

DISSERTATION

MODELING RIPARIAN VEGETATION RESPONSES TO FLOW ALTERATION BY  
DAMS AND CLIMATE CHANGE

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## ABSTRACT

### MODELING RIPARIAN VEGETATION RESPONSES TO FLOW ALTERATION BY DAMS AND CLIMATE CHANGE

As the interface between freshwater and terrestrial ecosystems, riparian vegetation is a critical influence on biodiversity maintenance and ecosystem service production along river corridors. Understanding how altered environmental drivers will affect this vegetation is therefore central to sound watershed management. A river's flow regime exerts a primary control on the type and abundance of riparian vegetation, as differing adaptations to changing discharge levels mediate plant recruitment and persistence. Models of the relationships between flow and vegetation, generalized across species in terms of flow response traits such as flood tolerance, provide a means to explore the consequences of hydrologic alteration resulting from dams and climate change. I addressed these issues through development of a stage-structured model of woody riparian vegetation driven by variation in annual high flows. Simulation experiments offered insight into the potential trajectories of competing vegetation trait types relative to scenarios of dam construction, re-operation and removal. Modifying the size and frequency of the floods responsible for both disturbance mortality and establishment opportunities altered the relative abundance of pioneer and upland cover. Yet, qualitative differences in simulated outcomes resulted from alternative assumptions regarding seed limitation and floodplain stabilization, illustrating the need to carefully consider how these factors may shape estimated and actual vegetation responses to river regulation. In addition, I linked this simulation approach with an integrated watershed-modeling framework to assess the relative risk of invasion by the

introduced plant *Tamarix* under multiple climate change scenarios. Though warming may increase the potential for *Tamarix* range expansion by weakening thermal constraints, the results of this work supported the expectation that hydrogeomorphic variation will control how this potential is realized. With simulated invasion risk strongly dependent on shifts in both the magnitude and timing of high flows, model outcomes underscored the importance of accounting for multiple, interacting flow regime attributes when evaluating the spread of introduced species in river networks. This research suggested the utility of simplified but process-based simulations of riparian flow-ecology relationships, demonstrating that such models can establish a first approximation of the potential consequences of management decisions and can highlight key questions for additional research, particularly where data are scarce and uncertainty is high.

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## DEDICATION

Leopold – may you float free flowing rivers.

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## INTRODUCTION

Riparian zones support reciprocal exchanges between freshwater and terrestrial ecosystems, and these interactions create the richly ‘tangled banks’ that provide vital habitat for a host of species. In addition to their biological profusion, riparian zones influence valuable ecosystem services along rivers, affecting nutrient and pollutant transport, flood energy attenuation, bank stability, and recreational appeal. The pattern of flow in a river is a primary control on the extent and composition of riparian vegetation communities, and the widespread modification of natural flow regimes has consequently altered the distributions and abundances of riparian plants, at times with detrimental effects on biodiversity and the benefits enjoyed by people. Human population growth and a changing climate are poised to intensify the demands placed on rivers, but the values associated with riparian vegetation justify protection and restoration of these communities. Planning and implementing sound watershed management strategies to meet societal needs while stewarding freshwater ecosystems will require assessments of the trade-offs between flow modification and riparian ecological condition. Complex feedbacks and novel ecosystem elements such as introduced species raise the likelihood of surprises and heighten the challenge of ecological prediction, but pressing water management decisions, inevitably framed by substantial uncertainty, warrant methods to explore these trade-offs by representing the potential effects of alternative scenarios. This work is an attempt to progress toward assessment approaches that account for the variation through time that is integral to flow regimes and riparian vegetation communities, but that simplify the ‘bio-hydro-geomorphic’ interactions in river corridors in order to meet pragmatic constraints on project duration and data availability.

My approach draws on the concept of riparian flow response traits to characterize the extent of different plant functional types relative to a sequence of annual high flows driving flood disturbance mortality and establishment opportunities. In Chapter 1, I review previous approaches to modeling riparian vegetation in order to contextualize this work. In Chapter 2, I describe my generalized model structure and apply it to questions of how dams may influence the relative abundance of flow response trait types by altering the size and frequency of overbank flows. The costs and controversy surrounding dams complicate direct experimentation and necessitate the use of models to represent their possible impacts. I use the simulations in this chapter to illustrate how a highly simplified representation of flow-vegetation dynamics can afford preliminary insight into the outcomes of decisions concerning dams and can highlight key considerations for more resource-intensive modeling. In Chapter 3, I relate the introduced plant *Tamarix* to hydrologic and geomorphic processes along rivers in the western United States and discuss how *Tamarix* may in turn influence these processes. In Chapter 4, I apply the model developed in Chapter 2 within the background presented in Chapter 3 as a means to examine the risk of further *Tamarix* spread. Where lower temperatures now limit the suitable habitat of introduced species such as *Tamarix*, climate change may render watersheds increasingly vulnerable to invasion. However, hydrologic and geomorphic variations throughout drainage networks are likely to govern the populations of introduced riverine organisms, and I accordingly analyze the relative risk of colonization associated with flow regime changes under different climate scenarios. My research demonstrates that a modeling approach based on the flow response traits of riparian plants is well suited to investigating trajectories of vegetation change relative to hydrologic alteration by existing water control infrastructure and future climate change.

## CHAPTER 1: RIPARIAN VEGETATION MODELING PRECEDENTS

### **Why model riparian plant communities?**

As the interface between terrestrial and aquatic habitats, riparian zones are critical features of the landscape, particularly in semi-arid and arid regions (Naiman et al. 2005). These ecosystems influence numerous goods and services valued by society (Loomis et al. 2000, Holmes et al. 2004), including the overall availability of surface water in a catchment, the movement of sediment and ensuing changes in channel form, the flux of nutrients and pollutants into drainage networks and other water bodies, the type and amount of fish and wildlife habitat, and the desirability of recreation within the river corridor. Fundamentally, vegetation communities within riparian zones are valuable as diverse, evolving assemblages containing species with unique adaptations to river-related processes. Consequently, these communities may offer readily observed signals of the undesirable consequences of hydrologic alteration (Nilsson and Berggren 2000, Rood et al. 2005, Capon et al. 2013).

Models represent relationships among key system components for the purposes of understanding observed patterns and anticipating the probability of future outcomes. Models codify scientific understanding of ecological processes and serve as virtual laboratories for otherwise impossible manipulations. The challenge of managing water to meet short-term needs without undermining long-term ones requires sound decision support information, and models can provide a rigorous means to compare management alternatives and to guide policy, planning and permitting. Rather than replicate the full complexity of reality, useful models offer a clear perspective on a critical but necessarily limited set of processes. As the number of parameters and functions included in a model increases, the benefits of exploring more realistic scenarios



must be weighed against the costs of greater data needs, larger budgets, longer project durations and the greater difficulty of understanding model behavior, such that more technical expertise is needed to initialize, run and interpret results. An ongoing challenge for the research community is the development of interdisciplinary, cost-effective modeling methods that represent biophysical processes with sufficiently mechanistic structure to allow the meaningful investigation of alternative futures.

Here, I review several alternative approaches to the task of representing riparian vegetation communities and their relationships with environmental drivers, in particular the pattern of discharge along rivers designated the flow regime. In structuring this chapter, I distinguish correlative models that fit observed vegetation patterns to a set of variables of hypothesized importance from process-based models that attempt to represent directly the hypothesized mechanisms generating those patterns. This conceptual distinction designates the ends of a spectrum rather than an inviolable division, but it offers a way to organize studies that reflects differences in both model structure and potential applicability. No single model of riparian vegetation is ‘best’, and the choice of an appropriate strategy along this spectrum will follow from considerations unique to each project.

### **Geographic species distribution models**

Correlative approaches quantify riparian ecosystem drivers as independent variables and vegetation outcomes as dependent variables without directly specifying the biophysical mechanisms governing their interaction. These methods reveal patterns in data and can enable hypothesis testing of how particular factors influence measured patterns. The selection of factors known or presumed to play a causal role in a response strengthens the inference from this mode

of investigation. Correlative relationships defined using a wide range of regression methods and similar techniques are well suited to predicting management outcomes if the proposed actions under consideration alter the examined factors within their range of prior measurement. The fairly widespread practice of applying statistical models beyond their domain of supporting data may also afford a useful first approximation of plausible consequences when the inherent limitations are understood (i.e., the possibility of basic structural shifts in the underlying system at a threshold outside of observed values).

Relating vegetation presence and species composition to environmental correlates, historical events and other niche dimensions is inherently spatial. The maturation of the discipline of landscape ecology and the advent of large-scale, spatially continuous environmental datasets have fostered the development of geographic species distribution models (SDMs). Although the underlying algorithms do not necessitate a particular spatial scale, SDMs are often constructed over a large extent (thousands of square kilometers), with a coarse grain (square kilometer tiles), and with independent variables that either provide the best fit to training observations or are pre-defined to measure physiological constraints of known importance (Kearney and Porter 2009). Several recent SDMs have focused on riparian plants and illustrate the approach of extending inference from the site conditions associated with known occurrences to unobserved sites for which comparable data are available (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006, Elith and Leathwick 2009).

Woody riparian plants in the *Tamarix* genus were introduced to western North America during the 19<sup>th</sup> and early 20<sup>th</sup> centuries, and efforts to model the distribution of *Tamarix* have demonstrated the utility of SDMs (Nagler et al. 2011). Morisette et al. (2006) based a nationwide estimate of suitable *Tamarix* habitat on recorded presences regressed against composite, remote

sensed indices of vegetation condition. At the smaller extent of Grand Staircase-Escalante National Monument (Utah, USA), Evangelista et al. (2008) demonstrated that several SDM algorithms accurately captured likely *Tamarix* habitat within the larger landscape matrix in terms of overland distance to water, slope and soil moisture. Stressing the need to update SDMs as new data become available, Jarnevich et al. (2011) built on these studies and additional occurrence records to construct a maximum entropy model (MAXENT, Phillips and Dudík 2008) for *Tamarix* habitat suitability throughout the western United States. Assessed against non-training data, this model accurately described *Tamarix* presence and absence (e.g., high sensitivity and specificity) at a resolution of 1 km<sup>2</sup> as a function of distance to water, warm season temperature and precipitation (both mean and event-magnitude). This research highlighted the importance of incorporating new observations into SDMs intended to support management of invasive or threatened species with expanding or contracting patterns of occurrence (Jarnevich and Reynolds 2011, Nagler et al. 2011). Established modeling protocols and shared public data repositories (e.g., the National Institute of Invasive Species Science; [www.niiss.org](http://www.niiss.org)) can facilitate this process.

Indeed, Kerns et al. (2009) applied this approach to the question of potential range expansion, extrapolating to future climate conditions with a *Tamarix* SDM developed for the Pacific Northwest region of the United States. When evaluating habitat suitability under existing conditions, these authors found that a climate envelope model limited to temperature and precipitation variables performed comparably to a model including distance to water and solar radiation. Implementing this climate-only SDM subject to spatially downscaled climate projections suggested that suitable area for *Tamarix* might expand substantially by the end of the 21st century. Strengthening confidence in this model outcome, the predicted increase resulted

primarily from a larger area of the conditions observed to support tamarisk under the historic range of values rather than from the effects of entirely novel environmental conditions.

Acknowledging the uncertainty associated with greenhouse gas emission scenarios, climate model projections, and SDM construction, the authors proposed that this approach nonetheless afforded a heuristically valuable ‘starting point’ for ongoing assessment of *Tamarix* range expansion.

Species distribution models rapidly characterize important landscape patterns, generate readily interpreted output such as habitat suitability maps, and may help refine further data collection or provide insight into the need for more detailed analyses. Regular updating with newly available data may also build confidence in the applicability of an SDM if the model successfully predicts novel occurrences. Nonetheless, SDM approaches for riparian vegetation are subject to conceptual and logistical limitations concerning spatial scale and temporal variation. Predick and Turner (2008) demonstrated that both composite regional variables and finer-scale measures of habitat quality (soil texture, land-use history) and hydrologic regime (proxies for inundation frequency) significantly contributed to models of the presence and abundance of invasive floodplain shrubs in Wisconsin (USA). Analyzing an extensive survey of 12 non-native riparian plants in the western U.S., Ringold et al. (2008) found that species occurrence, including that of *Tamarix* and Russian olive (*Elaeagnus angustifolia*), varied significantly among climate regions (e.g., mountains versus plains) and within river networks (e.g., between reaches distinguished by Strahler order). Despite these and other indications that spatial scale is highly likely to influence riparian SDMs (e.g., Jarnevich and Reynolds 2011), few studies to date have systematically quantified which environmental factors contribute most

strongly to SDM performance at reach, watershed and continental scales, or determined the appropriate resolution (grain size) for different categories of input data.

These concerns have direct implications for management choices or ecosystem service estimates based on SDMs. Results that neglect finer-scale population controls could be interpreted as a conservative over-estimate of the area susceptible to an invasive species, but could also constitute a dangerously misleading characterization of the declining range of a threatened species. In addition, SDM algorithms may resolve the incidence of habitat generalists less accurately than that of habitat specialists (Evangelista et al. 2008). Riparian plants are often habitat specialists at a landscape scale, but invasive species such as *Tamarix* may be generalists within riverine habitats (Merritt and Poff 2010). Given the relative paucity of spatially continuous, extensive, but fine-scale data for hydrologic and fluvial geomorphic attributes, this implies that the basic functional traits of many riparian species may limit the applicability of SDMs beyond continental scale assessments. Nonetheless, the approach merits further development to characterize riverine taxa within currently information-rich watersheds or as such data become more widely available.

However, static geospatial SDMs produce a single ‘snapshot’ of an environment-vegetation relationship, with limited capacity to represent temporal patterns other than the estimated riparian response to the long-term mean or maximum values of predictor variables. All models are subject to the inductive error of presuming that observed patterns will persist, but the SDM approach may restrict the exploration of alternative assumptions regarding the structure of system interactions (e.g., shifts over time in the importance of dispersal limitation). Comparison across a set of input scenarios is possible (i.e., ‘present’ versus ‘future’), but dynamic simulation

can provide greater flexibility and transparency in this regard and generally greater capacity to evaluate vegetation changes under novel circumstances.

### **The role of dynamic simulation**

Existing riparian populations are evolving in the context of environmental factors that have begun to shift away from the recent historical range of variability (Catford et al. 2013). Paleoclimatic reconstructions may provide valuable information about the long-term adaptive setting of a species, but recent human activity has created novel biological communities and altered flow and sediment regimes in ways that lack historical analogues (e.g., hydropeaking). In addition to climate shifts, ongoing evolution (Friedman et al. 2008, Gaskin and Kazmer 2009) and the continued adaptation of land and water management practices imply that the future of riparian ecosystems always has the potential to fall outside the range of the observed past.

This potential suggests the need for model frameworks designed to capture changes in vegetation, possibly as the rules governing those changes are themselves changing. I distinguish dynamic simulation as a modeling exercise that begins from a set of variables of interest (e.g., flow conditions and species abundance), and specifies functions or algorithms that state how they are assumed to interact through time. The resulting model object enables controlled, repeatable tests of system behavior within the specified parameter space, while also accommodating creative exploration of novel relationships (i.e., “What if...?” experiments). Models fit to historical observations and theoretical model experiments can both afford insight into the production of ecosystem services associated with the modeled riparian vegetation, thereby framing decisions within transparently derived, reproducible information. Stakeholders,

regulators and researchers may debate which factors to include, but the resulting model can serve as a common point of reference.

I focus on peer-reviewed studies undertaken to characterize and anticipate changes in the amount and type of riparian vegetation occupying floodplains, reaches and river networks. Abiotic and biotic factors such as light availability, temperature extremes, soil quality and herbivory may significantly influence riparian plant recruitment and persistence, but fluvial controls on surface and subsurface water availability are primary controls on the distributions of plants in riparian areas. Hydrologic variation is a key physical process in riparian ecosystems (Naiman et al. 2005). Fluctuating water levels favor riparian plant species over aquatic macrophytes and upland competitors with lower water requirements (in arid areas) or lower disturbance tolerance (in humid areas). More specifically, the sequence of high and low flows within and between years influences the establishment, survival and mortality of riparian vegetation. Flow and sediment regimes generate suitable germination sites, constrain dispersal and establishment, and govern mortality due to shear stress, anoxia and drought (Auble et al. 1994, Scott et al. 1996, Patten 1998, Nilsson and Svedmark 2002, Sandercock et al. 2007, Osterkamp and Hupp 2010). Thus, vegetation distribution patterns emerge from colonization and succession dynamics driven by the interaction of hydrogeomorphic heterogeneity with functional trait variation in plant species (Merritt et al. 2010).

In contrast to geospatial SDMs with limited temporal resolution, models incorporating hydrologic variation require a record through time of flow regime attributes such as magnitude, duration, frequency, timing and rate of change (e.g., a time series or probability distribution characterizing discharge) as well as assumptions regarding the effects of those flow attributes. Beyond a shared emphasis on features of the flow regime, the following models differ

considerably in spatiotemporal representation and structural complexity. For the purpose of organization, I classify simulations according to whether recruitment probability, a set of patch types or detailed community information describes the modeled vegetation. I note that these distinctions have quite limited precision and are not necessarily mutually exclusive. For instance, any Markov chain, such as a matrix population model that simulates detailed demography, including recruitment success, also embodies transitions between hydrologic states.

### **Hydrologic controls of recruitment and persistence**

Field observations made within floodplains or along longitudinal river gradients have established numerous associations between the flow regime and plant recruitment and persistence, often mediated by local topography (Campbell and Dick-Peddie 1964, Auble et al. 1994, Hupp and Osterkamp 1996, Toner and Keddy 1997, Shafroth et al. 1998). These observations have supported the development of both theoretical models to describe basic hydrogeomorphic controls on riparian vegetation and river-specific representations of the abundance or occurrence of particular species relative to particular flows. In addition to the general population and community ecology theory that bears on riparian vegetation dynamics (e.g., the influence of diversity on invasibility, mechanisms of competitive co-existence, etc.), a recent body of research has sought to derive mathematical expressions that synthesize the hydrogeomorphic controls specific to riparian zones. Collectively, this work views abundance and diversity patterns as the product of local forces interacting within the constraints imposed by drainage network form (Rodriguez-Iturbe et al. 2009).

