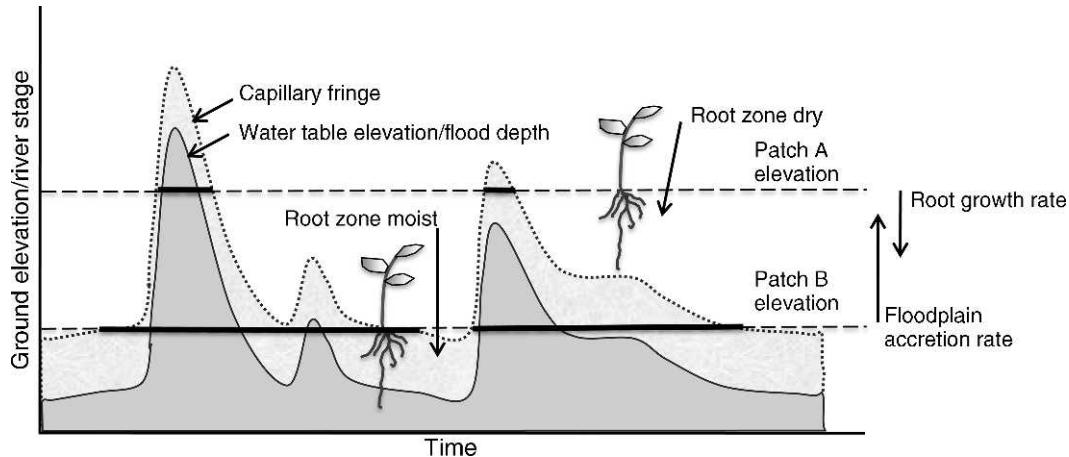


FIG. 1. Schematic of the interaction of model parameters determining seedling survival in the first year. Seedlings survive if (1) they have sufficient moisture and root growth rate for roots to maintain contact with the capillary fringe and (2) subsequent flooding does not exceed a threshold depth sufficient to scour/uproot plants, nor a threshold duration sufficient to kill seedlings via root anoxia. The contrast in conditions experienced by plants in two patches of different elevation (patch A and patch B) is illustrated by the horizontal dashed lines, with thick solid lines indicating periods of water availability to roots, and flood severity indicated by the height of the gray area above the patch surfaces.

Germination and survival of cottonwood on individual patches was governed at each model time step by a series of logical rules (Fig. 3). We assumed that seeds were available on all patches in all years. This assumption is typical of cottonwood population models (e.g., Lytle and Merritt 2004) and is supported by empirical data showing that cottonwoods produce abundant seeds that are widely dispersed via wind and water to distances of several kilometers (Braatne et al. 1996, Cooper et al. 1999). For seeds to germinate on a particular patch in a given year, the model required the surface of the patch to be above the river's flow stage (i.e., not underwater), but low enough for phreatophytic plants to access soil moisture directly from the gradually receding water table or from its capillary fringe. For germination to succeed, these conditions had to be met during a period of 20–80 days after seeds were released and before seeds were no longer viable (Fig. 3, Table 1 [Mahoney and Rood 1998, Stella et al. 2006]). To calculate the day of seed release for each year of every model run, we used a cumulative growing degree day (GDD) model developed for California populations of Fremont cottonwood (Stella et al. 2006) (Table 1) and historical daily temperature data for Chico, California (National Climatic Data Center: *available online*;⁴ see Appendix A for additional details).

Following successful germination, annual survival in the model required a narrow range of physical conditions that would provide sufficient moisture to prevent drought mortality, while simultaneously protecting seedlings from excessive discharge levels that

would lead to scour, sediment burial, or inundation. Drought mortality occurred in the model when roots were out of contact with the capillary fringe above the water table for 10 days or more (Fig. 1 [Stella and Battles 2010]). Seedling root depth was calculated daily from the day of germination to the end of the first calendar year. Sapling and adult root depth were calculated on an annual basis and were limited to a maximum rooting depth (Table 1). As a proxy for flood-induced sources of mortality in the model, including scour from excess shear stress and burial by sediment, we set a threshold for the maximum elevation of flow above the patch that could be tolerated by each age class (Table 1). Mortality from inundation occurred in the model when the elevation of the river's flow was 10 cm or more above the elevation of the patch for a threshold number of days depending on tree age (Fig. 3, Table 1 [Braatne et al. 1996, Friedman and Auble 1999]).

Statistical methods to rank parameter importance and evaluate interactions

After running simulations for a random subset of 2000 possible parameter estimate combinations, we used the Random Forest algorithm (R package *randomForest* 4.5-30 [Breiman et al. 2009]) to identify the parameter estimate uncertainties that had the greatest effect on each model output metric (i.e., the parameter estimates to which the model predictions were most sensitive). Random Forest was originally developed in the context of machine learning (Breiman 2001a) and has only recently been used in the analysis of ecological data (Cutler et al. 2007).