For meandering rivers, Perucca et al. (2006) proposed that the steady-state, transverse distribution of overall riparian biomass would follow a decreasing, increasing or unimodal form



at greater perpendicular distances from the channel according to whether water table depth, flood effects or a combination of the two acted as the dominant control at a particular position in the network. Incorporating simple expressions for these alternative conceptual functional forms into a simulation of planform channel morphology change, these authors then examined how the relationship between the rate of meandering and those of vegetation growth and decay determined patterns of overall abundance along a reach. In this and a subsequent study addressing the feedback of vegetation density on bank erosion susceptibility, the emergent, modeled patterns clearly resembled observations from rivers in a variety of hydro-climatic zones. These models demonstrated that mathematically tractable but mechanistic descriptions of channel migration and vegetation maturation (controlled by floods and water table depth) could reproduce empirically recognizable distributions of overall plant density in riparian zones, particularly as the time-scales of the basic biological and geomorphic processes converged.

Pursuing a similarly compact description of the effects of flow variation on riparian biomass, Camporeale and Ridolfi (2006) formalized the premise that water surface elevation determines vegetation growth and decay across a channel and riparian zone cross-section. They proposed a stochastic differential equation driven by dichotomic noise representing changes in river stage (i.e., continuous variation filtered to a binary state). The pattern of river stage fluctuations was characterized by the probability distribution and temporal autocorrelation of discharge at a cross-section, and this forcing switched the equation terms between a generalized logistic growth expression and a power function describing decay. Biomass at inundated positions declined according to parameters describing resistance to inundation, and biomass otherwise increased toward a carrying capacity determined by the depth to alluvial groundwater for elevations greater than river stage. These authors derived an analytical formulation for the

steady-state, transverse biomass distribution, and indicated how differences in statistical properties of flow could alter vegetation features such as the highest and lowest vegetation elevations. Although the model required biological and hydrogeomorphic simplifications for mathematical tractability, the resulting equations nonetheless captured important basic patterns such as a unimodal lateral distribution of riparian biomass due to the combined effects of flooding and groundwater tables.

The core expressions in the model of Camporeale and Ridolfi (2006) provided a platform for extension to additional questions such as the network-scale distribution of riparian vegetation and the effects of dam-induced changes in flow regime (Muneepeerakul et al. 2007b, Tealdi et al. 2011). Muneepeerakul et al. (2007b) demonstrated the potential for a decrease in riparian vegetation width with increasing variance in discharge, and described how the network scaling of floodplain dimensions and hydrologic variation could mediate this pattern. Tealdi et al. (2011) applied the model framework to examine changes in both the mean and coefficient of variation in flows, illustrating outcomes of management concern such as channel narrowing due to vegetation encroachment. These models elegantly represent generalized relationships between physical and ecological dynamics, reproducing key riparian vegetation responses to hydraulic and hydrologic forcing. This generality, however, has favored their application to broadly relevant research questions over parameterization for specific rivers and plant species.

In western North America, empirical research and models have responded to stakeholders' primary interest in the response of particular taxa. Seedling germination and survival requirements are well studied for native cottonwood species (*Populus angustifolia*, *Populus deltoides*, *P. fremontii*, *Populus trichocarpa*) and invasive species such as tamarisk that share recruitment traits. The "Recruitment Box" conceptual model associates cottonwood

recruitment with favorable rates of stage decline following annual spring snowmelt floods (Braatne et al. 1996, Mahoney and Rood 1998, Rood et al. 2003). The model hypothesizes that over the course of an annual cycle, gradual but consistent river stage recession following a flood peak (that may coincide with the timing of seed release) can increase the likelihood that young plants are neither stranded (as water table declines outpace root growth and cause drought mortality) nor saturated by standing water, after having germinated on bare, moist alluvial surfaces.

Subsequently, Braatne et al. (2007) quantified an extended set of criteria in order to account for inter-annual variation in peak flow magnitude. In addition to intra-annual recession rates favorable to seedling root growth, these authors observed that previous flows of sufficient magnitude were needed to reconfigure floodplain sediment, and that subsequent smaller floods were required to meet sapling water requirements without scouring new stands (empirical support for this idea is also described in Cooper et al. 2003, Birken and Cooper 2006). In conjunction with cross-sectional hydraulic modeling, Burke et al. (2009) implemented a subset of these criteria as numerical rules in order to examine the effects of dam-induced hydrogeomorphic change on riparian recruitment opportunities along the Kootenai River (Canada and USA). This watershed-scale study, along a 233 km longitudinal profile, focused on the dynamics of a local hydrologic driver: per-kilometer, daily river stage during the growing season. While not developed to evaluate specific management alternatives, the model revealed how dams had altered fluvial geomorphic conditions to inhibit cottonwood recruitment, and indicated that dam releases intended to benefit native fish might also promote cottonwood recruitment.

The recruitment box concept has also supported simulation of cottonwood stand age composition, a potentially important determinant of ecosystem service production (e.g., flood energy attenuation; recreational appeal). Incorporating age-based differences in susceptibility to flood and drought mortality, Lytle and Merritt (2004) developed a transition-matrix model to describe population dynamics for cottonwood within floodplains along the Yampa River (Colorado, USA). This study assumed that river meandering simultaneously generated and destroyed suitable habitat, thereby maintaining potential occupied area in quasi-equilibrium. Parameters for rates of reproduction, self-thinning and senescence were calculated from field observations, and used to determine annual changes in the proportional area held by 6 seedling and adult stage classes. Yearly peak discharge magnitude and rate of decline modified the probabilities of persistence and recruitment, resulting in periodic establishment pulses at a frequency related to the hydrologic variation included in model runs. Model behavior illustrated the likelihood of cottonwood population declines as flow regulation either reduced or increased inter-annual flood frequency, respectively limiting recruitment opportunities or imposing more regular mortality. Furthermore, the discrimination of age classes permitted an evaluation of differential vulnerability to flow alteration, and the potential benefits of conservation efforts targeting particular life stages.

Models focused on hydrologic recruitment controls have also provided insight into the potential consequences of flow management for riparian protection or restoration in other regions. Ahn et al. (2004, 2007) modeled recruitment relative to intra-annual stage fluctuations for herbaceous and woody species occupying Illinois River (USA) floodplains. These studies used the STELLA framework to examine how plant distributions along a lateral floodplain elevation gradient might respond to proposed dam releases of a given duration and timing. Dixon

and Turner (2006) investigated the implications of flow modification for within-floodplain recruitment of 5 species along the Wisconsin River (Wisconsin, USA). Their detailed simulation translated extensive field data into functions for seed dispersal, deposition, germination and over-winter survival due to water availability, inundation and scour. In addition to implementing recruitment box concepts for multiple species, this work extended prior studies by addressing the likelihood of overwinter seedling survival. Simulated outcomes indicated that regulated flows favored greater overall recruitment in this humid system, corroborating historical observations. Comparison to model runs driven by an unregulated flow regime illustrated how this pattern resulted from the combination of reduced spring peak flow mortality, increased late-season baseflow, and decreased variability. The process of model construction and assessment also revealed knowledge gaps, highlighting the need for further quantification of shear stress thresholds and other sources of hydrologic mortality.

The recently introduced HEC-EFM platform seeks to provide a means to quantify and assess possible ecological consequences of future water allocation decisions, within any river basin for which hydrology and biology data are available (<http://www.hec.usace.army.mil/software/hec-efm/index.html>). Although not developed specifically for riparian vegetation, the graphical user interface and ease of combination with standard hydraulic and geographic analysis tools (i.e., HEC-RAS and GeoRAS) are intended to facilitate study of the consequences of known flow-ecology relations such as the links between floods and riparian vegetation recruitment. Demographic flow-ecology models have been empirically parameterized for a limited number of species, but work to date suggests that multi-species implementations are feasible (Dixon and Turner 2006). Glenz et al. (2008) applied a fuzzy logic method to formalize qualitative flood tolerance descriptions for a 65 European

riparian trees and shrubs, proposing that these functions could support further dynamic models of inundation effects on community composition. Yet studies at the guild level have only weakly addressed how different hydrologic recruitment traits may influence riparian vegetation composition. When multiple species have been included, recruitment models and tools such as HEC-EFM have typically assumed independent populations, such that limiting germination resources are not explicitly partitioned according to an hypothesized mode of competition. Thus, additional research is required to clarify how best to simulate interspecific differences in hydrologic response traits (Merritt et al. 2010).

### **State and transition models**

Rather than characterizing the likelihood of establishment or mortality for particular species, a simulation may involve transitions between pre-defined, categorical vegetation states. For the purpose of organizing this review, the designation “state and transition” implies a strongly spatial component to supporting data, simulation implementation (i.e., cellular or geographic), or both. The number of states may vary substantially, from major cover differences (i.e., bare sediment, pioneer vegetation and mature stands) to classes that discretize site-specific canopy successions, but within-class changes are not usually modeled. Input flow records or other environmental changes trigger transitions, and models may represent disturbance by resetting a progression through sequential vegetation states.

Richter and Richter (2000) applied this approach to a study of riparian vegetation specifically in the context of river management. Understanding potential consequences of damming and storing the flow of the Yampa River (Colorado, USA) motivated this research, and the authors sought to position their model development within the larger social process of

determining desirable flow regimes. Building on extensive field observations, they modeled a sequence of vegetation classes that progressed from the colonization of newly formed point-bars and meander cut-offs. Class transition probabilities were derived from aerial photos and analysis of the effective discharge associated with geomorphic changes in this minimally regulated system. These authors compared simulated cover proportions under natural and regulated flow conditions in order to estimate the flood duration needed to maintain an historic riparian cover mosaic. This work demonstrated how the goal of evaluating alternative environmental flow schedules justified the capacity to conduct meaningful model experiments.

Patch proportions were spatially implicit in the model constructed by Richter and Richter (2000), but subsequent studies have refined the spatial representation of riparian vegetation transitions. For a geographic representation of the Grande Ronde watershed (Oregon, USA), Fonnesbeck (2007) defined a range of vegetation states (e.g., pioneer forbs to mature, multi-strata forest) within channel units distinguished by gradient and network position. These different geomorphic contexts modified the effects of a variety of stochastic transition events (e.g., floods, debris flows, fires). Alternative management scenarios and parameters for the spatial extent of impact further controlled the effects of these events. This model structure addressed the propagation of class transitions via both overland and in-network connections. For example, a debris flow affecting an upstream patch could alter vegetation states in downstream channel units during subsequent model iterations. While unsuited to examining specific modes of hydrologic alteration (e.g., shifts in flood timing) or local management interventions, this model demonstrated an approach to accounting for the intersection of hydrologic factors with broader landscape disturbances. Such interactions may have important influences on riparian dynamics,

especially at the drainage network scale, but have received limited attention in models emphasizing hydrologic variation.

Benjankar et al. (2011) modeled the succession through three vegetation classes (cottonwoods and willows, reeds and marsh forbs, and shrubs) within bank and floodplain zones in a study of the consequences of hydrologic alteration caused by dams and levees on the Kootenai River. At a relatively high spatial resolution (10x10m grid cells) along a large braided reach, a hydraulic model of water surface elevation defined inundation and shear stress inputs used to transition between vegetation states. A combination of topography, discharge and current vegetation state determined whether cells reverted to bare gravel and sand available for colonization or progressed toward maturity. The model reproduced overall differences in proportional cover between pre- and post-dam flow regimes well, but a much stricter cell-by-cell comparison between simulated results and a surveyed map suggested the need for further refinement in the prediction of fine-scale distribution patterns. These authors noted that the model assumptions of fixed topography and uniform susceptibility to flood duration within a cover class, in combination with the limited representation of shear stress thresholds, might have reduced spatial accuracy. Despite these sources of uncertainty and the site-specificity of the initially modeled vegetation states, Egger et al. (2012) recently adapted the model structure and parameters to the monsoon-driven Nakdong River (Korea) and García-Arias et al. (2012) implemented this platform for several European rivers, indicating its applicability to scenario evaluation in other hydroclimatic zones.

Emphasizing model parsimony to minimize data requirements, but still seeking to maintain management relevance, Perona et al. (2009b) derived a differential equation to describe the creation and colonization of bare surfaces within a defined floodplain extent (Equation 11



gives the final, unexpanded form). This work focused on the statistical properties of floodplain cover types rather than representing the location of specific classes (i.e., “patches” were spatially implicit). These authors built on a series of aerial photographs, discharge records and hydraulic modeling for a 2.8km reach of the Maggia River (Switzerland) to specify the rate of change in bare sediment and open water (and conversely vegetated area) as a combined function of randomly recurring floods above a magnitude threshold and the ongoing colonization of “low” vegetation (i.e., grasses). In addition to deriving an analytical solution for the cumulative distribution function of the area of bare sediment under steady state assumptions (Equation 22, Perona et al. 2009b), these authors simulated estimates of this key riparian attribute under different assumptions for the statistical properties of flood recurrence and magnitude.

Perona et al. (2009a) subsequently distinguished grasses, shrubs and trees as separate cover types, noting that the behavior of the corresponding system of equations illustrated a progression toward mature cover if flood magnitudes were maintained below the disturbance threshold. The formulation of these models supported a compact expression of the steady-state probability that a given flow regime (characterized by flood magnitude and recurrence parameters) would result in a particular extent of floodplain vegetation, depending only on parameters for the daily rate of colonization and the critical discharge at which vegetated area was converted to bare sediment. Despite simplifying assumptions regarding the processes of inundation, scour, establishment and survival, this model framework therefore provided a theoretically sound, mechanistic tool with which to calculate possible consequences for vegetation cover under future flow alteration (Perona et al. 2009a, b). The development of these simulations (and the related, previously described work of Camporeale and Ridolfi 2006) involved sophisticated mathematical concepts, but the final functional expressions include a

limited number of parameters and could serve as the underlying “engine” for decision support and service evaluation tools that include appropriate user interfaces “wrappers”.

Simulating transitions among classes offers a flexible means to investigate the effects of hydrogeomorphic processes on riparian vegetation. Studies to date have generally concentrated on the local spatial scales of individual reaches and floodplains, but these methods may be applied to network or regional scales in contexts where geomorphic units and corresponding vegetation states are adequately discriminated (Fonnesbeck 2007). Patch-based transition models invite visually realistic implementation, with a corresponding increase in data requirements over tools in which vegetation locations are implicit. The number of class divisions may also strongly affect model complexity and parameterization requirements, with the number of separately specified transition rules possibly growing rapidly as classes are added (depending on the scope of “looping”). Coarse class distinctions such as water, sediment and plants are likely robust to the duration of simulations, but categories that assume homogeneous responses (i.e., early versus late successional cover) may represent vegetation behavior less effectively if evolutionary or biogeographic processes such as species introductions or losses alter the set of functional traits represented within a class.

### **Stand simulators**

Virtual stand models share a conceptual lineage rooted in the pioneering forest simulators of the 1970’s (i.e., JABOWA Botkin et al. 1972). However, unlike forest simulations focused on representing competition for light and soil nutrients (e.g., SORTIE, <http://www.sortie-nd.org>), fewer studies have emphasized the hydrologic and geomorphic variability characteristic of riparian systems (Perry and Enright 2006). This class of models varies substantially in spatial

grain and extent as well as temporal resolution, but generally requires greater structural complexity and detailed information concerning species or individual level growth, reproduction, dispersal and mortality.

Adapting the JABOWA conceptual template, Phipps (1979) developed the SWAMP model to investigate differences in tolerance to flooding and water table depth for bottomland trees occupying the White River National Wildlife Refuge (Arkansas, USA). SWAMP recorded size and species identity for more than 30 trees and shrubs divided into understory, sub-canopy and canopy levels within a spatially implicit 20x20m plot. Growth and survival of the simulated vegetation were subject to yearly water availability, crowding, logging or other disturbance, and establishment was flood-regulated. Application of the model to examine the combined effects of commercial cutting and upstream flood control provided an early demonstration of the usefulness of translating field observations into a simulation tool for assessing management alternatives.

Pearlstone et al. (1985) combined functions from SWAMP with the FORET platform (Shugart and West 1977) to generate FORFLOW, a model capable of examining intra-annual flood duration and frequency effects on small plots along the Santee and Cooper Rivers (South Carolina, USA). In addition to temperature and crowding influences on growth, survival and reproduction, FORFLOW introduced functions describing the effects of inundation on these processes at a bi-weekly time step. Although within-plot tree locations were not specified (spatially-implicit dynamics), the model was run for a range of elevations relative to a stage-discharge relationship, facilitating an early demonstration of geographically realistic output at the larger between-plot scale. FORFLOW was motivated by the applied goal of assessing a U.S. Army Corp of Engineers proposal to re-divert flows that had led to undesirable harbor sedimentation following a previous diversion. Model output suggested that a re-diversion

schedule modified to improve establishment conditions might support more extensive cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) forest than the originally proposed pattern of flow releases which resulted in primarily open, marshy soils. Nonetheless, simulation indicated that either re-diversion program was likely to decrease the area of mixed hardwood forest, thereby illustrating and quantifying one of the potential trade-offs associated with further flow alteration.

Several subsequent applications of the FORFLOW/SWAMP platform have focused on basic ecological questions. Hanson et al. (1990) included functions to explicitly represent several dispersal modes (anemochory, hydrochory, barochory and zoochory) as SEEDFLO, and demonstrated that structured, directional dispersal altered species diversity relative to the assumption of “ubiquitous” seed availability. Similarly, Nuttle and Haefner (2007) combined functions based on SWAMP with detailed modeling of wind-borne seed dispersal within a spatially-explicit, individual-based simulation of bottomland forests along the lower Mississippi (YAFSIM). Simulation experiments indicated that seed availability contributed significantly to longer-term patterns of stand diversity (e.g., century-scale declines in richness), indicating the importance of modeling dispersal constraints, particularly in floodplain forests subject to less frequent disturbance. Liu and Malanson (1992) implemented a version of FORFLOW to investigate the relationship between long-term periodicity in vegetation abundance and characteristic environmental conditions specified as mean annual growing degree-days and natural and regulated flood regimes. Analyzing the dominant frequency of the spectral density calculated from simulated time series of stand composition, these authors observed that differences in the species favored by climate shifts and flow regime alteration ultimately produced different cycles of overall stand density. While this study did not examine the

consequences of increased climatic variance (e.g., larger standard deviation in annual growing season temperature), the controlled, mechanistic simulation approach provided a valuable perspective on the complex interactive effects of temperature and discharge patterns (Perry et al. 2012).