Random Forest has several advantages that are particularly useful in analyzing GSA output: it is

⁴ (<http://www.ncdc.noaa.gov/oa/ncdc.html>)

nonparametric and can easily handle both categorical and continuous data; it is highly accurate; it can efficiently model the complex interactions among a large number of variables, and it offers an “importance value,” a succinct metric for quantifying the relative influence of each parameter in determining model predictions (Breiman 2001a, Cutler et al. 2007). Random Forest uses classification and regression trees (CART), which classify data by repeated binary partitioning of the data into groups with increasingly similar outcomes. In CART, the variable used as the predictor at each node of the classification tree (i.e., for each binary partition) is chosen based on an optimization process designed to minimize classification error. When error can no longer be reduced, the tree is considered fully grown. In CART, the single fully grown tree is then pruned to remove imprecise lower branches, optimizing tree size and ensuring that the remaining branches are robust (Rejwan et al. 1999). The Random Forest method takes a different approach to the process of creating classification and regression trees. It uses bootstrap samples of the data to create multiple classification trees (Breiman 2001a, Liaw and Wiener 2002). As each tree is created, the variable used as the predictor at each node is the optimal predictor chosen from a random subset of one-third of the predictors rather than from all predictor variables, as in CART. Each tree is then fully grown and is *not* pruned. Error rates can then be calculated by comparing the predictions of each tree to the data not included in the bootstrap sample. These error rates are then aggregated for each data point, and an overall prediction error rate is calculated (see Breiman [2001a] for further details). Overfitting is not a concern in Random Forest as compared to a single unpruned CART tree, because the error rate converges as the number of trees increases (Breiman 2001a).

To quantify variable importance, Random Forest essentially performs a sensitivity analysis across all trees, calculating the change in prediction error that occurs when a single variable is moved while all remaining variables are left unchanged (Liaw and Wiener 2002). Because bootstrap sampling is used, the variable importance values can vary slightly each time Random Forest is run, but the order in which the variables are ranked typically remains unchanged (Liaw and Wiener 2002). These importance values incorporate not only the effects of individual parameter uncertainties, but also all higher-order interactions among the input parameters that best explain the variance in model predictions. This ability to consider all higher-order parameter interactions in calculating relative importance among parameters is particularly useful in global sensitivity analysis for complex mechanism-based models. In the traditional local sensitivity analysis approach, these interactions cannot be determined by varying one factor while holding all others at arbitrarily determined values (Fieberg and Jenkins 2005, Cariboni et al. 2007).

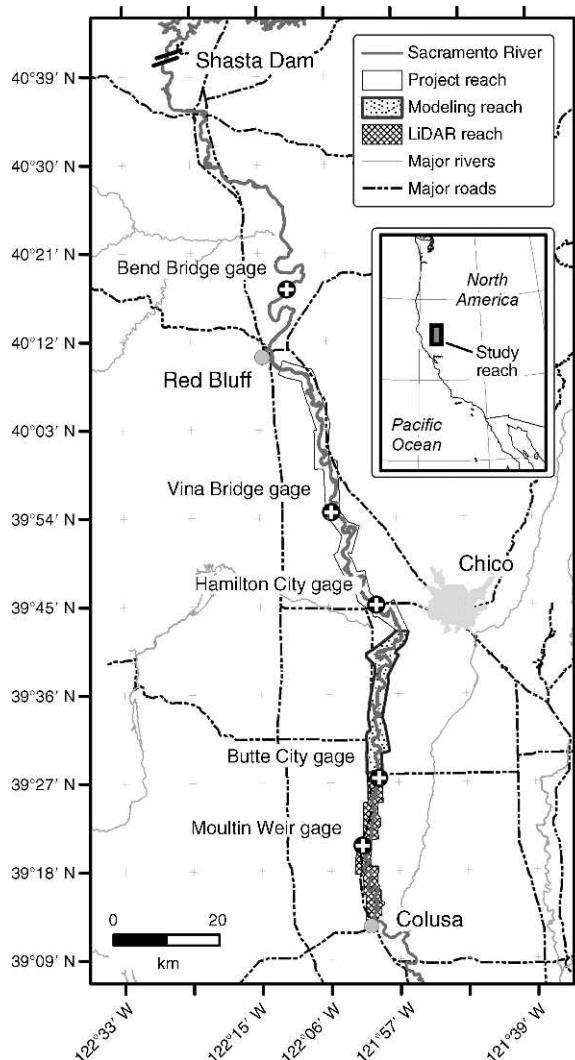


FIG. 2. A map of the study site on the Sacramento River in California, USA. We performed a global sensitivity analysis on a model of Fremont cottonwood population dynamics for the reach from Hamilton City to Butte City. Model parameterization data came from existing data gathered along the river primarily between Red Bluff and Colusa. However, the lidar data were only available for the reach from Butte City to Colusa.

Local sensitivity analysis may be sufficient for models in which input parameters are unlikely to interact; however, in models that include several ecological mechanisms, interactions among parameters are likely to be important (Naujokaitis-Lewis et al. 2009).