Recent studies have sought to refine the spatiotemporal resolution of stand dynamics while maintaining relevance to both the management and basic ecology of floodplain forests. Addressing proposed reservoir operations designed to increase baseflow in support of river navigation, Ye et al. (2010) represented the consequences of hydraulic fluctuations for three competing species in riparian zones of the Lijiang River (southwestern China). This model described vegetation changes in a cellular automata implemented over a triangular mesh of elevations and driven by a combination of daily hydrology across the riparian zone and competition for a non-specified resource within cells (as spatially implicit dominance rules). Simulation of stabilized flow conditions illustrated a likely decline in the distribution and abundance of herbaceous, annual species following replacement by a competitively superior phreatophyte species. Hoepfner and Rose (2011) focused on cypress-tupelo stand dynamics within Mississippi River bottomlands, developing an individual-based model describing inundation and salinity effects relative to elevation across a grid of 10m cells. Weekly iteration of tree growth, reproduction and mortality nested within annual cycles of establishment and survival supported comparison of stands simulated under different levels of flooding and saltwater intrusion. Although modeled basal area and stem density agreed with field observations, relative dominance was not as well predicted. Noting the well-resolved spatiotemporal depiction of stand behavior, these authors concluded that the model could guide

future restoration planning, particularly following improved specification of interspecific differences and dispersal processes.

### **Research priorities and opportunities**

Riparian vegetation models to date have enabled theoretical tests of empirically inferred processes controlling plant distribution and abundance. Simulations have also supported the evaluation of management alternatives, including the likely consequences of flow regime alteration. These studies have made considerable progress toward the general objective of describing and anticipating riparian vegetation dynamics. However, further research is needed to characterize the basic behavior and associated ecosystem services of complex river-floodplain systems subject to climate change, land use modification and species introductions.

The task of prediction requires confronting the challenges of non-stationary environmental forcing and uncertainty that compounds with time and layers of modeled input. The unsurprising prevalence of ecological surprises (Doak et al. 2008) may favor a modeling approach that includes stochastic implementations and flexible functional structures. Despite inefficiency relative to convergence on a single modeling platform, expanding the currently diverse suite of approaches to modeling riparian vegetation will increase the collective probability of capturing seemingly unlikely changes in system behavior and increase opportunities for comparison.

Existing research has addressed diverse spatiotemporal domains (i.e., floodplain transects to channel networks and daily to multi-decadal durations), but applied forecasts of vegetation in the context of increasing computing power and data availability likely warrant advances toward finer spatial grain. Hydrologic modeling already extends the availability of key inputs to ungaged

locations throughout entire basins, and correspondingly extensive calibration data may emerge if the automated interpretation of satellite images becomes cost-effective at sub-kilometer resolutions. More fundamentally, models may benefit from improved specification of ecological interactions and trait evolution, and from the structural integration of plant feedbacks on the hydrologic and geomorphic processes affecting floodplain form. In addition to these concerns, eco-hydrologic models applied in a predictive mode will also require tighter coupling to models of the human economic behavior associated with rivers.

Competitive effects have informed some stand simulations and are implicit in several population approaches, but greater attention to multiple trophic levels may refine predictions of density and composition significantly, particularly in settings where mechanical removal of biomass (e.g., herbivory or harvest) exerts a strong influence over establishment or reproductive output. Regardless of the methodological approach, models of the plant populations occupying riparian zones have largely neglected evolutionary processes. The neutral and competition-colonization trade-off models of Muneeppeerakul et al. (2007a, 2007c) are a notable exception, but even these simulations present a limited perspective on changing traits. If logistical constraints have imposed the implicit assumption in most recent models that genetic variability plays no appreciable role in determining vegetation patterns, then relaxing this assumption is a priority for a rigorous, “mature” characterization of the mechanisms controlling plant distributions and densities. Rapid evolutionary processes such as the hybridization of previously distinct invasive species may influence important physiological and phenotypic functional traits over short durations (Sexton et al. 2002, Gaskin and Kazmer 2009). At a minimum, the exclusion of natural selection and drift demands explicit recognition. Representing riparian populations as interacting, evolving entities offers a tremendous opportunity to link important conservation

questions to specific adaptations. Scarce conservation resources could be prioritized according to the likelihood that a species will “save itself” or show such vulnerability or limited allelic variability as to be irredeemable over the long term, thereby increasing the likelihood of effective and efficient intervention.

Feedbacks between riparian vegetation and hydro-geomorphic processes substantially influence channel morphology and stage-discharge relations, altering the appearance of river corridors and modifying floodplain response to flows of a given magnitude (Gurnell et al. 2012, Merritt 2013). Yet, relatively few models have explicitly linked functions for plant recruitment, growth and persistence with functions for erosion and accretion that alters riparian surfaces, despite broad recognition of the importance of reciprocal causality. Typically, ecologists have developed models in which the physical template for intra- and interspecific interactions is ignored or held constant, while fluvial geomorphologists have tended to ignore or oversimplify biological changes. Simple disciplinary divisions are partly to blame, but progress toward integrated models may require confronting more fundamental differences in the spatiotemporal units of ecological and geomorphic pattern and process (Post et al. 2007). Nonetheless, the model of river meandering interacting with vegetation growth and decay proposed by Perucca et al. (2006) revealed the compelling behavior displayed by even a first approximation of the coupled system.

Although policy considerations have motivated many of the models reviewed, little evidence exists to gage the models’ impacts on management decisions. A recent survey of stakeholder attitudes toward hydropower impacts suggested the importance of presenting scenario evaluation information from a combination of biophysical and socioeconomic perspectives (Tullos et al. 2010). As simulation tools develop toward richer integration of



hydrogeomorphic, ecological and evolutionary mechanisms, incorporating functions to describe the socio-economic context of riparian zones will likely increase the relevance of forecasting efforts. Ongoing research into coupling hydrologic and economic models can facilitate this progress (Brouwer and Hofkes 2008), and greater political and societal relevance is the basic goal of improving the representation of riparian ecosystem services. All models must be interpreted within the context of their conceptual and technical limitations, yet forthcoming tools that build on the strengths of current models will certainly justify the effort to communicate their application to management audiences.

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## CHAPTER 2: USING FLOW RESPONSE TRAITS TO CHARACTERIZE THE EFFECTS OF HYDROLOGIC ALTERATION BY DAMS ON RIPARIAN VEGETATION TYPES

### Summary

Dams profoundly affect riverine ecosystems. Good stewardship of freshwater biodiversity and ecosystem services therefore requires evaluating the potential consequences of management decisions involving water control infrastructure such as dams. Flow response traits – shared adaptations to natural flow variability – provide a process-based means to structure models that link the hydrologic alteration resulting from dams and watershed change to the riparian population and community dynamics that mediate habitat quality, nutrient influx, flood damage, and recreational appeal. In order to investigate how river regulation might influence woody riparian vegetation distinguished by flow-response and life history traits, I developed a stage-structured, discrete-time model forced by annual peak discharge. I simulated two hypothetical trait types reflecting different ‘flow niches’: a ‘pioneer’ that depended on flooding to establish seedling cover and an ‘upland’ type that established in unflooded areas. Relative to the upland type, the pioneer was more tolerant of flood disturbance, matured more rapidly into the adult stage, and established on a larger portion of available suitable area. However, a larger portion of the upland seedling cover had the potential to mature into the juvenile stage. I subjected these trait types to stochastic sequences of scaled peak discharge that represented a shift from a ‘natural’ flood regime to a pattern of reduced magnitude and variability characteristic of ‘dam’ conditions. Adult abundances of the pioneer and upland type were comparable under the natural forcing scenario, but the imposition of smaller, less frequent disturbances decreased seedling cover for the pioneer while relaxing the limitation of flood



mortality for the upland type. Regular forcing sequences representing artificially scheduled flood releases did not recover the pre-dam distribution of vegetation types, but the system exhibited resilience under a full return to the natural scenario. However, manipulating the model structure clarified the importance of assumptions regarding dispersal limitation and geomorphic interactions that may qualitatively alter the trajectories of riparian vegetation change following dam construction or removal. This highly simplified depiction of riparian vegetation dynamics illustrated how flow variation may interact with traits controlling recruitment and persistence to influence stage structure and community composition in riverine environments. This work suggested that a theoretical model based on flow response traits can be used as a first approximation or null hypothesis of how future environmental conditions and management may alter riparian vegetation, particularly where input and parameterization data are scarce or unavailable.

## **Introduction**

Ecological conditions in rivers and streams inherently change through time, as regional hydro-climatic differences produce both predictable and unpredictable flow variation over hours to decades (Poff et al. 1997, Sabo and Post 2008). Riverine organisms have adapted to take advantage of this variation through diverse behaviors and morphology (Lytle and Poff 2004), resulting in a rich and fascinating flora and fauna. Yet, the widespread construction of dams and diversions has altered discharge patterns over continental scales (Nilsson et al. 2005, Poff et al. 2007), and this flow regulation interacts with watershed land use change and pollutants to pose a global threat to riverine and floodplain biodiversity (Tockner and Stanford 2002, Naiman and Dudgeon 2010, Strayer and Dudgeon 2010, Carpenter et al. 2011). Dams differ in their purposes

and their effects on flow (Poff and Hart 2002, Graf 2006), but infrastructure designed to meet human needs interferes with the requirements of riverine species when water is both scarce and plentiful (Baron et al. 2002, Bunn and Arthington 2002). For example, summer diversions that reduce base flow may harm fish and invertebrates by limiting in-channel habitat area and increasing stream temperatures, while flood control through levees and reservoir storage may disrupt reproductive cues, restrict access to side-channel rearing habitat, and reduce flushing of salts or renewal of nutrients from disconnected floodplains (Bayley 1995, Tockner and Stanford 2002). In broad terms, flow alteration affects aquatic biodiversity by impairing the physical habitat template, interfering with life history adaptations, and increasing vulnerability to biological invasion (Bunn and Arthington 2002).

Plant communities along rivers are sensitive to these impacts due to the fundamental influence of hydrologic variation on the abundance and diversity of riparian vegetation (Gurnell 1995, Naiman and Decamps 1997, Tabacchi et al. 1998, Nilsson and Berggren 2000, Nilsson and Svedmark 2002, Naiman et al. 2005, Rood et al. 2005). Impoundments that convert upstream reaches into lentic systems may submerge formerly productive bottomlands while possibly generating new riparian habitats in drawdown zones at their margins (Nilsson and Berggren 2000). The specific consequences for riparian vegetation downstream of dams are mediated by latitude, aridity, fluvial geomorphic form (e.g., braided vs. meandering channel types), watershed land cover (e.g., agricultural extent and intensity), and infrastructure use (e.g., irrigation, flood control, hydropower, transportation), but plant community changes have been consistently associated with altered high and low magnitude flows (Patten 1998, Nilsson and Svedmark 2002). Floods can kill and remove vegetation, but may simultaneously flush salts, refresh soil moisture and nutrients, reconfigure floodplain surfaces and redeposit sediment to support

vegetation renewal (Hughes 1990, Scott et al. 1996, 1997). Consequently, reservoirs that reduce peak flow magnitude and trap sediment may lower the likelihood of plant mortality while altering the transient and long term availability of recruitment surfaces, potentially increasing or decreasing the overall area of riparian vegetation and shifting the relative abundance of pioneer, later successional and upland species (Friedman et al. 1998, Johnson 1998, 2000, Shafroth et al. 2002b). Not all dams exert a major effect on vegetation (Katz et al. 2005), but in semi-arid western North America, for example, native species declines and exotic species spread have been associated with shifts in the size, timing and frequency of floods following dam construction (Rood and Mahoney 1990, Rood et al. 1995, Sher et al. 2000, Merritt and Poff 2010, Mortenson and Weisberg 2010, Johnson et al. 2012).

These changes may directly threaten valued vegetation types and may adversely affect other taxa that rely on riparian plants as an essential source of habitat or nutrients (Gregory et al. 1991, Naiman and Decamps 1997, Naiman et al. 2005). Furthermore, flow alteration that modifies the composition of riparian vegetation communities may diminish the production of ecosystem services related to food and fiber, recreation, cultural traditions, flood attenuation, and pollution (Strange et al. 1999, Loomis et al. 2000, Brismar 2002, Holmes et al. 2004). Conservation and restoration efforts that seek to avoid or remedy such undesirable consequences of river regulation will conflict with calls for new dam construction prompted by intensified water and energy scarcity under a warming climate and growing human population (Baron et al. 2002, Poff et al. 2003, Gleick 2010, Sabo et al. 2010, Vorosmarty et al. 2010). Characterizing the trade-offs in biodiversity and service provision that may result from dam management alternatives is therefore necessary in the face of differing views of the value of riverine

ecosystems and water control infrastructure (Poff et al. 2003, Korsgaard et al. 2008, Richter 2010, Kareiva 2012).

Evaluating the potential effects of dam construction, operation, or removal on riparian vegetation and river ecosystems requires a modeling framework to organize assumptions about system interactions and to explicitly relate altered drivers to potential outcomes. Species distribution models relating the suitability of unobserved locations to environmental variables measured at known occurrences (and sometimes absences) are a widely used modeling method that has been successfully applied to riparian vegetation (Nagler et al. 2011). This approach can yield useful information regarding potential range shifts and regional vulnerability, particularly as distribution models incorporate variables involved in the mechanisms of population change and are updated with additional data (Kearney and Porter 2009, Jarnevich et al. 2011). However, dynamic population models that incorporate fluvial process may better represent the variable biophysical conditions in rivers and can support investigating vegetation responses outside of the range of past correlation support, as may often be necessary in the context of anticipated flow alteration (Anderson et al. 2006, Shenton et al. 2012, Yen et al. 2013). For example, Richter and Richter (2000) and Benjankar et al. (2011, 2012) used patch transition models to relate the incidence of flooding to observed turnover in regionally dominant cover classes along western U.S. rivers, thereby providing insight into the flows required to meet conservation goals. Tealdi et al. (2011) and Perona et al. (2009) applied the stochastic differential equations describing cross-sectional vegetation biomass derived by Camporeale and Ridolfi (2006) to investigate the consequences of dam-induced changes in the statistical properties of discharge time series, reproducing both widening and narrowing trends in riparian cover. Taking a spatially implicit approach, Lytle and Merritt (2004) translated field observations of cottonwood (*Populus*

*deltoides*), an important native species in the western U.S., into a stage-structured matrix population model driven by recorded high and low flows. This model indicated the potential for flow regulation to alter intraspecific population structure in addition to overall patterns of abundance.

Such detailed representations of biophysical mechanisms that draw on extensive data collection can bolster confidence in assessment estimates (Shafroth et al. 2010b, Benjankar et al. 2012, García-Arias et al. 2012), but an illustration of the relationship between flow alteration and riparian vegetation may be required in settings with a very limited budgets, timelines and access to information. Current watershed assessment approaches may either insufficiently incorporate the flow variation essential to representing riparian vegetation or demand substantial data for parameterization and calibration (Richter et al. 2011, Vigerstol and Aukema 2011). Despite the complexity of reciprocally interacting hydrologic, geomorphic and ecological processes along river corridors, a pragmatic need exists for tools that adequately represent basic flow-vegetation dynamics on the basis of minimal input information.

Methods based on riparian flow response traits can meet this need. Merritt et al. (2010) reviewed the important contributions made to understanding flow-vegetation relationships through models focused on individual species and system-specific plant assemblages. However, noting the conceptual and applied utility of functional trait classifications for fish and benthic macroinvertebrate species (Poff and Allan 1995, Poff et al. 2006) as well as those for general vegetation strategies (Grime 1977), these authors proposed the use of flow response traits as a means to extend inference across basins when assessing the impact of river regulation on riparian zones. Flow response traits designate the shared attributes of riverine species that mediate mortality and regeneration relative to the disturbance, stress and recruitment opportunities

resulting from high and low flows. For example, riparian species in different regions may tolerate flood disturbance with adaptations such as flexible stems and furrowed bark that confer the ability to withstand scour and burial under alluvial sediment. Similarly, deep, extensive roots and high water use efficiency may buffer plants from low water stress in various arid and semi-arid settings. In addition, multiple species release copious, widely dispersing seeds or re-sprout from branch fragments to establish new individuals on the moist, freshly exposed surfaces that can follow floods. The idea that flow regime alteration may favor or disfavor the population growth of riparian vegetation with alternative trait profiles therefore serves to structure models that indicate potential effects of water management on entire functional plant classes (Figure 2.1). If trait types also differ with respect to their habitat value or service production, then this conception can serve to link flow alteration to riparian ecosystem benefits.

I used the riparian flow response trait concept to initiate development of a generalized, exploratory simulation approach. My primary objective was to visualize change through time in the relative abundance of co-occurring vegetation types in order to demonstrate how a model grounded in basic stream ecology principles might provide heuristic insight into the effects of flow alteration where data are highly limited. Focusing on woody pioneer and upland vegetation types subject to annual flood disturbance, I examined two questions through a sequence of simulation experiments: (1) How does dam construction that alters the intensity and frequency of flood disturbance affect the adult abundance and stage structure of these trait types and (2) To what extent may intentionally scheduled flood releases or dam removal mitigate these effects? After introducing the model structure, I discuss the simulated behavior related to these questions in the two sections that follow, before concluding with a general discussion.