The randomForest package in R does not currently offer a method for averaging the multiple trees that it produces; therefore, to complement the Random Forest analysis, we used CART to create a pruned classification tree (R package rpart 3.1-45 [Therneau and Atkinson 2009]) to provide a graphical understanding of how parameters interact to affect patch occupancy and to compare outcomes between model runs with different

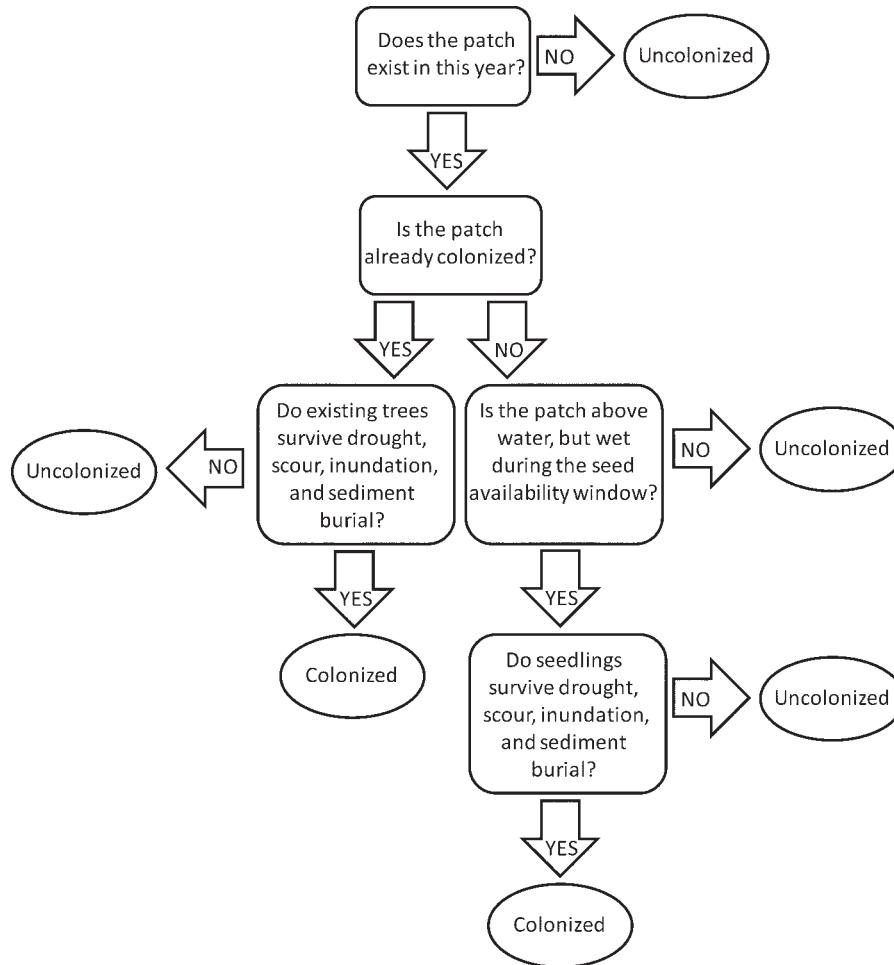


FIG. 3. A simplified flow chart of the decision rules embedded within the patch-based population model for Fremont cottonwood on the Sacramento River, California, USA. The model begins with a physically based model of river channel migration that predicts the creation of 10 550 habitat patches over the 175 years of the simulation (Larsen et al. 2006a). For each year that each patch exists, the population model determines if conditions are suitable for germination and survival. The conditions required for survival are age-specific (seedlings, saplings, and adults). The model tracks the age class of trees on each occupied patch and calculates aggregate output variables for the river-wide population.

combinations of parameter estimates. We specified a Poisson distribution in the CART analysis because the patch occupancy data were skewed and fitted this distribution. We pruned the tree using a 10-fold cross-validation technique to generate an optimally sized tree that maximizes model fit while limiting cross-validation error. This was achieved using the standard 1 SE rule, which states that the tree with the most nodes should be selected as long as the corresponding cross-validation error is within one standard error of the minimum cross-validation error (Breiman et al. 1984). Based on this rule, we pruned the CART tree to 12 terminal nodes (further details can be found in Appendix B).

RESULTS

The Random Forest analysis explained >80% of the variance in model predictions (83–86% depending on the

output metric) and revealed multiple important patterns in the GSA output. Most importantly, we found that parameters to which the model predictions were most sensitive were not necessarily those that were based on the least amount of data (Table 2). The three parameters with the greatest effect on patch occupancy were physical factors including the height of the capillary fringe, the rate of floodplain accretion, and the stage–discharge relationship (Fig. 4a). These parameter estimates were all based on high-quality data sets, either with multiple years of data, multiple published studies, or a high degree of spatial replication. Conversely, some of the parameters with the least amount of empirical data available, and correspondingly wide ranges of estimates in the sensitivity analysis, had importance rankings in the bottom third of all parameters (Fig. 4).