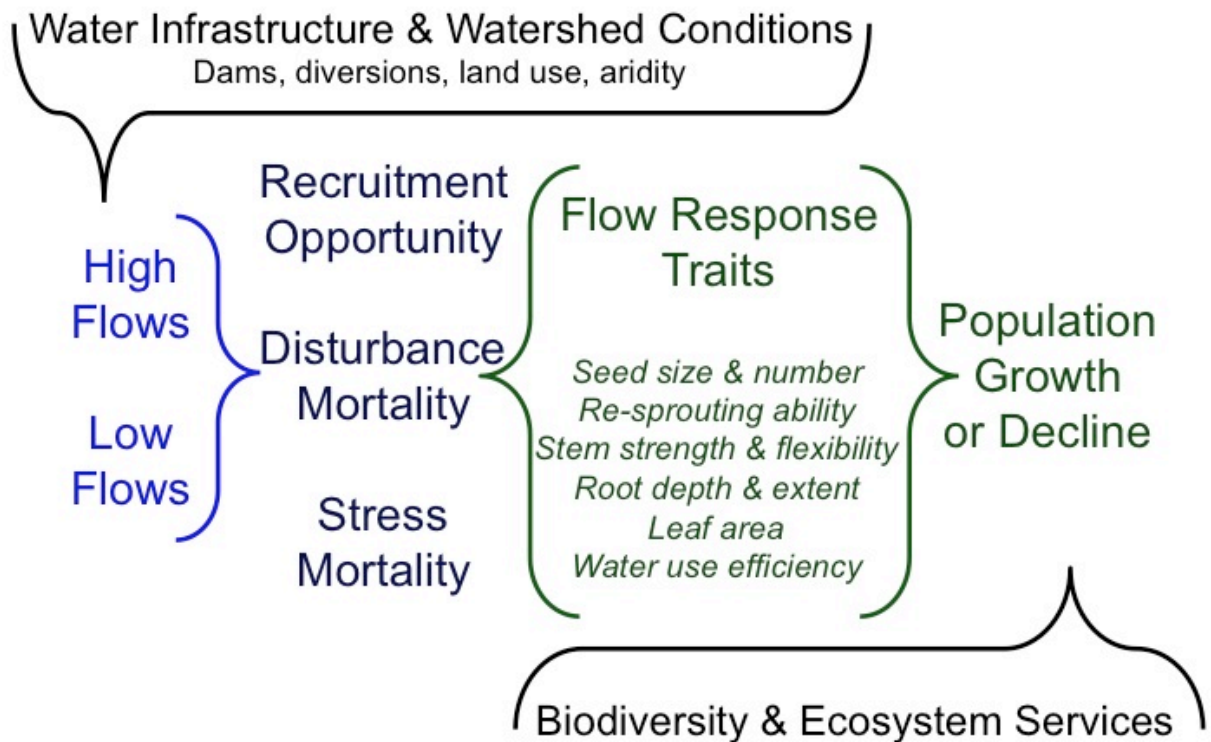


Figure 2.1: Environmental and management changes that alter flow regimes may detrimentally affect riparian vegetation and associated biodiversity and ecosystem services. The flow response trait concept offers a means to structure a general assessment of these effects, particularly where limited resources or information are available to support detailed or complex modeling.

## Model structure

I defined the modeled riparian zone as a finite area along a river reach regularly inundated by overbank flows. I focused on representing woody vegetation within this area, due to the importance of trees and shrubs in structuring habitat for riparian fauna and influencing ecosystem service production. Flow response traits may differ substantially among the life stages of woody riparian vegetation. For example, resistance to tractive stress may increase over the transitions from vulnerable green seedlings to progressively larger and more deeply rooted saplings and mature plants. I therefore distinguished the spatially implicit cover area of seedling, juvenile, adult and dead stages as state variables in a system of forced difference equations, with

trait differences expressed as parameter values that varied between stages and vegetation types (Figure 2.2a, b; equations below).

In order to examine patterns over a half-century or longer, and due to the multi-decadal life span of many riparian trees and shrubs, I updated these stages on a yearly time step. Each within-year model cycle consisted of flood disturbance mortality, maturation between stages, and establishment of new seedling cover (Figure 2.2a, b). This sequence is broadly relevant to rivers that experience a seasonal flood pulse but particularly reflects processes in arid and semi-arid western North American rivers with a snowmelt hydrograph. Though many flow regime attributes affect riparian plant communities (i.e., timing, duration, frequency and rates of change; Poff et al. 1997), annual peak flow magnitude can exert a strong influence on woody vegetation if high flows suffice to remove existing cover and create suitable establishment sites for trees with the appropriate traits (Scott et al. 1996, 1997). Accordingly, I drove the model system with series of values of an extrinsic environmental forcing variable  $Q_t$  that represented annual peak flow divided by an overbank threshold associated with bankfull discharge  $Q_{bf}$  (so that  $Q_t > 1$  designated overbank flow). Notwithstanding considerable variation in the physical meaning and recurrence intervals attributed to ‘bankfull discharge’ (Williams 1978), scaling to the  $Q_{bf}$  threshold translated peak discharge magnitude into a flow descriptor more directly relevant to riparian vegetation and allowed model implementation from very limited hydrologic information (i.e., an annual peak distribution), given the generally accepted approximation of  $Q_{bf}$  by  $Q_{1.5}$  (Dunne and Leopold 1978).



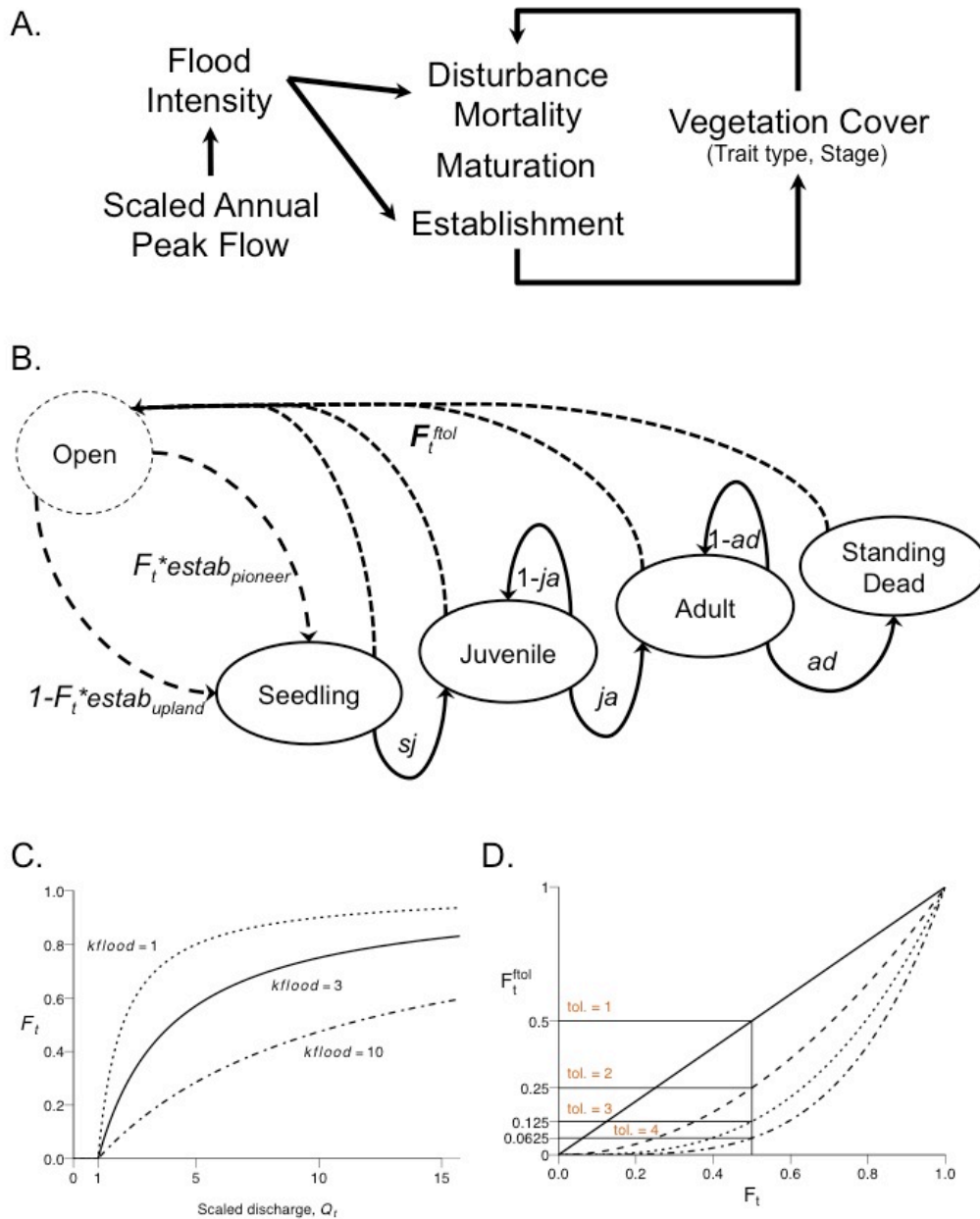


Figure 2.2: Conceptual overview of model structure. A. During each annual cycle, simulated vegetation within the riparian zone is subject to flood disturbance mortality, transitions between life stages, and potentially gains new seedling cover area. B. These events are governed by the interaction of a forcing variable  $F_t$ , representing flood intensity, with parameters controlling tolerance of flood disturbance (*ftol*) and establishment success (*estab*) as well as life history characteristics not directly influenced by flow (*sj*, non-flood seedling cover loss; *ja*, maturation to the adult stage; and *ad*, non-flood adult mortality). C. The *kflood* parameter controls how disturbance intensity increases and saturates with larger overbank scaled annual peaks. Larger values reduce flood effects for a given multiple of the bankfull discharge threshold. D. Flood tolerance parameters specific to each stage of each vegetation type reduce disturbance mortality. Assigned values reflect the assumption that increasing survival due to morphological adaptations is greatest in the transition out of the seedling stage, so that larger absolute reductions occur per increment at smaller parameter values.

Numerous interacting factors determine flood disturbance intensity relative to discharge magnitude (e.g., bed and bank substrate, suspended sediment load, longitudinal gradient, cross-sectional profile). However, I implicitly modeled the rate at which burial and scour intensity rose then saturated with increasing discharge as a single parameter function of the scaled peak forcing:

$$F_t = F(Q_t) = \begin{cases} 0, & Q_t \leq 1, \text{below bank} \\ \frac{Q_t - 1}{k_{flood} + Q_t - 1}, & Q_t > 1, \text{over bank} \end{cases}$$

$$k_{flood} > 0, \quad F_t \in [0,1]$$

Values of the *kflood* parameter conceptually relate to the floodplain classification suggested by Nanson and Croke (1992), with smaller values corresponding to high energy, non-cohesive classes (on which disturbance intensity might rise rapidly with larger magnitude flow; Figure 2.2c), and intermediate and larger values respectively associated with medium energy, non-cohesive classes and low energy, cohesive classes. I assumed that fluvial geomorphic conditions were in dynamic equilibrium, so that the total riparian zone area (i.e., the potentially occupied area) and the relationship between scaled discharge magnitude and flood disturbance remained constant through model runs (i.e.,  $Q_{bf}$  and *kflood* values were fixed except where noted). This simplifying assumption is likely to be violated on the many rivers in disequilibrium states of biogeomorphic progression (Corenblit et al. 2007), but it permitted the initial investigation of model behavior as I focused on the responses of different vegetation types in the absence of feedback or trends in channel-floodplain form.

Noting the importance of floods in determining the effects of river regulation on vegetation, Nilsson and Berggren (2000) observed, “Many upland species are normally excluded from growing in and near free-flowing river channels because of intolerance to sedimentation, erosion, submersion, physical damage, and low soil fertility ... Riparian pioneer species, on the other hand, are adapted to or need such processes; they have easily dispersed seeds, rapid germination, and rapid root and height growth.” (p.787). Following this distinction, I defined a modeled ‘pioneer’ type as referring to trees and shrubs adapted to take advantage of the plentiful light, moisture and nutrients available in the flooded portion of the unoccupied riparian zone. In contrast, I defined an ‘upland’ type as capable of establishing in the unoccupied portion of the riparian zone that was not flooded. I assigned trait parameter values to reflect additional relative differences between these types, generalized from the literature describing woody riparian vegetation (Figure 2.2b, d; Table 2.1). Relative to the upland type, juvenile and adult stages of the pioneer had greater tolerance of flood disturbance, and maturation to the adult stage was faster. When suitable establishment area was available to each type, the pioneer established on a larger portion than the upland type, but lost more seedling cover prior to the juvenile stage (e.g., due to high reproductive output of many weak seedlings versus lower reproductive output of fewer but hardier seedlings). These vegetation types were assumed not to evolve during model runs (i.e., trait parameter values were time invariant), and the numerous other abiotic and biotic factors affecting riparian populations were not explicitly represented (e.g., ice scour, fire, herbivory, etc.).

For a vector  $\mathbf{v}$  of vegetation indexed by stage ( $s, j, a, d$ ) and type ( $i = \text{pioneer, upland}$ ), the system of updating functions representing these interactions may be written:

$$\text{seedling}_{\text{pioneer}}: v_{t+1,si} = \text{estab}_i \left(1 - \sum_i v_{t,i}\right) F_{t+1}$$

$$\text{seedling}_{\text{upland}}: v_{t+1,si} = \text{estab}_i \left(1 - \sum_i v_{t,i}\right) (1 - F_{t+1})$$

$$\text{juvenile}: v_{t+1,ji} = (1 - ja_i) v_{t,ji} (1 - F_{t+1}^{jftol,i}) + sj_i v_{t,si} (1 - F_{t+1}^{sftol,i})$$

$$\text{adult}: v_{t+1,ai} = (1 - ad_i) v_{t,ai} (1 - F_{t+1}^{aftol,i}) + ja_i v_{t,ji} (1 - F_{t+1}^{jftol,i})$$

$$\text{dead}: v_{t+1,di} = v_{t,di} (1 - F_{t+1}^{dftol,i}) + ad_i v_{t,ai} (1 - F_{t+1}^{aftol,i})$$

These equations state that, during each model cycle, the prior cover of each stage and type survived according to the level of flood disturbance affecting the riparian zone, as modified by a tolerance parameter that reduced cover loss (e.g., for the adult stage:  $v_{t,i}(1 - F_{t+1}^{aftol,i})$ ;  $0 \leq v_{t,i} \leq 1$ ,  $0 \leq F_{t+1} \leq 1$ ,  $f_{tol} \geq 1$ ). This expression offered a simple means to capture the potentially non-linear differences between stages in susceptibility to mortality that may result from various morphological attributes (Figure 2.2d). Cover that survived flooding then matured or persisted in the current stage relative to parameters controlling seedling loss unrelated to flooding ( $0 \leq sj \leq 1$ ), the rate of transition to the adult stage ( $0 \leq ja \leq 1$ ), and adult mortality not due to flood disturbance (e.g., drought or disease;  $0 \leq ad \leq 1$ ). Flooding ( $F_t$  or  $1 - F_t$ ) allocated the unoccupied portion of the riparian zone from the prior time step ( $1 - \sum_i v_{t,i}$ ) into suitable establishment area for the pioneer and upland types, which formed new seedling cover according to a type-specific parameter controlling establishment success ( $0 \leq \text{estab} \leq 1$ ).

I used this model system to examine how altered flow regimes might effect vegetation through simulations that addressed hypothetical dam construction and management alternatives. Dams and diversions often limit annual peak magnitude and variability relative to the natural flow regime of a river (Magilligan and Nislow 2005, Graf 2006, Poff et al. 2007, FitzHugh and

Vogel 2011). Accordingly, I synthesized scenarios of natural forcing as random draws from a lognormal distribution representing theoretical annual peak magnitude for an intermediate size river ( $\mu = 5$ ,  $\sigma = 1$ ; median annual high flow  $\approx 150$  cms), and drew dam-altered forcing values from a distribution adjusted to generate peaks that were smaller and less variable ( $\mu = 4.71$ ,  $\sigma = 0.5$ ; median annual high flow  $\approx 111$  cms). Series of natural and dam-altered peaks were scaled to a fixed bankfull threshold given by the magnitude within the natural cumulative distribution at an exceedance probability of 0.66 (i.e.,  $Q_{bf} \approx Q_{1.5}$ ,  $T=1.5$  and  $1/T \approx 0.66$ ), and were truncated at the 10<sup>th</sup> and 99<sup>th</sup> percentiles of each distribution to avoid unrealistically extreme values (i.e., peaks  $< 10\%$  or  $> 5000\%$  of the overbank scaling threshold). No temporal autocorrelation was assumed, but sequences of several higher or lower flows did occur stochastically under both natural and dam scenarios. Furthermore, scaled discharge values were potentially lower than the  $Q_{bf}$  threshold under both scenarios, but were less frequently overbank under the dam altered forcing.

All simulation runs were initialized at 10% adult cover of both types, and *kflood* was held equal to 3 (except where noted) to represent overbank conditions leading to an intermediate intensity of flood disturbance. Simulations consisting of 50 years under the natural scenario followed by 50 years under the dam forcing were replicated 500 times. This set of runs was extended by alternative sequences of small floods at fixed intervals to examine the effects of intentional releases. An additional set of 500 runs combined sequences of stochastic natural to dam forcing with a return to 50 years of the natural scenario as a representation of dam removal. Model development and all simulations were performed in R 3.0.0 (R Core Team 2013).

Table 2.1: Flow response and life history parameters assigned to the two vegetation trait types. Tolerance parameter values indicate relative differences in the morphological adaptations conferring resistance to flood disturbance, while life history parameter values represent relative differences in fecundity, growth, and life span. In addition to different establishment requirements, the pioneer trait type was distinguished from the upland type by greater tolerance of flood disturbance, establishment on a higher percentage of suitable area but a greater loss of seedling cover prior to the juvenile stage, and faster maturation from the juvenile to adult stages. Numbers in parentheses below *ftol* parameter values indicate the effective mortality for  $F_t = 0.5$ .

Parameter	Pioneer	Upland	Parameter effect
<i>sftol</i>	1 (0.5)	1 (0.5)	Controls flood removal of seedling cover as exponent on $F_t$
<i>jftol</i>	2 (0.25)	1.5 (0.354)	Controls flood removal of juvenile cover as exponent on $F_t$
<i>aftol</i>	3 (0.125)	2.5 (0.177)	Controls flood removal of adult cover as exponent on $F_t$
<i>dftol</i>	3 (0.125)	2.5 (0.177)	Controls flood removal of standing dead cover as exponent on $F_t$
<i>estab</i>	0.6	0.1	Percentage of suitable establishment area assigned to the seedling stage
<i>sj</i>	0.25	0.75	Percentage of seedling cover that matures to the juvenile stage following any flood disturbance mortality; 1- <i>sj</i> is lost
<i>ja</i>	0.3	0.1	Percentage of juvenile cover that matures to the adult stage following any flood disturbance mortality; 1- <i>ja</i> remains juvenile
<i>ad</i>	0.01	0.01	Percentage of adult cover that converts to standing dead; 1- <i>ad</i> remains adult

### Question 1: How does flow regulation that alters the intensity and frequency of flood disturbance affect the adult abundance and stage structure of vegetation trait types?

Merritt et al. (2010) proposed the general hypothesis that: “The proportion of the riparian community with adaptations to disturbance should be higher in systems with high frequency and magnitude of disturbance. Shifts in this guild will occur in accordance with magnitude and direction of the change at a rate determined to some degree by the life-history traits of those species included in the guild.” (p. 219). The shift from the hypothetical natural to dam flow scenarios produced model behavior in agreement with this expectation and previous observations. Under the natural scenario, frequent and occasionally large floods created regular

establishment pulses for the pioneer trait type (Figures 2.3 and 2.4, light green traces in seedling panels). The dam scenario reduced the size and frequency of seedling establishment opportunities, but simultaneously decreased the flood disturbance mortality experienced by both immature and adult stages. As a consequence, the average adult pioneer cover increased and stabilized through time (Figures 2.3 and 2.4, light green traces in adult panels). However, the regulated flow regime favored the upland type to a greater extent. As a result of less disturbance mortality, average adult upland cover rose from a level comparable to or lower than the pioneer under natural conditions to nearly double that of the pioneer under the dam scenario (Figures 2.3 and 2.4, dark green traces in adult panels). In addition, the total live upland cover was often more than double that of the pioneer due to greater juvenile upland cover. Yet, perhaps counter-intuitively, upland seedling cover was lower under reduced flooding (Figure 2.3, dark green trace in seedling panel). In contrast to the density-independent mortality limitation imposed by flooding under the natural scenario, greater adult cover rendered the upland trait type establishment-limited under the dam scenario, as suitable area for new seedling cover declined.

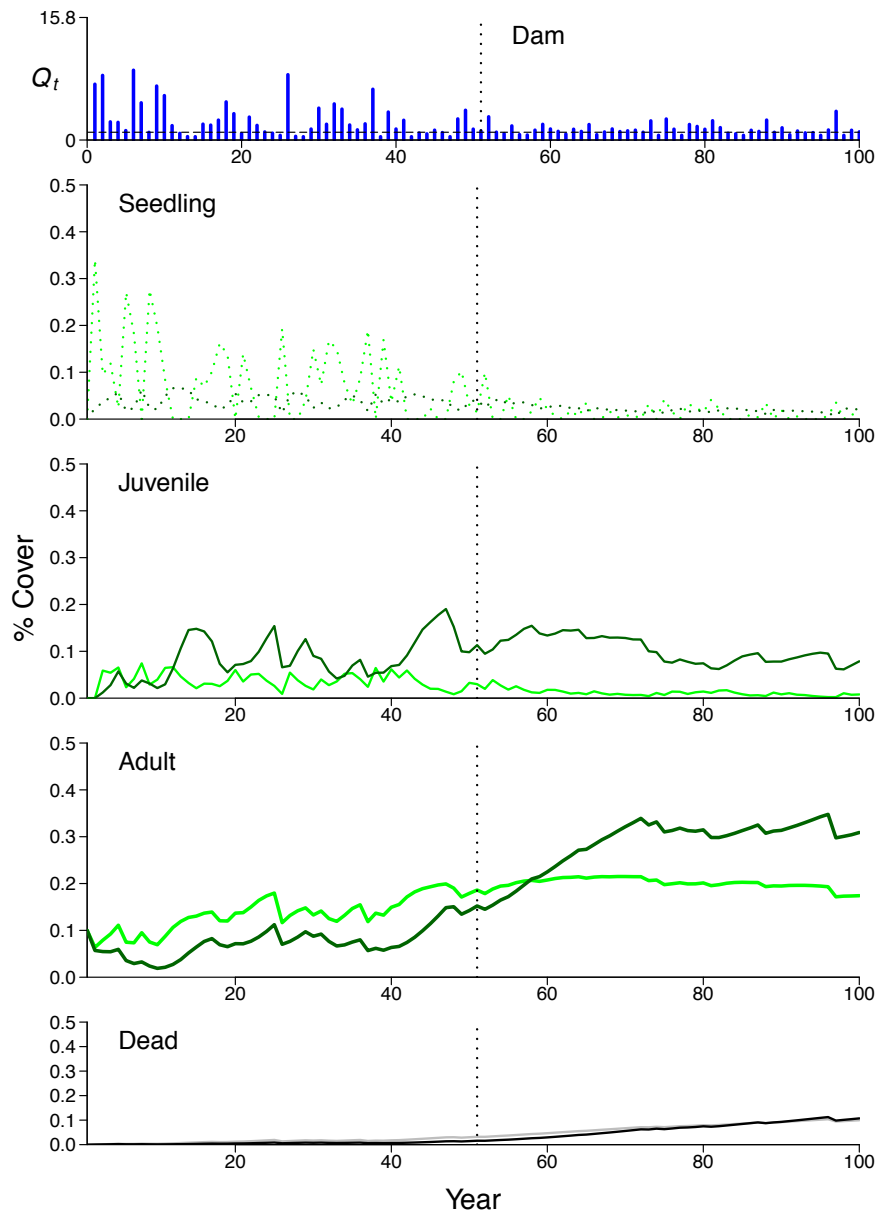


Figure 2.3: Scaled discharge and vegetation cover by stage for an example simulation under the natural and dam-altered forcing scenarios. The uppermost panel shows the scaled annual peak discharge values during each model year, with overbank flows that produced disturbance mortality and permitted pioneer establishment indicated by the dashed horizontal line at  $Q_t = 1$ . Remaining panels illustrate the cover area through time of each stage of the pioneer (light green and grey) and upland (dark green and black) vegetation types. Imposition of the dam forcing at year 51 reduced flood magnitude and the frequency of overbank annual peaks. This change was most evident for the vegetation in the reduced pioneer seedling cover (due to fewer, smaller establishment opportunities) and the increased upland adult cover (due to less flood disturbance mortality of persisting adults and maturing juveniles). However, pioneer adult cover also stabilized with the reduction in disturbance, and upland seedling cover gradually decreased as suitable establishment area declined. In addition, the standing dead cover of both types increased through the combination of greater live adult area and decreased removal by large floods.



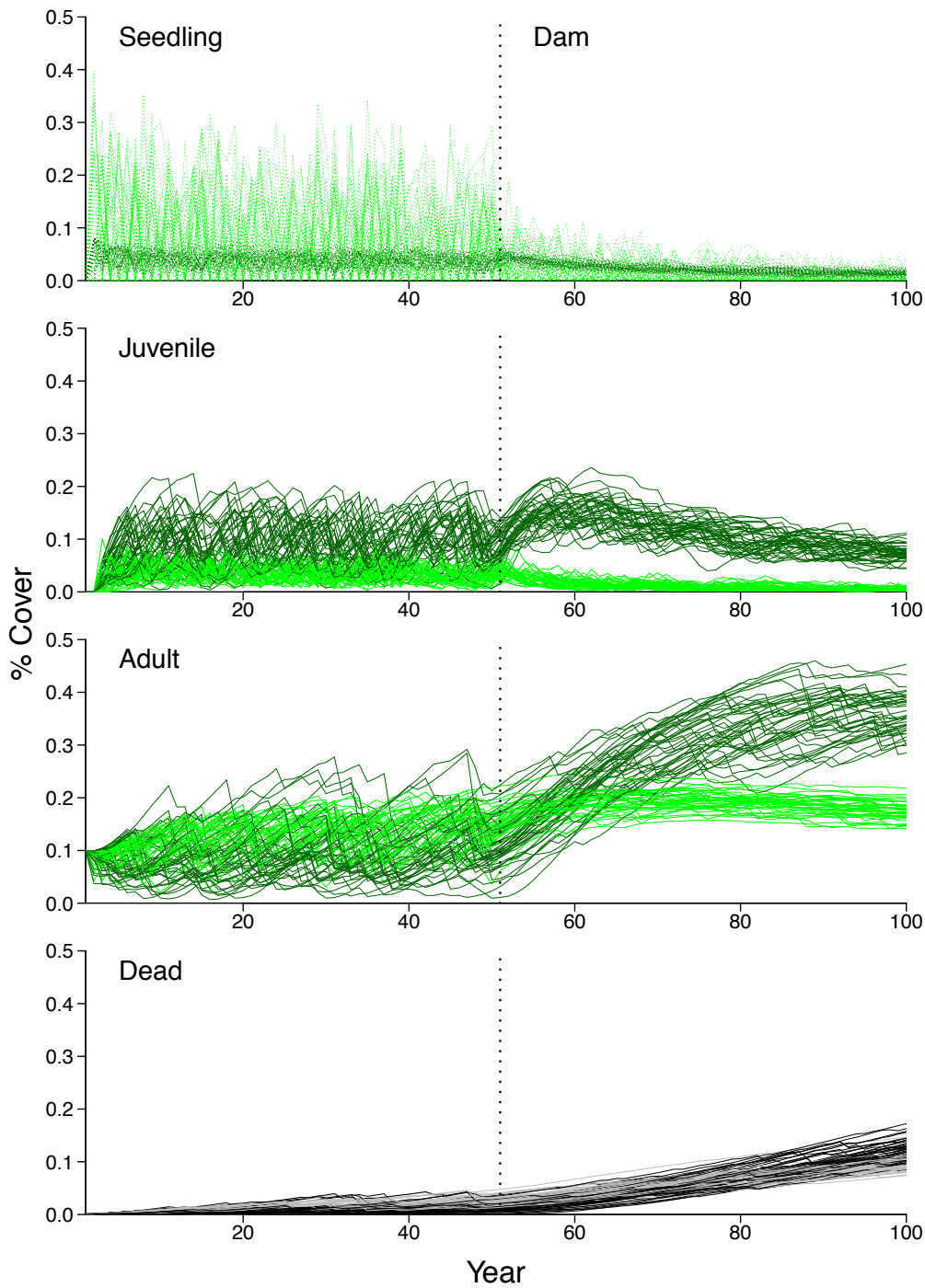


Figure 2.4: Overlaid results of distinct simulation runs. Panel conventions follow Figure 2.3, showing the stages of the pioneer type (light green) and upland type (dark green). Only 40 runs are shown for visual clarity, but patterns are consistent over greater numbers of replicates. Despite differences among runs caused by the stochastic forcing sequences (e.g., occasionally high adult upland cover under the natural scenario), the pattern of reduced seedling establishment and greater, more stable adult cover under the dam scenario was consistently evident.

Demonstrating the interacting role of life history traits, the faster juvenile-to-adult maturation of the pioneer conveyed less advantage under the dam conditions. Less frequent and lower disturbance intensity reduced the importance of developing to a stage with greater flood tolerance. Furthermore, the greater percentage of upland seedlings reaching the juvenile stage after flood losses was more beneficial as such losses decreased in frequency. These effects were evident in the relatively stable juvenile upland cover under the dam scenario (Figure 2.3, dark green trace in juvenile panel). The low and identical rates of non-flood adult mortality did not influence the relative adult abundance of the two trait types, but the increased adult cover and the lack of sufficiently large floods did allow standing dead cover to accumulate steadily under the dam conditions.

Under the natural scenario, the particular year-to-year sequence of high flow magnitudes influenced modeled population growth in a manner similar to previous empirical and theoretical observations for woody riparian pioneers (Lytle and Merritt 2004, Birken and Cooper 2006). Adult cover increased through time during periods of several smaller annual peaks that followed a seedling pulse from a larger flood year (Figure 2.3, pre-dam). Comparing tree ages determined through growth ring counts with long term discharge gage records for the Green River (UT, USA), Birken and Cooper (2006) found that episodic recruitment of woody riparian pioneers in the *Tamarix* and *Populus* genera was significantly favored by the pattern of lower magnitude peaks subsequent to larger ones. In a stage structured population model for *P. deltoides* based on field measures from the Yampa River (CO, USA; a major tributary to the Green), Lytle and Merritt (2004) also reported that several years of low flood disturbance and drought stress after a favorable high flow year led to the greatest increase in mature cover. Thus, the present simulation approach indicates that low information demands for discharge forcing and response

trait parameters may suffice to capture this consistent flow-vegetation relationship in qualitative terms. If the planned intent of a dam is to stabilize downstream high flows between years, but protecting pioneer riparian trees is desirable (e.g., as wildlife habitat or recreational amenities), then a simple model may adequately reveal the likely conflict between these objectives and reinforce the need for a closer examination of probable trade-offs.

The divergent trends in average seedling (decreased) and adult (increased) cover of the riparian pioneer under the simulated dam scenario were also in agreement with previous studies. For example, in a survey of 64 reaches along 13 rivers in the southwestern United States, Merritt and Poff (2010) observed that the woody riparian pioneer tamarisk (*Tamarix* spp.) had high establishment in the absence of flow regulation and lower abundance on free-flowing rivers with more large floods (elevated magnitude of 10-year recurrence interval peak flow). Similarly, Stromberg et al. (2010) reported younger (smaller median stem size) riparian pioneer cover at sites on the San Pedro River (AZ, USA) subject to higher intensity flooding (elevated total stream power of the 10-year flood).

My model did not capture the transient pulse in pioneer establishment described by Johnson (1998) along the previously braided Platte River (NE, USA) and by Friedman et al. (1998) for a number of braided rivers in the Great Plains that experienced decreased flood disturbance mortality following flow regulation. However, the simulated behavior did partially correspond to the potential for a new quasi-equilibrium consisting of greater adult cover but limited ongoing seedling regeneration in these systems (Johnson 2000). Again, this modeled pattern suggests that, in the context of initial planning or evaluation of water management options, even a basic flow response trait modeling approach can inform the discussion about what may be lost and gained. Simply illustrating the dual role of flood disturbance as an agent of

both mortality and regeneration for woody riparian plants (or other riverine taxa) may serve to remind stakeholders that a dam may suppress renewal of some trees and skew stand structure towards adults. Indeed, if pioneer trait types are viewed as undesirable ‘weedy’ elements of the river corridor, then model results could bolster the position of dam proponents seeking to argue that fewer establishment opportunities will be an additional benefit that complements more consistent water supply or reduced flood damage.

The decreased relative abundance of the pioneer type under the dam scenario was congruent with the general expectation articulated by Merritt et al. (2010) and others, particularly along formerly meandering rivers (Johnson 1998, Nilsson and Berggren 2000). Yet, despite reduced recruitment and greater standing dead cover, adult pioneer cover remained quasi-stable and upland dominance plateaued in the modeled representation of this change. Though transient lag effects may mask the possibility of pioneer declines relative to hydrologic alteration (Andersen et al. 2007), an eventual decrease is probable if mortality (including non-flood losses) outpaces regeneration (Johnson 1998). Regardless of whether greater upland cover is viewed positively or negatively, the underlying assumptions that produced this behavior highlight important considerations for assessing the potential effects of flow regulation. The qualitative nature of these patterns was not due to the short window of simulation chosen for relevance to management timeframes, nor the assigned level of non-flood mortality (*ad* parameter values). Long-term simulation of the illustrated parameter values under the dam flow forcing did result in dead cover of both types that was greater than that of the live adult pioneer, but live adult upland area was comparable and the pioneer was maintained in the system (Figure 2.5a). Altering the rates of conversion from live adult to standing dead cover in order to represent a shorter lifespan

due to increased stress or disease for example, shifted the quasi-stable distribution these stages but did not fully eliminate the trait types (not shown).

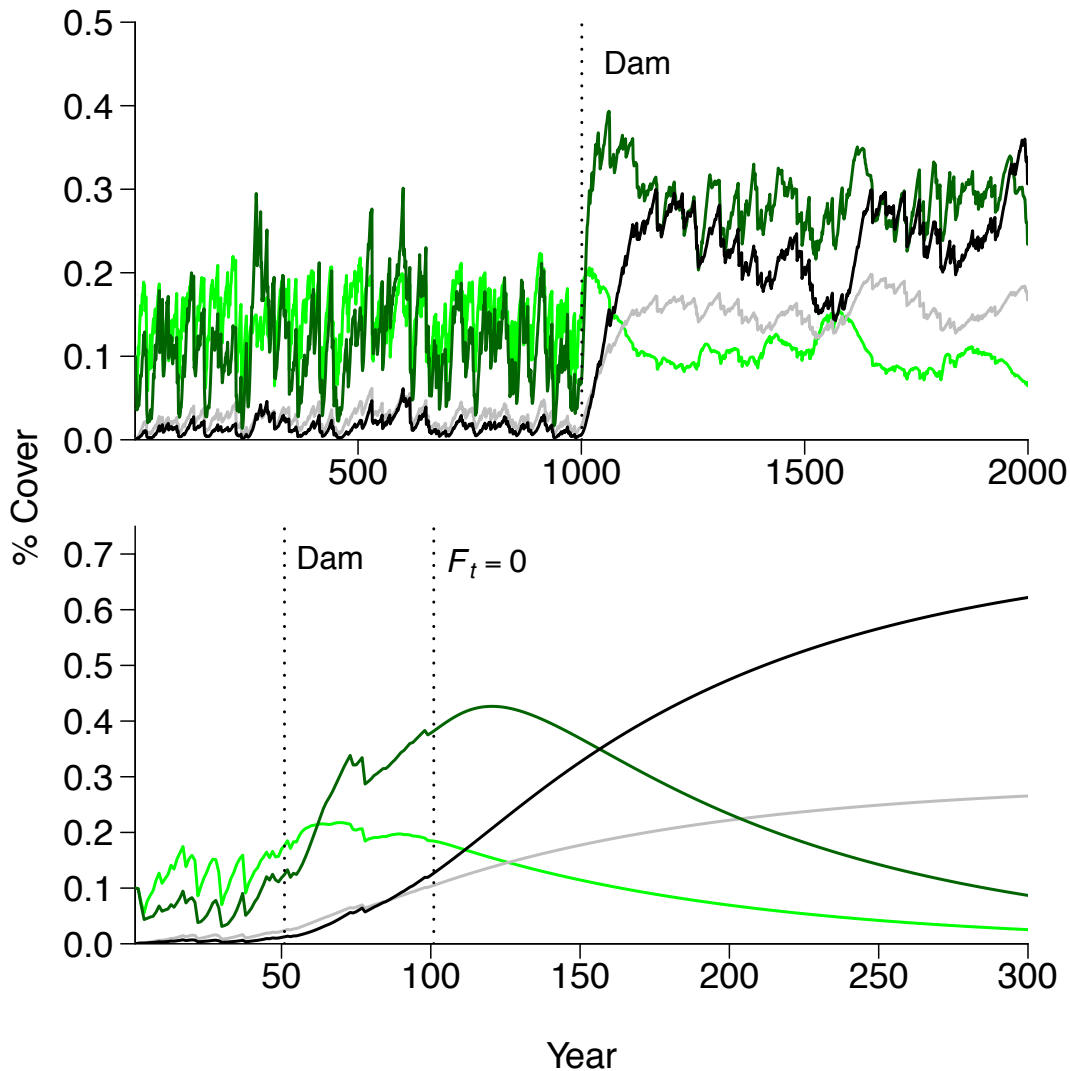


Figure 2.5: A. An example of a longer simulation run, illustrating 1000 years under the natural and dam conditions respectively. Only adult and dead stages of the pioneer (light green and grey) and upland (dark green and black) vegetation types are shown for clarity. Though dead cover of both types exceeds that of the adult pioneer stage, this stage remained present due to the assumption of an open system without dispersal limitation and a moderate level of ongoing disturbance under the dam forcing scenario. This quasi-equilibrium stage distribution remained consistent for longer runs (e.g., 50,000 years, not shown). B. Complete elimination of flood disturbance following the dam scenario resulted in convergence to a riparian zone consisting entirely of the standing dead stages. Non-flood mortality controlled by the *ad* parameter continually generated additional dead cover that was not removed by flooding. Color conventions are identical to the above panel, but note the y-axis change of scale.