TABLE 2. The sensitivity rankings and the quantity of data available for 14 parameter estimates included in the patch-based model of Fremont cottonwood populations.

| Sensitivity rank | Estimate based on: | | |
|---------------------------------------|-----------------------|-------------------|---|
| | “Expert opinion” only | A single data set | Multiple published studies and/or experiments |
| 1) Height of the capillary fringe | | | X† |
| 2) Floodplain accretion rate | | X† | |
| 3) Stage–discharge relationship | | X† | |
| 4) Seedling inundation threshold | X | | |
| 5) Seedling root growth rate | | | X† |
| 6) Sapling inundation threshold | X‡ | | |
| 7) Adult tree inundation threshold | X‡ | | |
| 8) Seed availability window | | X | |
| 9) Sapling scour threshold | X‡ | | |
| 10) Seedling scour threshold | X‡ | | |
| 11) Timing of seed release | | | X |
| 12) Adult tree scour threshold | X‡ | | |
| 13) Root growth rate after first year | | | X |
| 14) Maximum rooting depth | | | X |

Notes: Sensitivity rankings were determined using Random Forest importance values for each parameter in determining the number of patches occupied at the end of each 175-year simulation. Importance values consider the effect of each parameter and its interactions with all other parameters in the model. The quantity of data on which the parameter estimate is based is indicated with an X.

† Parameter estimates based on a large quantity of data by whose uncertainty had a disproportionately large effect on model predictions.

‡ Parameter estimate with a large degree of uncertainty, but with little effect on model predictions.

Examples include scour thresholds for all age classes and inundation thresholds for adult trees (Table 2).

Second, we found that not all output metrics were most sensitive to the same parameter estimates (Fig. 4). Random Forest importance values indicated that three of the four output metrics were most sensitive to variation in the height of the capillary fringe, including patch occupancy, proportion of years with successful germination, and proportion of patches occupied by adult trees (Fig. 4a, b, d). However, predictions of the proportion of years with successful first-year survival (i.e., survival of seedlings to the end of the first calendar year) were most sensitive to different parameters, primarily the seedling inundation threshold followed by the seedling root growth rate (Fig. 4c). The relative importance of parameters also varied among output metrics. Capillary fringe height was over four times as important as any other parameter in determining the frequency of successful germination, but was only slightly more important than floodplain accretion rate in determining patch occupancy (Fig. 4).

Last, Random Forest and CART results indicated that model predictions were sensitive to complex combinations of parameter estimates. This is shown in the pruned classification tree (Fig. 5) illustrating the complex interrelationships among parameters that led to variation in model predictions. The terminal nodes in Fig. 5 indicate the predicted proportion of patches occupied at the end of each model run that contained a given combination of parameter estimates.

No individual parameter estimate prevented successful patch occupancy; however, the interactions among certain parameter estimates led to zero patch occupancy for many model runs (Fig. 5). For example, seedlings

were prevented from surviving to maturity in model runs with a capillary fringe of ≤ 30 cm (i.e., on patches with a pure gravel or sand substrate), a slow seedling root growth rate of 2 mm/d, and a seedling inundation threshold of ≤ 30 days (Fig. 5).

Other parameter estimate combinations did result in some degree of patch occupancy, but the predicted number of patches occupied varied substantially depending on parameter interactions (Fig. 6). For example, the stage–discharge relationship alone did not determine patch occupancy, but when interacting with other parameter values that exacerbated drought mortality (e.g., a low capillary fringe) or increased risk of inundation and burial (due to low floodplain accretion rate), this parameter became highly important. Interactions among these factors were evident from the CART output and emphasized the role of the stage–discharge relationship as a latent factor. When the height of the capillary fringe was 100 cm (e.g., the right side of the tree in Fig. 5), the number of patches occupied differed over an order of magnitude depending on the sediment accretion rate and stage–discharge relationship.

In addition, the classification tree indicated the importance of the height of the capillary fringe in determining patch occupancy. When the height of the capillary fringe was minimal (5 cm, corresponding to a gravel substrate), a long series of five other conditions had to be met for patch occupancy to be $>18\%$ (left side of the tree). However, in finer substrates that support a capillary fringe >30 cm (right side of the tree), a high proportion of patches are occupied as long as one or two additional conditions are met (slow-to-moderate flood-

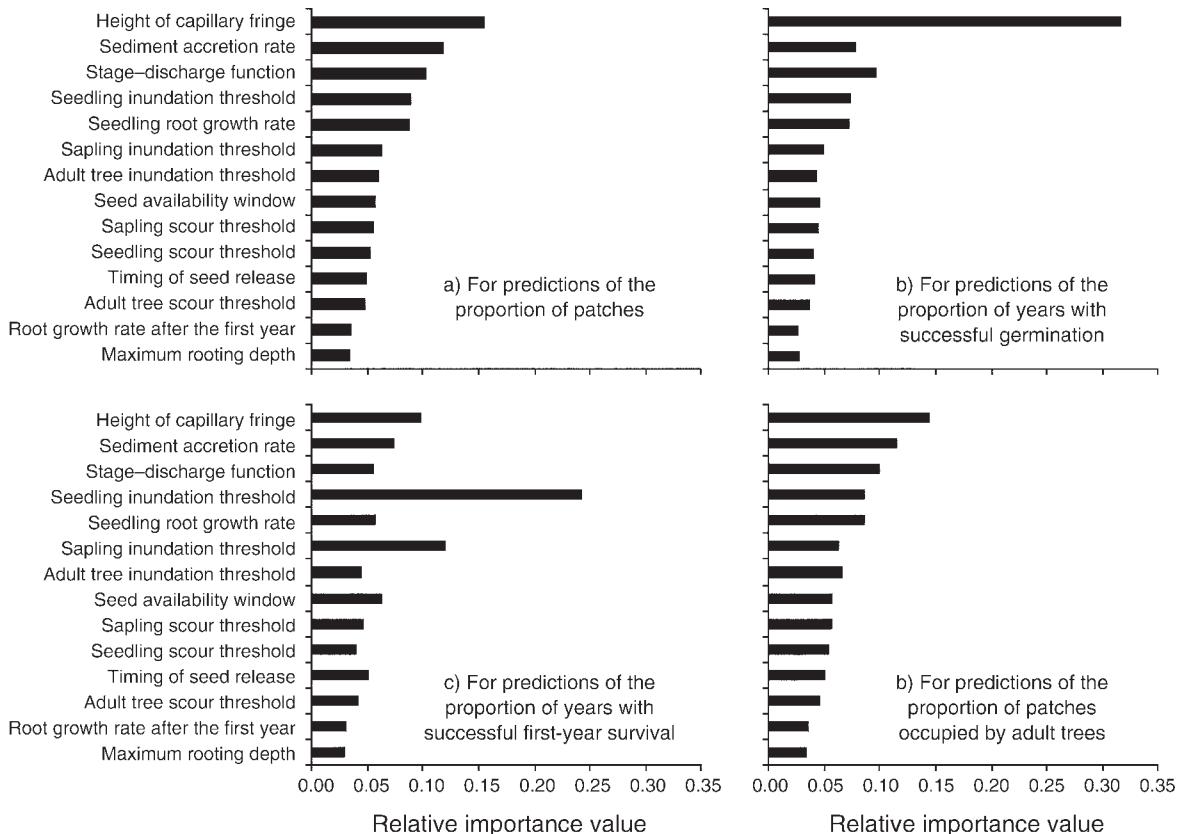


FIG. 4. Normalized Random Forest importance values for each parameter in 2000 simulations of 175 years. Values indicate the relative importance of each parameter and its interactions with all other parameters in determining: (a) the number of patches occupied at the end of each simulation; (b) the frequency of years with successful germination; (c) the proportion of years with successful first-year survival; and (d) the number of patches occupied by adults (trees older than 5 yr) at the end of each simulation.

plain accretion rate and a low stage–discharge relationship; far right series of binary splits in Fig. 5).

Collectively, the 2000 GSA simulations do not reflect the range of predictions that would be expected in the natural system, but rather represent the range of possible model predictions resulting from the combined uncertainty around multiple parameter estimates in the model. Most model runs (65%) resulted in zero patch occupancy after 175 years (Fig. 7a), because in each run there was a high probability that the worst-case-scenario estimate was chosen for at least one of the 14 parameters. Depending on the combination of parameter estimates used in each model run, the proportion of patches occupied ranged from 0% to 100% (Fig. 7a). Other output metrics yielded similarly wide-ranging estimates, although some were much wider than others. Germination frequency ranged from 10% to 100% of years, with 57% of model runs resulting in germination on at least one patch in every year (Fig. 7b). The range of estimates was narrower for first-year survival frequency (0–50% of years), with the majority of model runs resulting in successful first-year survival approximately once every 10 years (Fig. 7c). The proportion of

patches occupied by adult trees at the end of model runs ranged from 0% to 99%.

A large proportion of model runs resulted in either no occupancy (i.e., the random combination of parameter estimates likely prevented successful germination) or occupancy exclusively by seedlings (the random combination of parameter estimates were favorable for germination, but did not allow survival beyond the seedling stage). When the parameter combinations did result in patch occupancy, however, a large proportion of those runs resulted in an age structure dominated by adults (Fig. 7d). Age structures dominated by adults typically occurred when parameter estimates allowed moderate to high rates of sapling and adult survival, and when there was complete seedling mortality in the final year of the model (0% seedlings at the end of the 175-year simulation). In the majority of model runs that resulted in patch occupancy, the age structure was either 80–99% adult trees or 100% seedlings. Saplings rarely occurred on >20% of occupied patches. Age structures with 100% seedlings at the end of 175 years resulted from combinations of parameter estimates that allowed for successful