Rather, the persistence of live cover of both types could be attributed to the assumptions of an open system without restricted seed availability and the continuation of some minimal level of disturbance even as flood intensity was reduced. The latter ensured that some establishment space was freed, and the former that it was occupied. Ubiquitous dispersal of riparian pioneer types is not implausible, as anyone who has watched cottonwood seeds float past will attest, nor is the idea that some dams still permit low magnitude flooding. However, neither claim is likely to be universally valid, particularly at smaller spatial and shorter temporal scales. Adjusting the annual peak forcing to completely prevent disturbance resulted in convergence to a riparian zone effectively covered in only the standing dead stages, as all cover eventually died but was never removed by floods (Figure 2.5b; recall that the *ad* parameter represented ongoing non-flood mortality and no other forms of disturbance were modeled). Though this outcome was clearly unrealistic, it suggested the value of the model for generating a counterfactual of use in considering what other factors may determine riparian cover if a dam strongly suppresses disturbance. For instance, this behavior implied that previously rare or absent vegetation types with greater fire and shade tolerance could become increasingly important along dammed reaches.

More relevant to questions of riparian invasion or species loss, introducing terms into the establishment functions to represent dispersal limitation fundamentally altered the model behavior. For example, the seedling updating functions could be adjusted with a simple additional term to weight the establishment of new cover by the relative abundance of adult cover in the prior year:

$$\begin{aligned} \text{seedling}_{\text{pioneer}}: v_{t+1,si} &= \text{estab}_i \frac{v_{t,ai}}{\sum_i v_{t,i}} \left(1 - \sum_i v_{t,i}\right) F_{t+1} \\ \text{seedling}_{\text{upland}}: v_{t+1,si} &= \text{estab}_i \frac{v_{t,ai}}{\sum_i v_{t,i}} \left(1 - \sum_i v_{t,i}\right) (1 - F_{t+1}) \end{aligned}$$

This change potentially yielded effective extirpation of the upland type under the natural scenario or the pioneer type under the dam scenario (Figure 2.6). The dispersal limited model configuration was not necessarily more accurate – the mismatch between model assumptions and empirical flow-vegetation relationships will differ with the river and plants under consideration – but it highlighted the importance of an ongoing source of seedling cover for desirable but less common species. Furthermore, it suggested the value of active planting or actions to maintain connectivity with areas of greater adult cover (i.e., as a seed source) for riparian zones that act as population sinks. Conversely, it also indicated that efforts to eradicate undesirable species may have little long-term success if such species are widely dispersing and capable of ongoing re-establishment.

My objective of minimizing the complexity of represented processes in order to reduce information demands led to a model lacking explicit treatment of numerous other factors that affect the interaction of pioneer and upland trait types and the composition of riparian zones (water stress, consumption by herbivores, fire, canopy shading, etc.). Yet, these alternative structural possibilities serve to underscore the dependence of any assessment on the specific model attributes included, and suggest that a strength of an exploratory simulation approach based on flow response traits may be the capacity to straightforwardly reconfigure the model and thereby investigate the implications of different assumptions in the face of process uncertainty. Given the pronounced shifts in vegetation under the regulated forcing scenario, I turn now to what the model framework suggested might result from efforts to restore a degree of the natural flow variability.

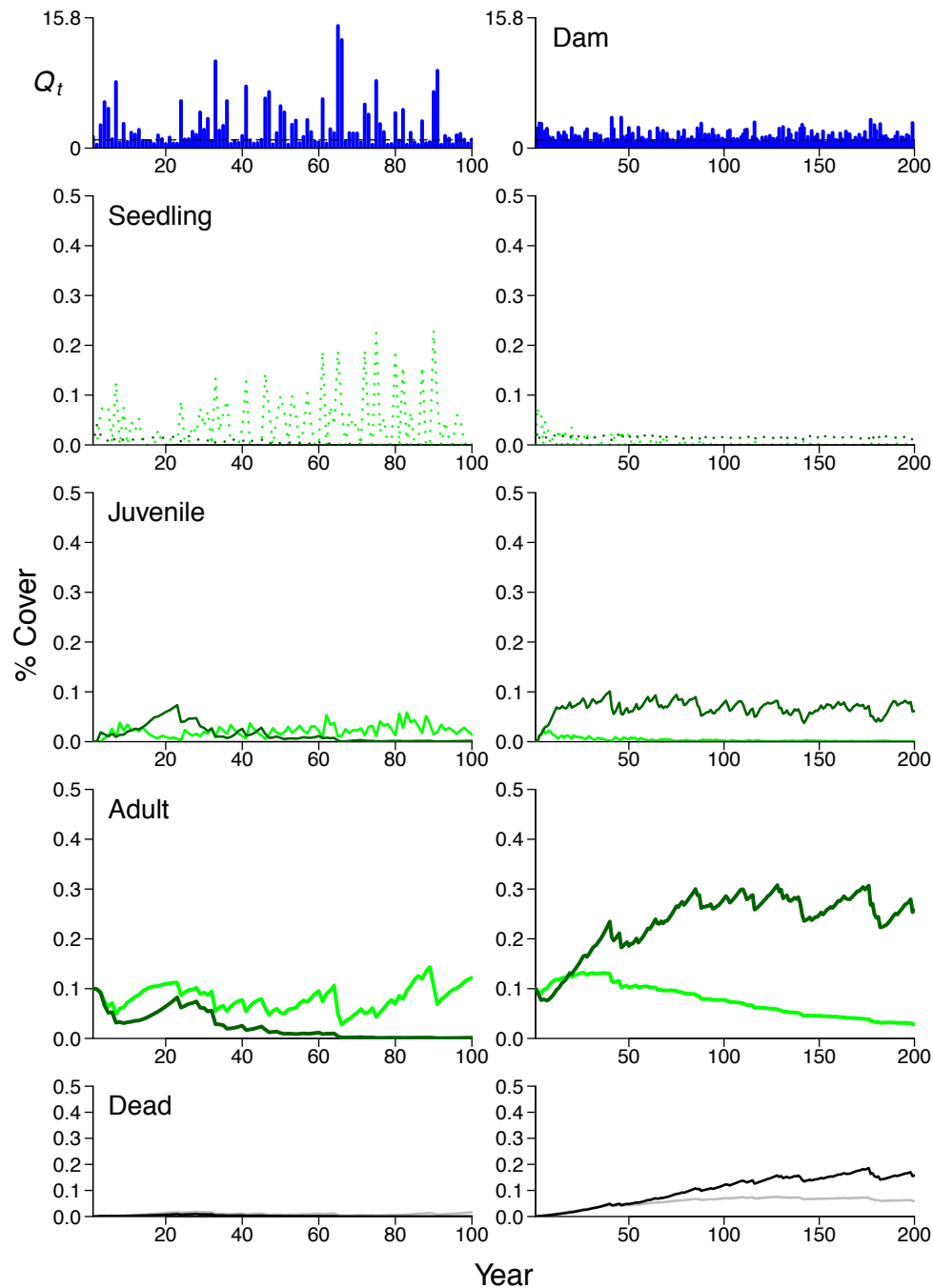


Figure 2.6: Adjusting the model to represent dispersal limitation resulted in qualitatively different simulated outcomes. Panels illustrate the scaled annual peaks and cover by stage for example runs under the natural (left column) and dam (right column) forcing scenarios. The seedling updating functions were adjusted to include a term that weighted establishment by the relative abundance of the adult pioneer (light green) and upland (dark green) vegetation types in the prior year. The upland type was effectively extirpated under the greater flood disturbance of the natural scenario, and reduced establishment under the dam conditions gradually excluded the pioneer (the adult pioneer decline was slower due to lower overall removal of cover).



**Question 2: To what extent may scheduled flood releases and dam removal mitigate the effects of flow regulation on vegetation?**

Amidst growing recognition of the socially and ecologically detrimental effects of river regulation, recent decades have seen considerable advances in research into the design of flow regimes that balance human and ecological needs, termed ‘environmental flows’ (Tharme 2003, Acreman and Dunbar 2004, Arthington et al. 2006, Richter and Thomas 2007, Poff et al. 2010). Incorporating flow regime targets into riparian restoration plans can greatly increase the likelihood of success (Stromberg 2001), and large-scale environmental flow programs such as the Sustainable Rivers Project, initiated as a partnership between the U.S. Army Core of Engineers and The Nature Conservancy, have demonstrated the feasibility of addressing conservation goals through flow management (Konrad et al. 2011). Ideally, after gathering information on the current uses and historical discharge patterns for a river or set of similar rivers, a group of stakeholders from diverse backgrounds (i.e., academia, agriculture, governance, industry, law, etc.) can carefully negotiate compromise flow levels over the full year (Poff et al. 2010). However, in more time and resource limited settings, simpler rules such as an acceptable percentage deviation from the natural hydrograph may also substitute (Richter et al. 2011). In addition, because high flows play such an important role in structuring the physical habitat template and biological composition of river corridors, intentional flood releases may constitute a worthwhile management option even for dams where a fuller environmental flow regime is not possible.

Indeed, managed floods have been used to attempt to manipulate vegetation on a number of rivers to varying degrees of success (Rood et al. 2003, 2005, Shafroth et al. 2010b, Mortenson et al. 2012). During the 20<sup>th</sup> century, declines in stands of cottonwood along many Western

ivers have elicited concern and spurred efforts to protect and restore native gallery forests (Rood et al. 2005, Johnson et al. 2012). At the same time, the spread of tamarisk has prompted debate and research into the consequences for evapotranspired water loss, soil chemistry, bird habitat, recreational appeal, and channel dimensions due to the capacity of these trees to form dense, monotypic stands (Shafroth et al. 2010a, Sher and Quigley 2013). In the western U.S., although other targets may take precedence in the design of flows (e.g., endangered native fish), intentional flood releases have commonly had two goals related to trees and shrubs: remove or prevent the establishment of non-native species and promote the establishment of natives, particularly *Populus* and *Salix* (Shafroth et al. 2005, 2008). However, in settings where pioneer trait types co-occur or where adult tamarisk occupy positions that are unlikely to experience appreciable scour and disturbance from managed floods, giving precedence to the second objective may involve accepting less success on the former (Shafroth et al. 2008, Merritt and Poff 2010, Mortenson et al. 2012). Though flow requirements for different riverine and riparian taxa may sometimes align (Rood et al. 2003), the likelihood of trade-offs associated with attempts to control and promote species will warrant research in most settings.

As a prominent example of research into the effects of adaptive flow management, the Bill Williams River (AZ, USA) has served as the venue for catchment-scale ecological experiments testing the relationships between artificial floods and organisms including macroinvertebrates, beaver, and riparian trees and shrubs (Shafroth et al. 1998, Shafroth et al. 2010b). Larger reservoir releases following abundant rainfall have had sufficient power to scour trees and rework channel form in some reaches, and smaller flood pulses in subsequent years have also reduced *Tamarix* seedling density relative to *Salix*. Long term monitoring of hydrologic, geomorphic and biological conditions has enabled detailed biophysical modeling of

this system, although predicted shear stresses and observed vegetation patterns have not necessarily aligned, even for data-intensive reach scale hydraulics modeling. The results of particular flood releases are certain to depend on the unique biogeography and antecedent hydrogeomorphic characteristics of the river under consideration, as well as uncontrollable variables such as subsequent precipitation events (Mortenson et al. 2012). Nonetheless, despite some disagreements between modeled and observed patterns, the effort to represent potential flood outcomes has significantly contributed to understanding of the system and, perhaps most importantly, model outcomes have informed on-the-ground management decisions. These achievements indicate how process-based models of riverine dynamics can effectively inform the design and implementation of environmental flows (Richter and Richter 2000, Anderson et al. 2006).

Indeed, a variety of factors may present challenges to empirical experimentation and limit the scope of managed floods. For example, engineering design may constrain the maximum release, the financial consideration of opportunity costs from lost power generation may restrict flood frequency, and the legal risk of property damage or difficulty of securing adequate water rights under a prior appropriation doctrine may limit flood size. Exploratory simulation can therefore afford useful initial insight into the potential effects of managed floods when such floods must confront social opposition and before resources are committed to more complex and mechanistic evaluation (e.g., models of reservoir operations linked to surface and groundwater routing, sediment transport and habitat suitability). Consider a regulated river where diversion and storage of flows have resulted in annual peak magnitudes that are consistently below the overbank threshold barring intentional flood releases ( $Q_t < 1$ ). If a primary goal of scheduled releases is to increase the abundance of a desirable native riparian pioneer while reducing the

cover of an undesirable upland type in the riparian zone, then an important preliminary question concerns the frequency of feasible high flows that will balance sufficient establishment opportunities against disturbance mortality that removes upland stages but possibly harms newly recruiting pioneer cover. I extended the regulated flow simulation runs of the previous section in order to gain perspective on this question. Following 50 years of the stochastic dam forcing scenario, I imposed sequences of scaled annual peaks that represented small but overbank flows ( $Q_t = 2.5$ ) at 2-, 5- and 10-year fixed intervals and slightly larger floods ( $Q_t = 5$ ) at a 10-year interval.

Scheduled floods shifted the relative abundance of pioneer and upland stages, but did not recover the vegetation distribution characteristic of the simulated pre-dam period. As expected, the highest frequency of flooding generated the most pioneer seedling cover (Figure 2.7 and 2.8). Under this 2-year flood interval, pioneer establishment was adequate to counter disturbance mortality, the non-disturbance related loss of seedling cover ( $sj$ ) and the conversion of live adult to standing dead ( $ad$ ). Consequently, adult pioneer cover remained stable (Figure 2.7). In contrast, the short interval between overbank scaled peaks combined with the lower flood disturbance tolerances of the juvenile and adult upland stages to drive upland adult cover moderately lower (Figure 2.7, dark green trace). Although the lower flood frequency in the 5- and 10-year schedules produced less disturbance mortality, diminished pioneer regeneration resulted in a lower quasi-equilibrium for adult pioneer cover than under the stochastic dam scenario (Figure 8, light green traces). However, these forcing sequences stabilized or slightly increased the adult upland cover due to ongoing recruitment for this type during the non-flood intervals (Figure 2.8, dark green traces). Larger floods at the 10-year interval temporarily removed more adult upland cover, but were too infrequent to maintain these reductions or to

increase pioneer cover. In addition, with few clearing floods, standing dead cover of both trait types increased and was more abundant than the live pioneer adult (not shown).

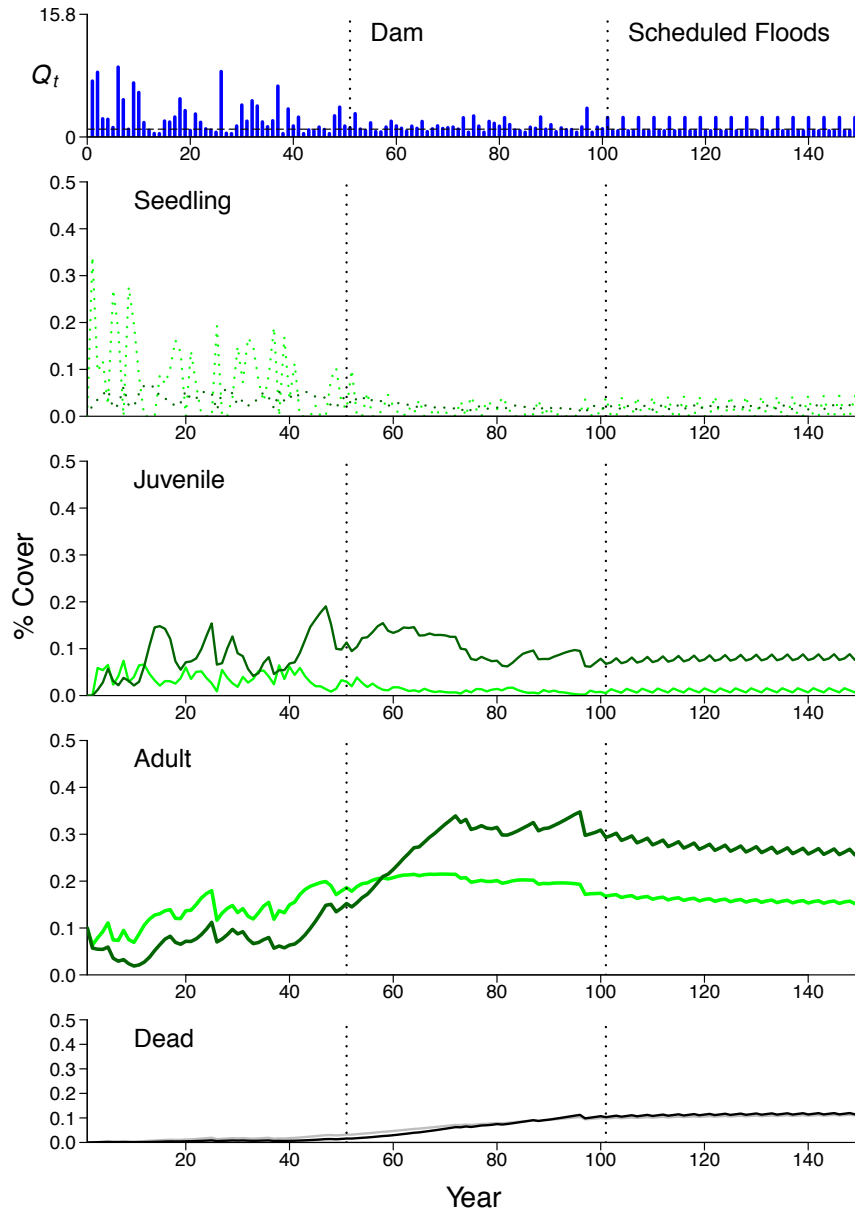


Figure 2.7: A regular sequence of small overbank annual peaks did not restore the pre-dam distribution of vegetation types but did provide more frequent establishment opportunities for the pioneer (light green). The regeneration of seedling cover sufficed to compensate for disturbance and non-flood mortality, maintaining a quasi-stable adult pioneer cover area. In addition, the low intensity but persistent clearing floods limited the abundance of the adult upland stage (dark green) and stabilized standing dead cover.