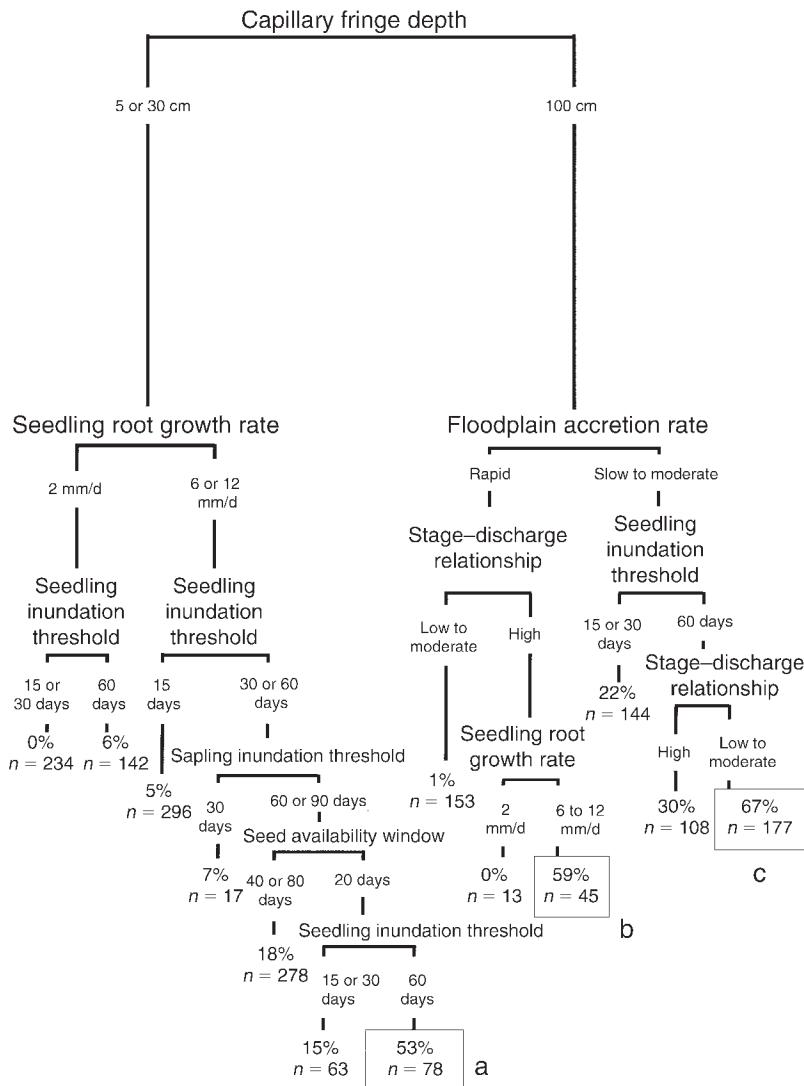


FIG. 5. Classification tree illustrating the complex relationships among parameters in defining decision rules that predict percentage patch occupancy at the end of each 175-year simulation. Percentage values at the ends of each terminal node indicate the estimated percentage of patches occupied, and *n* indicates the number of observations (i.e., model runs) in each category. There are three pathways (a, b, and c) that can lead to high patch occupancy of >50%. Two pathways result in 0% patch occupancy.

germination and survival of seedlings in the final year of the model, but low sapling and/or adult survival.

DISCUSSION

Performing a GSA on our mechanism-based model of Fremont cottonwood population dynamics revealed nonintuitive patterns that underscore the importance of understanding how interactions among factors drive model behavior for complex systems. In the case of the Fremont cottonwood model, we found that the degree of uncertainty around a parameter estimate was not proportional to its importance in determining model predictions. For example, the scour thresholds tolerated by each cottonwood age class were crude estimates based solely on “expert opinion”; yet, despite the wide

range of these estimates due to uncertainty about the true parameter value, these three parameters ranked low (9th, 10th, and 12th out of 14 parameters) in their importance in determining the number of patches occupied at the end of the model. Conversely, predictions of patch occupancy were highly sensitive to uncertainty in parameters that were based on high-quality data, including the floodplain accretion rate (which used lidar data) and the stage–discharge relationship (based on multiple years of USGS gage data). Thus, efforts to improve model accuracy in predicting cottonwood patch occupancy should focus on understanding the variability within the best-known parameters rather than those for which there are no empirical data. During the model-building process it is not