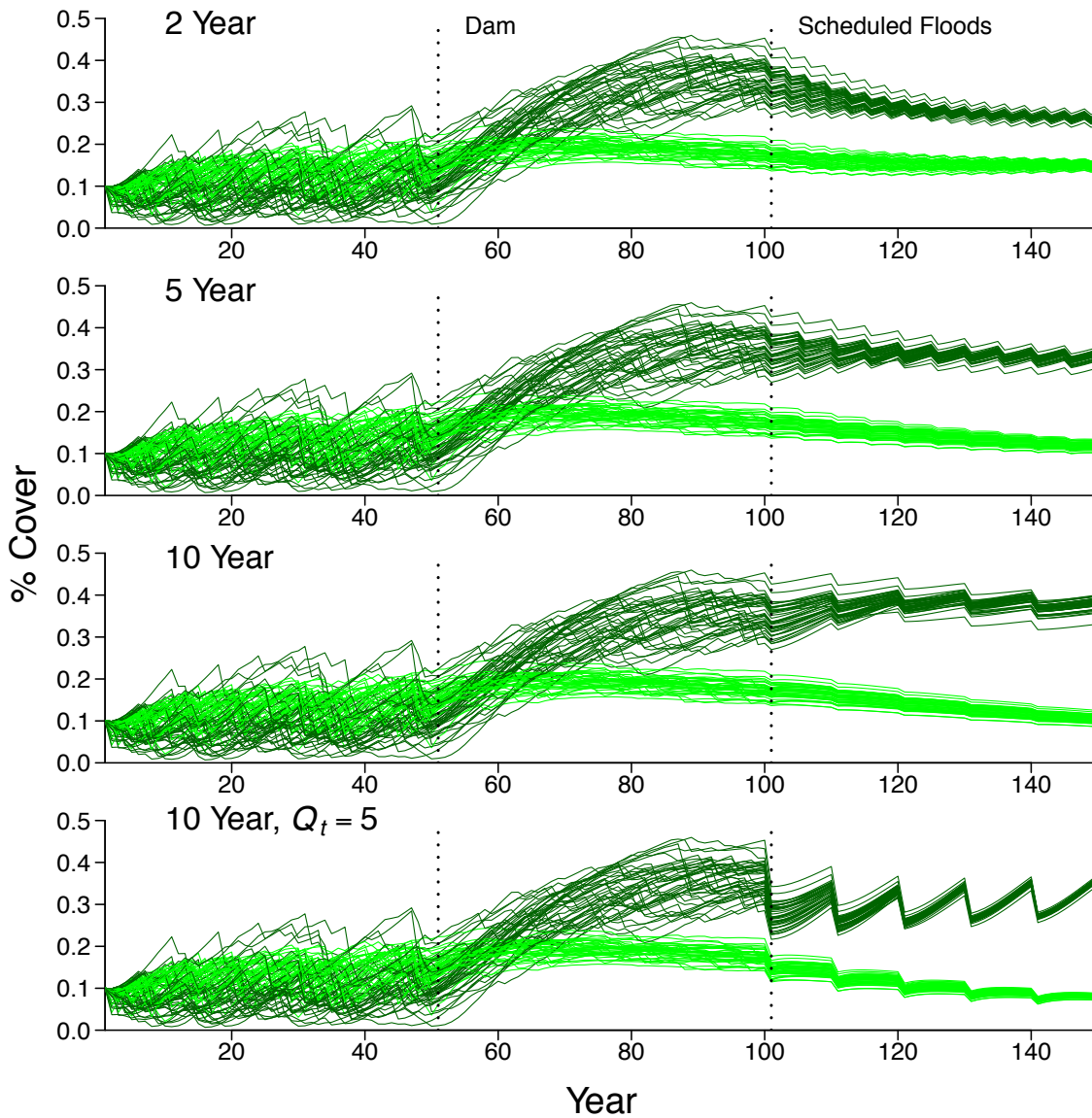


Figure 2.8: Overlaid simulation runs at alternative flood schedules for identical replicates of the stochastic dam forcing scenario. Only the adult stages of the pioneer type (light green) and upland type (dark green) are shown for clarity. Longer intervals between floods resulted in lower adult pioneer cover and less reduction in the upland type. Larger intentional releases at the 10-year interval did not change this pattern, as ongoing establishment of upland seedling cover enabled the adult stage to recover from additional disturbance mortality but pioneer establishment was inadequate to compensate for mortality.

For a dam constrained to only modest magnitude releases, these simulated patterns suggested that greater regularity of managed floods could partially meet the objective of limiting upland cover. However, model behavior indicated that infrequent intentional high flows could have the unintended consequence of introducing enough disturbance mortality to slightly reduce desirable pioneer populations but failing to generate enough recruitment opportunity to compensate for these losses. Nonetheless, interpretation of these results certainly depends on the alternative flow regimes being compared, and the 10-year schedule could be viewed as an improvement on an even longer interval between floods that would result in lower pioneer or more dead cover. Furthermore, the risk of unintended outcomes of managed floods on any real river will depend on factors not included in the model. For instance, the timing, duration and rate of change of managed floods will also interact with their frequency and magnitude to influence riparian and other ecological outcomes (Rood et al. 2005, Shafroth et al. 2010b, Mortenson et al. 2012). Successful pioneer recruitment will depend on whether suitable establishment sites are made available as seed release occurs and whether the post-peak stage decline meets the requirements of newly germinated plants as described in ‘Recruitment box’ models (Shafroth et al. 1998, Braatne et al. 2007).

More generally, the model behavior suggested the need for cautiously controlled expectations regarding the potential ecological benefits of managed floods. Occasional artificial high flows are likely preferable to a complete lack of floods that flush accumulating salts from riparian soils or reconfigure channel and floodplain form. However, simulated dam releases could not fully mitigate the effects of flow regulation, and may be better viewed as a critical ‘life support’ instrument rather than a panacea. The limitations of scheduled flooding raise the

question of whether complete dam removal could restore a greater degree of the pre-dam function to river corridor ecosystems.

Obsolete dams become candidates for removal, and a great deal of aging water infrastructure is becoming increasingly obsolete (Doyle et al. 2008). Safety concerns and maintenance costs that exceed the removal project costs are often motivating factors, but detrimental ecological impacts such as aquatic habitat fragmentation are now seen as sufficient justification to begin assessing the viability of deconstruction (Pohl 2002, Whitelaw and MacMullan 2002, Doyle et al. 2003, Stanley and Doyle 2003). Dam and barrier removal (e.g., culverts, levees) can play an important role in a whole-watershed, process-based approach to freshwater conservation (Bednarek 2001, Beechie et al. 2010). In addition to the many smaller removal projects in the Northeast and Midwestern United States, recent years have seen the elimination of larger infrastructure, such as the Elwha and Glines Canyon dams on the Elwha River (WA, USA; AR 2013). Reducing the risk of catastrophic failure provides an immediate benefit, but assessing the conservation uplift from removal is more complicated. The fundamental complexity of ecological responses and the likelihood of persisting fluvial geomorphic changes such as narrowed, incised channels hinder projections of rapid, unequivocal improvements in habitat quality, species richness or other metrics of ecological integrity.

In an important discussion of issues relating to riparian vegetation, Shafroth et al. (2002a) postulated that, “Dam removal should not always be expected to restore riparian ecosystems to their pre-dam condition...Legacies of flow regulation such as altered channel morphology, species composition, and age structure may result in a delayed response of the system to naturalized flows” (p. 708). Furthermore, these authors noted the risk of a fallacy comparable to the “if you build it, they will come” approach of structural stream restoration efforts that fail to



account for watershed-scale hydrologic alteration and dispersal limitation. Referring to the potential for dam removal to reduce cover of a species like Russian olive (*Elaeagnus angustifolia*; non-native and viewed as undesirable in western U.S. riparian zones), they suggested that “if you remove it, they will go” may not be a valid expectation: “even if dam removal reduces available habitat for seedlings of exotic species, established adults may persist for decades until a flood, drought, age-related factors, or some other agent kills them” (p.706).

Yet, riparian systems have been proposed to be quite resilient because of the naturally high variation under which their flora and fauna evolved (Naiman and Decamps 1997, Capon et al. 2013, Stromberg et al. 2013). This perspective recognizes that some forms of human watershed alteration have historical or spatial analogs to which populations may have already adapted, at least at the whole-network or sub-continental scale. The implication for dam removal is that some aspects of the pre-dam ecological state may recover fairly rapidly, particularly with assistance during community assembly phases, such as intentional planting of desired species on former reservoir sediments. However, novel riparian ecosystem states caused by no-analog species pools (e.g., introduced herbivores) or flow conditions (e.g., stage fluctuations due to daily ramping of hydropower production) weaken the expectation of riparian resilience, as does the uncertainty associated with ongoing climate changes (Capon et al. 2013, Catford et al. 2013). For example, if a decade of drought follows the removal of a dam that elevated low flows, then not only might floods remain suppressed (i.e., from lower precipitation), but existing vegetation could actually experience additional water stress due to the loss of dam-related moisture subsidies.

Though many factors interact in the rationale to remove or retain a dam (Pohl 2002, Whitelaw and MacMullan 2002), changes in riparian trees and shrub communities deserve

attention given their influence on the downstream flux of stored sediment, the post-dam in-channel habitat condition (e.g., large woody debris input, temperature), and the recreational appeal of restored reaches. As for intentional flood releases, the financial, legal and social difficulties of conducting removals are likely to necessitate modeling of possible outcomes, and heuristic simulation experiments can serve to illustrate basic patterns of vegetation responses that merit closer examination. I therefore simulated an additional set of 500 model runs involving a return to the naturally variable scaled annual peak scenario after a period of dam forcing as a first approximation of the effects of removal on the balance of the pioneer and upland trait types.

Model behavior illustrated both the potential for a rapid return to pre-dam vegetation patterns and the potential for a prolonged transient phase if a post-dam flow regime does not regain the full range of variation of pre-dam peak magnitudes. Larger, more frequent floods in the post-dam period reversed the trends toward lower pioneer seedling cover, temporally stabilized adult cover and greater relative abundance of the upland trait type (Figure 2.9 and 2.10). Standing dead area also declined, as clearing by disturbance was again greater than conversion from the live adult stage (Figure 2.9). Following the initial transition from the natural to the dam forcing scenario, population growth of the upland trait type required several years for existing and newly recruited seedling and juvenile stages to mature before the increased adult cover began to limit the availability of suitable establishment area. In contrast, increased flood disturbance mortality shortly after the simulated removal could eliminate much of the increased upland cover area. As a result, with suitable establishment area for the pioneer type more abundant, the pace of the shift back to the pre-dam vegetation distribution was typically faster than that from the natural to the dam forcing (Figure 2.10).

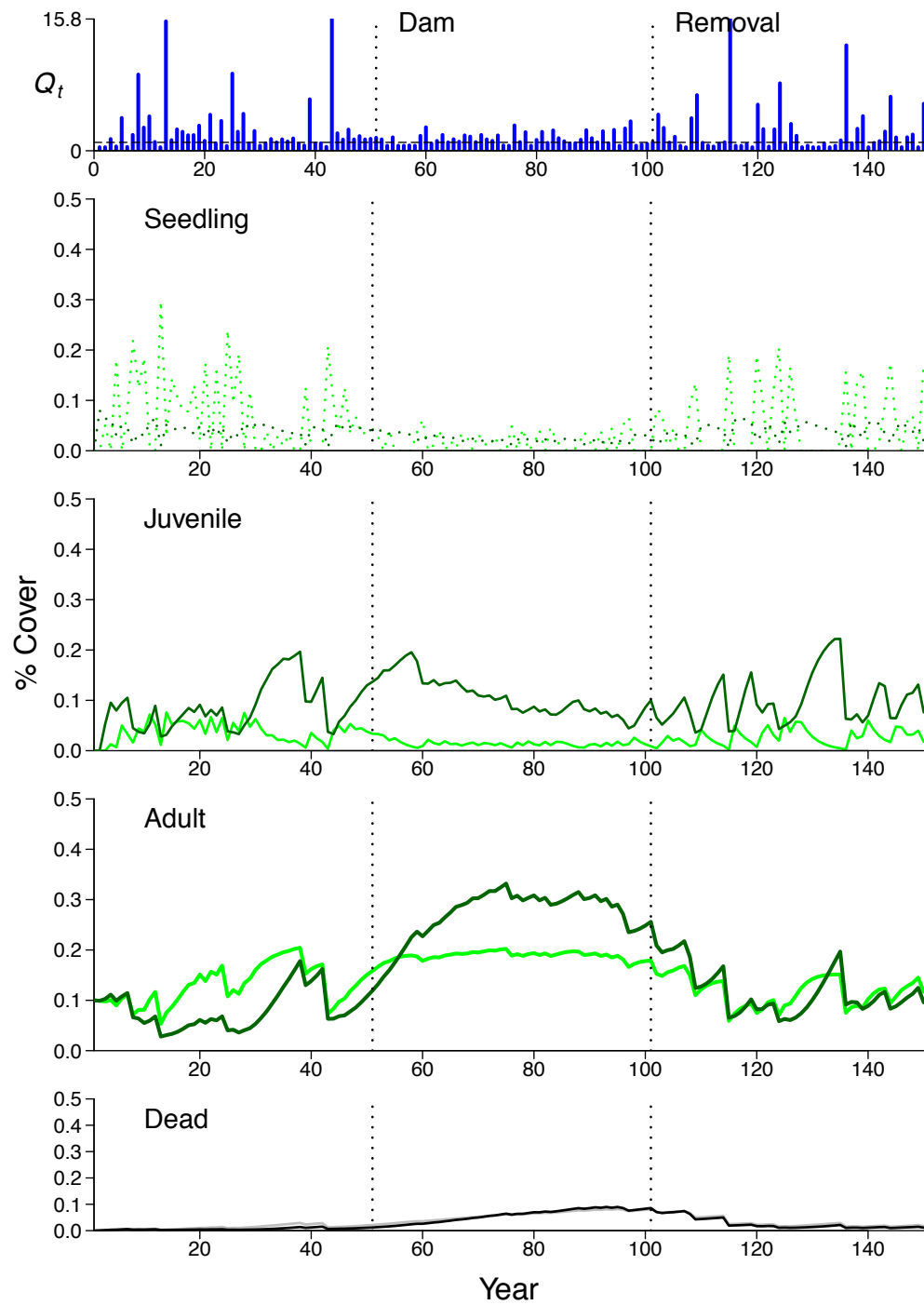


Figure 2.9: An example simulation run illustrating how a return to the natural forcing scenario after a period of the dam forcing could recover the pre-dam vegetation patterns. Cover of the adult upland type (dark green) and pioneer type (light green) reverted to comparable relative abundance, immature stages of the pioneer increased with greater establishment opportunities and standing dead cover was again cleared more effectively.

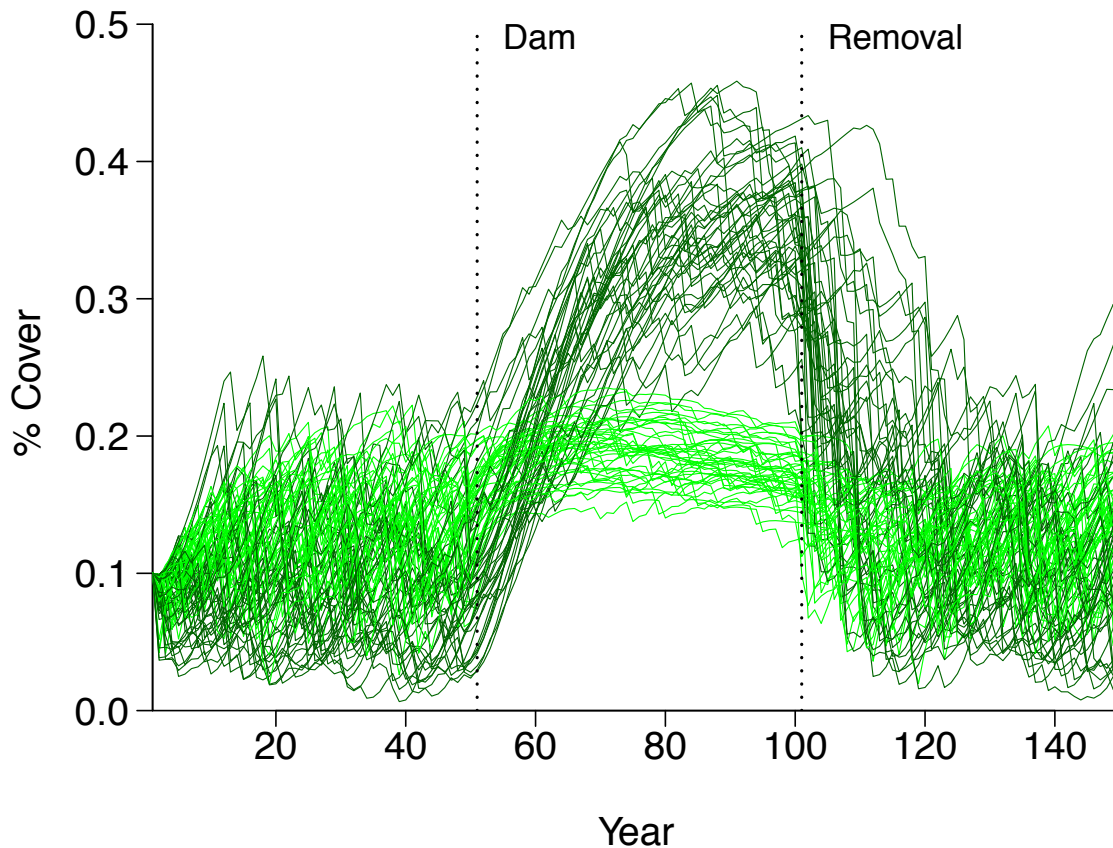


Figure 2.10: Following dam removal, a return to the pre-dam relative abundance of the adult pioneer (light green) and upland (dark) vegetation types occurred consistently over multiple simulations. Increased upland cover under the dam scenario required time for seedling and juvenile cover to mature (years 50 to 80). In contrast, stochastically generated sequences that included greater flood disturbance mortality immediately after the return to the natural scenario produced a rapid decrease in the adult upland (years 100 to 110).