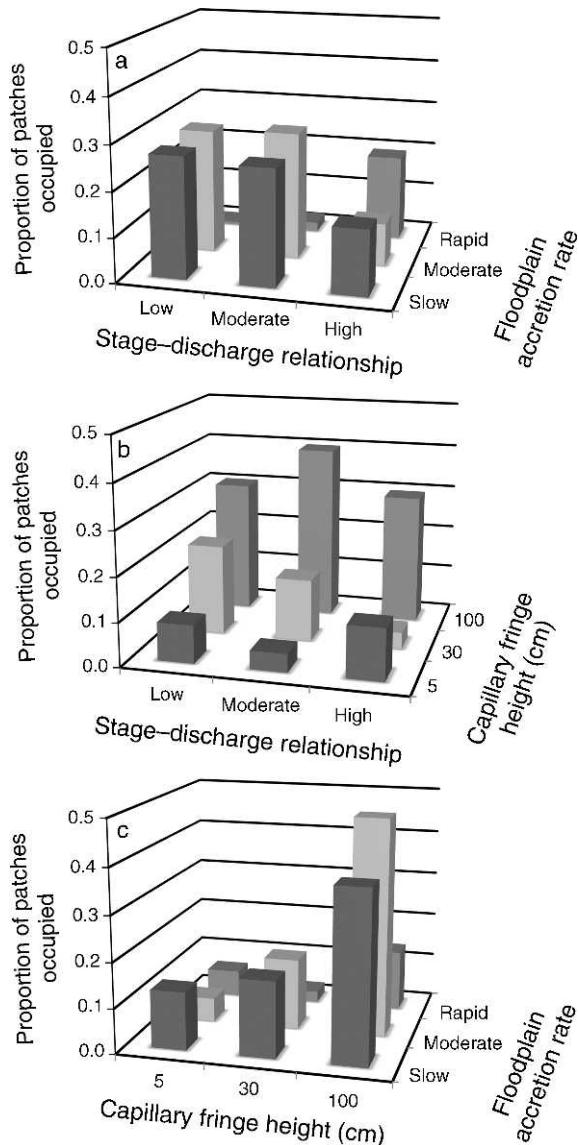


FIG. 6. The average proportion of patches occupied at the end of 2000 simulations of 175 years of cottonwood population dynamics was largely determined by nonlinear interactions among three physical factors: (a) the stage–discharge relationship and floodplain accretion rate; (b) the stage–discharge relationship and capillary fringe height; and (c) the height of the capillary fringe and floodplain accretion rate.

difficult to determine which parameter estimates are based on more or higher quality data than others, but it can be a mistake to assume that future research should focus primarily on the parameters for which there are the least available data (Fullerton et al. 2010). These are not necessarily the parameters that are limiting the precision of model predictions.

Another insight that emerged from the sensitivity analysis was that, depending on the research question of interest, priorities for model improvement differed. Random Forest importance values indicated that

uncertainty in estimates of the height of the capillary fringe had the greatest effect on predictions of patch occupancy, frequency of germination, and age structure, but that survival through the first year was most sensitive to the seedling inundation threshold. This suggests that if it is not feasible to improve estimates of important parameters to a degree that they yield precise predictions for a particular output metric, then the usefulness of that output metric should be reevaluated. For example, in the case of Fremont cottonwood, if it is not possible to accurately predict the spatial variation in the height of the capillary fringe over time, then it may be unreasonable to attempt to predict the spatial distribution of patch occupancy 100–200 years into the future. On the other hand, if additional experimental or empirical measurements can narrow the uncertainty around the estimate of the seedling inundation threshold (the parameter to which first-year survival was most sensitive), then the frequency of successful first-year survival events (a metric that the model already predicts with relatively good precision) might be a better metric to use in future applications of the model. It is important to recognize that while models can be extremely useful tools in informing conservation policy and resource management, there will always be a degree of uncertainty around parameter estimates, so that some predictions can be made with sufficient accuracy and others cannot (Beissinger and Westphal 1998). GSA provides a tool to identify and quantify these limits, allowing the important distinction to be made between useful and unrealistic predictions in complex ecological systems.

One of the challenges in making useful conservation recommendations for many populations, including Fremont cottonwood, is that future conditions are expected to change (Cayan et al. 2008). The most pressing conservation concerns surrounding Fremont cottonwood populations and populations of other riparian and riverine species on the Sacramento River result from the fact that water is the limiting resource for both the ecosystem and California's human population. Future conditions, including human population growth and increasing drought frequency due to climate change, will only exacerbate the problem (Gleick and Chalecki 1999). Caution must be used when making predictions about the future based on models that were parameterized using data collected under current conditions (Araújo et al. 2005). For example, in the case of Fremont cottonwood, the “recruitment-box model” suggests that cottonwood recruitment occurs on suitable substrate 0.6–2 m above low flow as long as stream stage decline does not exceed 2.5 cm/d (Mahoney and Rood 1998). These conclusions provide a good general guideline for managers, assuming that current conditions are similar to past conditions; however, if the mechanisms leading to these estimates are not explicitly quantified in a model, then the estimates cannot be adjusted to changing conditions, for example, increased

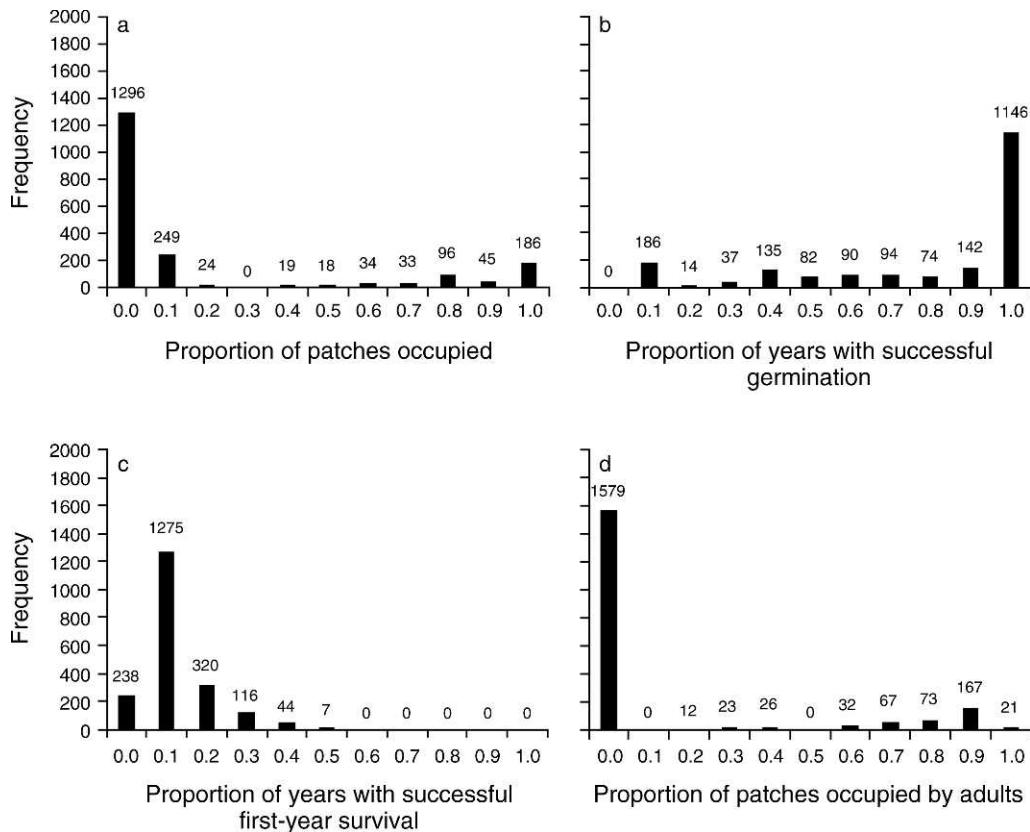


FIG. 7. Frequency histograms of four output metrics from 2000 simulations of 175 years of cottonwood population dynamics. Output metrics include (a) the proportion of patches occupied at the end of each simulation; (b) the proportion of years with successful germination on at least one patch; (c) the proportion of years with successful first-year survival on at least one patch; (d) the proportion of patches occupied by adults (trees >5 yr) at the end of each simulation. Numbers above the bars indicate frequency out of 2000 simulations.

atmospheric temperatures that alter the timing of seed release. Mechanism-based models, therefore, have the potential to outperform “black-box” models in this context, because their predictions have the potential to change accordingly when conditions shift (Breiman 2001*b*). However, introducing complexity into a model without acknowledging the accompanying increase in parameter uncertainty can reduce its accuracy and value to real-world applications (Nelson et al. 2008). The sensitivity analysis framework that we developed for the Fremont cottonwood model is particularly useful in this circumstance. From our model output it was clear that cottonwood recruitment and survival can only occur under a narrow range of conditions that are defined largely by physical factors. Within this range we found that certain interactions among parameters were especially important (capillary fringe, floodplain accretion rate, and the stage–discharge relationship), giving us the opportunity to improve our estimates of these key parameters and reduce uncertainty before using the model to make predictions about future conditions.

Within our GSA approach, Random Forest importance values were particularly useful for quantifying the

effects of parameters that, when interacting with other parameters, had a much larger influence on model predictions than would be expected if each factor were considered separately. For example, in the cottonwood model, the stage–discharge relationship, which defines the depth of the water table and height of surface flooding, was not in itself responsible for a large proportion of the variation in model predictions. However, when combined with extreme estimates of capillary fringe height or floodplain accretion rate, this parameter became very important, because all three factors in concert control the vulnerability of seedlings to drought scour and flood mortality. The shape of the stage–discharge relationship became the tipping point in determining survival of trees under marginal conditions. However, because the stage–discharge relationship in itself did not explain a large proportion of the variation in model predictions, its importance under these conditions would have been easily overlooked had our sensitivity analysis not considered the interactions among all of the variables in the model. The insights from our analysis suggest that improved estimates of the stage–discharge relationship, in addition to the height of

the capillary fringe and floodplain accretion rate, will be necessary before applying the model to make management recommendations.

For our mechanism-based model of Fremont cottonwood, we found that GSA coupled with Random Forest and CART is an efficient tool for identifying the parameter estimates that should be improved to increase model precision. However, we recognize that it is not able to indicate whether or not the model structure includes all the important drivers in the system. Therefore, model validation using field data is necessary to evaluate model accuracy, but is beyond the scope of the present study. It is important to recognize, however, that model validation that focuses exclusively on the final outcome of model predictions is not sufficient to validate a model that contains multiple complex interactions. As illustrated by the classification tree, there are multiple combinations of parameter estimates that can yield the same outcome. Therefore, evaluating the accuracy of a mechanism-based model based solely on whether or not its predictions match an observed population can be misleading. Because there are multiple means to the same end, the key to creating a useful mechanism-based model is to home in on the few parameter estimate combinations that truly reflect the natural system (e.g., Wiegand et al. 2004). This can be achieved through a combination of (1) global sensitivity analysis, (2) limiting parameter estimates to those that yield biologically reasonable results, (3) focused research to improve model precision, and (4) model validation using field data that validate the model's subcomponents as well as its final predictions.

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APPENDIX A

Additional details of cottonwood model structure and parameterization (*Ecological Archives* A021-056-A1).

APPENDIX B

Classification and regression tree (CART) pruning using the rpart package in Program R (*Ecological Archives* A021-056-A2).