Yet, random variation in the sequence of discharge forcing values also generated alternative outcomes during the 50 years following removal. As noted, the system quickly reverted to greater relative abundance of the adult pioneer stage if a large flood produced high disturbance mortality shortly after removal (Figure 2.11, top panel). However, if only low to moderate magnitude peaks affected the vegetation types over the 20 to 30 years post-removal, then a much more gradual decline in upland cover took place (Figure 2.11, middle panel). Furthermore, if the post-dam sequence of flows included no large floods during the simulated

period, then the combination of continued low disturbance mortality and non-flood years favoring the upland type prevented the vegetation from returning to the pre-dam state (Figure 2.11, bottom panel). In addition, even coarsely accounting for altered fluvial geomorphic conditions during and after the dam forcing scenario illustrated the substantially enhanced potential for a delayed vegetation response to removal (Figure 2.12). I imposed an arbitrary linear increase in the *kflood* parameter during the dam period to decrease the disturbance intensity for a given discharge magnitude. This modification implicitly represented the interaction of physical factors such as channel incision or sediment starvation with vegetation feedbacks such as reduced current velocity and stabilized near-channel surfaces. Despite a comparable linear decrease in *kflood* in the years following removal, the same flood forcing sequences that produced a rapid or gradual return to the pre-dam distribution of the trait types were then incapable of reducing the upland cover within the simulated post-removal period (Figure 2.12).

These results illustrated the contention by Shafroth et al. (2002a) that dam removal, while a necessary step toward the full functional rehabilitation of a regulated river, cannot address contextualizing changes in climate, land use, or the regional species pool that will influence post-dam trends in vegetation. As on relatively free flowing rivers, factors such as introduced competitors and consumers, loss of forested watershed area, or increasingly extreme precipitation events may all interact to determine tree and shrub abundance following removal. Though I did not seek to directly incorporate such factors, this generalized flow response trait modeling approach could be adjusted to accommodate additional vegetation types or alternative hydrologic forcing as a preliminary means of investigating such novel conditions. The initial model results could then serve as structured hypotheses for subsequent studies.

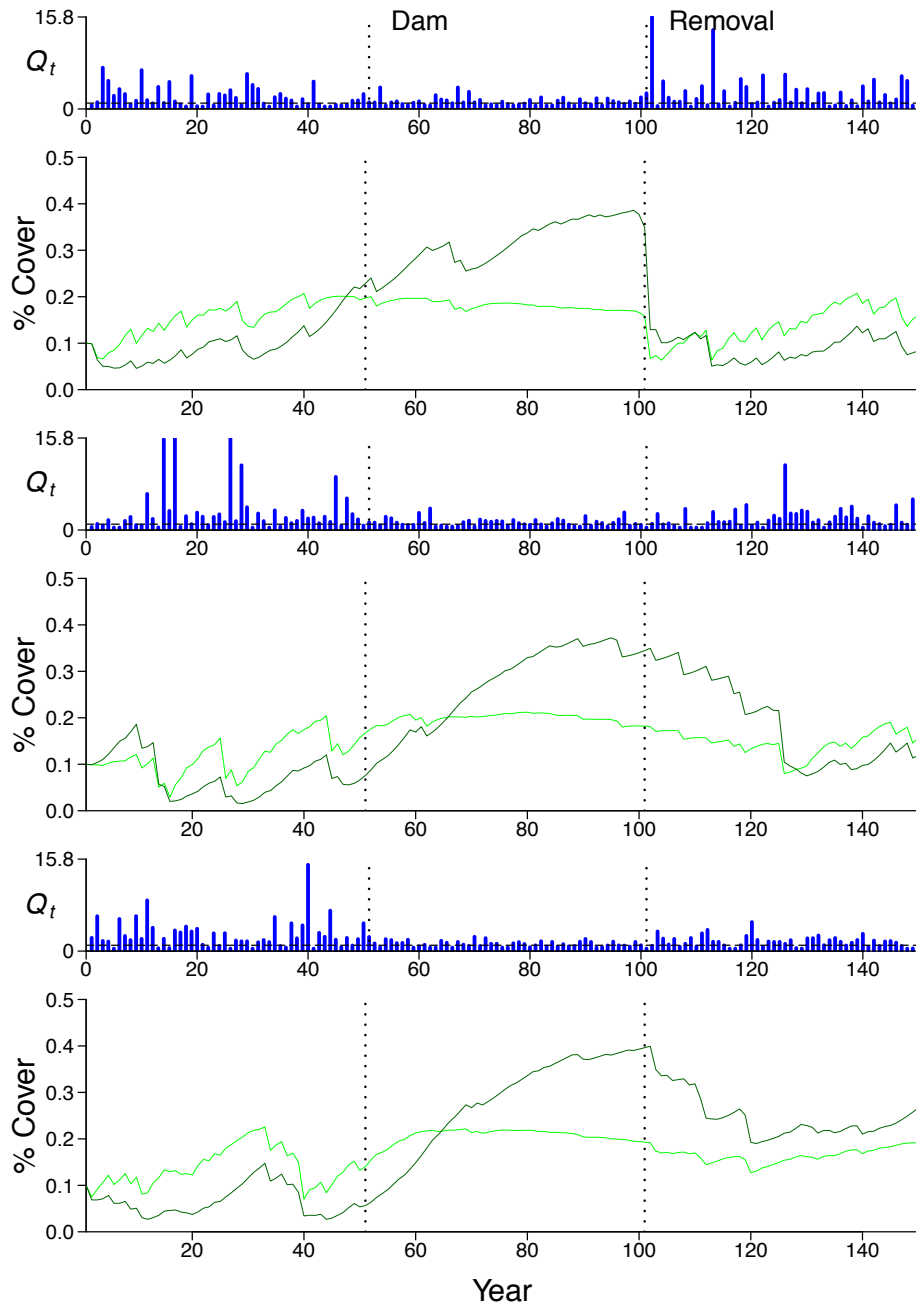


Figure 2.11: Random differences in the sequence of post-dam forcing produced alternative vegetation outcomes. Paired panels depict the forcing sequence and adult cover of the pioneer (light green) and upland (dark green) trait types for three example simulation runs. The top panels illustrate how a single large flood early in the post-dam period ‘snapped’ the system back, clearing adult cover and regenerating ample pioneer seedling cover. The middle panels show how a prolonged period without a large flood (approximately 30 years) and only moderate subsequent peaks resulted in a slower decline of the upland type. In the lower panels, despite declining upland cover with the return to more frequently overbank peaks, the absence of a major disturbance event prevented full recovery of the relative abundance of the pioneer type within the simulated period.

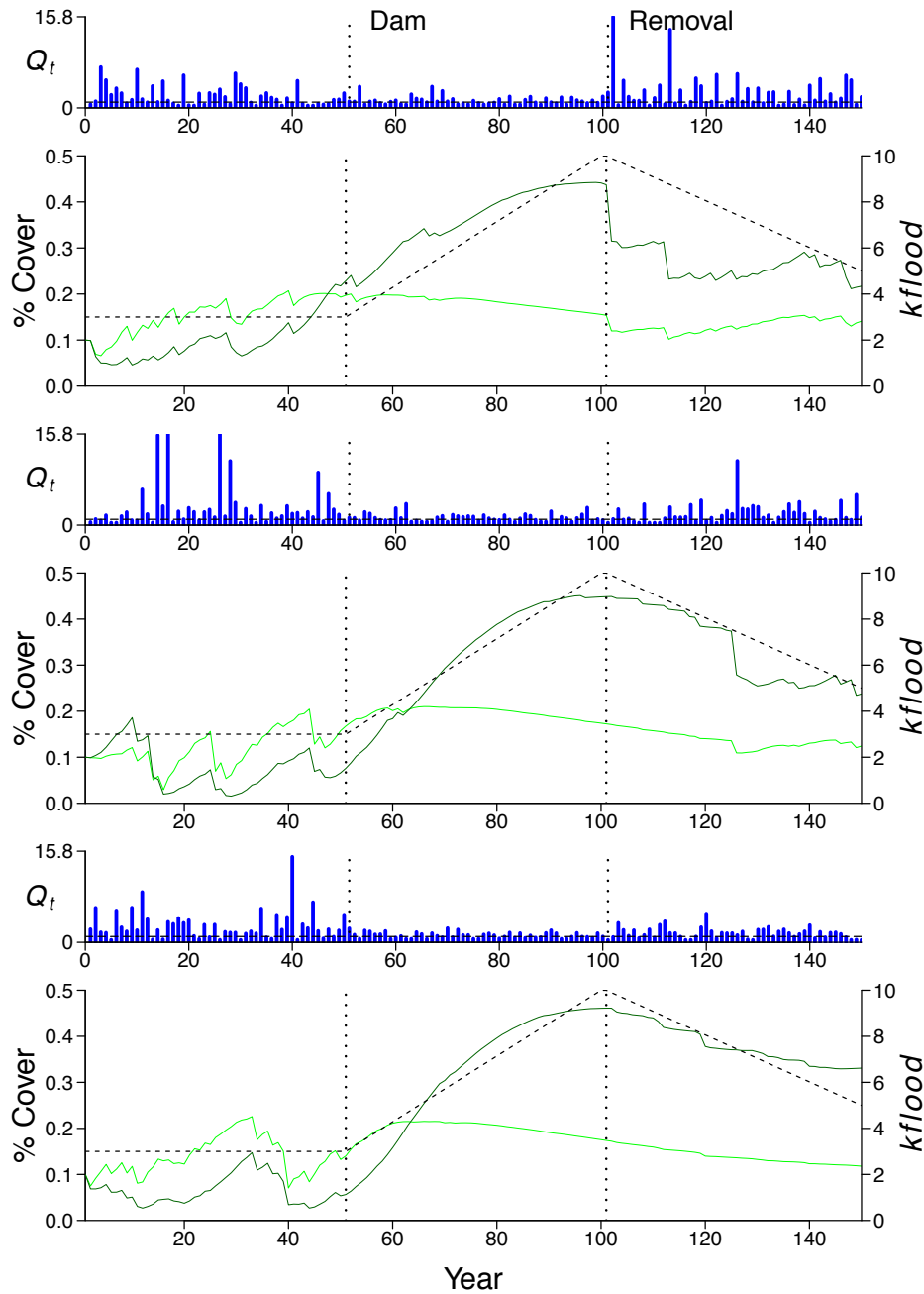


Figure 2.12: Adjusting the  $k_{flood}$  parameter through time (horizontal dashed line) to represent geomorphic shifts and vegetation feedbacks under the dam scenario further illustrated the potential for delayed or limited vegetation recovery following removal. Annual peak forcing sequences are identical to those in Figure 2.11, but the reduced flood disturbance intensity for a given scaled discharge suppressed the removal of adult upland cover (dark green) even for sequences in which larger magnitude flows occurred (top and middle panels). In conjunction with the absence of large overbank events (bottom panels), the adult upland type remained at considerably greater abundance than the pioneer.

## Discussion

In this work, I sought to demonstrate how the flow response and life history traits that mediate riparian vegetation abundance could serve as a means to link stream ecology principles to applied water management issues such as the potential outcomes of intentionally scheduled floods or dam removal. My generalized model was suited to exploring how trait differences influenced the prevalence and population stage structure of woody riparian vegetation types under alternative scenarios of flow variation. This approach was congruent with recent calls for a “demographic meta-species” framework for addressing environmental flow needs that might simultaneously capture population dynamics while remaining applicable in relatively data-limited settings (Shenton et al. 2012). With vegetation parameters assigned according to relative ‘trait profiles’, simulation runs were driven by hypothetical estimates of the distribution of annual high flows and the relationship between overbank flow and disturbance intensity. Yet, given these minimal inputs, the model behavior captured patterns relevant to assessing the effects of river regulation on riparian biodiversity and ecosystem service production, and clarified important assumptions regarding these responses.

Simulations lent further support to the principle that the loss of discharge variability due to dams and diversions alters the diversity of riparian zone vegetation, as reduced high flow magnitude and variation increased the viability of an upland type relative to a pioneer type better adapted to flood disturbance (Nilsson and Berggren 2000). In contrast, stochastic sequences of larger more frequent floods promoted greater cover of immature stages and less disparity in adult abundance between these types. In agreement with observations, adult pioneer cover increased when several years of reduced flood disturbance followed a pulse of recruitment in a high peak magnitude year (Birken and Cooper 2006). Simulated series of intentional floods were



insufficient to recover pre-dam vegetation patterns, but a higher frequency of low magnitude peaks generated more pioneer establishment opportunities and reduced upland cover. According with the expectation of riparian resilience to altered environmental conditions, pre-dam vegetation patterns recovered when dam removal was simulated as a return to higher magnitude and variability of peak flow forcing. However, this recovery was contingent on how quickly large floods again occurred, as well as the assumed degree of change in vegetation-geomorphic interactions affecting disturbance intensity. In addition, both recovery following removal and persistence under the dam-altered flows depended on the assumption that no dispersal limitation prevented pioneer seeds from reaching the system.

The differences in simulated vegetation responses relative to the inclusion of a very limited representation of geomorphic dynamics highlight the importance of incorporating information regarding valley type (e.g., unconstrained vs. canyon), channel form (e.g., braided versus meandering), substrate characteristics (e.g., sand vs. silt), and dominant fluvial geomorphic processes (e.g., erosion vs. aggradation) into flow-vegetation models (Corenblit et al. 2007, Shafroth et al. 2010b). Within this model framework, critical directions for further research regarding fluvial geomorphic effects would involve the appropriate functional form for changes in the  $Q_{bf}$  overbank scaling threshold with time and the appropriate adjustments to the  $k_{flood}$  parameter to represent the feedback of vegetation on overbank velocity and sediment stabilization. The relationship between dam construction or removal and channel incision or erosion is likely complicated and dependent on factors such as the antecedent sediment load, the reservoir capacity and the proximity of downstream tributaries. Nonetheless, given an expectation of downcutting or aggradation, the model platform could provide a means to explore the potential implications for vegetation. The general hypothesis that disturbance intensity is

negatively related to riparian plant cover could also direct model development. However, the morphology (e.g., single trunk versus many stems), density (e.g., many juvenile plants versus fewer adults), and root architecture (e.g., shallow and wide versus deep and narrow) of different life stages and trait types may influence the feedbacks that vegetation exerts on scour and burial during flooding. The simplicity of the current model could facilitate investigating the simulated results of these presumed differences through alternative linear or non-linear forms of the relationship between disturbance intensity and the vegetation included in functional terms (e.g., iteratively updating  $k_{flood}$  as a step function of adult and dead cover area in the prior time step).

The basic model structure could also accommodate further development to incorporate other flow regime dimensions or population controls unrelated to discharge, as more information is available. For instance, prolonged inundation or several smaller peaks may compound or substitute for the mortality effects of flood scour and burial related to a single annual high flow. Similarly, the timing of peak flows may influence population growth as a control on the availability of suitable germination surfaces relative to the period of seed release (Shafroth et al. 1998, Braatne et al. 2007). Flood timing may also affect seedling mortality if high flows later in the growing season scour young plants that have not reached a size and rooting depth sufficient to withstand disturbance. The effects of flood duration or timing could be incorporated into the model by making disturbance intensity a function of the number of days of discharge over a particular recurrence interval flow or by making the establishment success parameter a function of the date of high flow (Chapter 4). However, capturing these or other flow attributes would require additional forcing inputs as well as further specification of functional forms (e.g., continuous or threshold changes in germination with date) and covariance with magnitude (i.e.,

the relative ecological effects of short large floods versus long moderate ones), and this information may not be forthcoming outside of well-studied river basins.

Adjusting the stage transition parameters ( $sj$ ,  $ja$ ,  $ad$ ) could permit the implicit investigation of differences between vegetation types in susceptibility to non-flow mortality sources. However, traits mediating the effects of temperature extremes, precipitation patterns, herbivores, disease, fire, ice scour, harvest and other forms of removal (i.e., mechanical clearing for restoration) could also explicitly enter the model according to the same basic functional structure as flood disturbance mortality: persistence calculated relative to a forcing variable raised to the power of stage-specific tolerance parameters. The representation of the standing dead class could then account for ongoing spatial limitations on establishment due to vegetation structure remaining after mortality, for example due to insect herbivores or fire. Yet such adjustments again imply that data regarding these environmental drivers are available to incorporate into the modeling effort. The interaction of hydrologic variation with other environmental regimes and ecological community interactions remains an important area for future research.

The objective of achieving greater ecological realism in the representation of flow-vegetation relationships warrants extensive model development, but such detail may be unnecessary for the purpose of stimulating greater consideration of those relationships in the first place. In the context of challenging water resource decisions, a plainly ‘wrong’ model risks dismissal by stakeholders, but such an approach may also lead to discussion of the fundamental limitations of all predictive models, the uncertainty associated with other forecast estimates of project benefit and cost, and the importance of a precautionary perspective regarding the trade-offs associated with river regulation. A generalized, heuristic approach may suffice to illustrate

the primacy of dynamic, variable flow conditions for the composition of riparian vegetation communities, and therefore the need to account for change through time in assessments of river regulation.

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## CHAPTER 3: RECIPROCAL RELATIONSHIPS BETWEEN *TAMARIX*, HYDROLOGY AND FLUVIAL GEOMORPHOLOGY ALONG WESTERN U.S. RIVERS<sup>1</sup>

### Introduction

Flowing water, sediment and vegetation interact to form diverse and dynamic riverine landscapes. In arid and semiarid regions such as the western United States, variation in this biophysical regime shapes banks and channels (Poff et al. 2006a, Miller and Friedman 2009), alters the flux of nutrients (Molles et al. 1998, Fisher et al. 2007) and governs the composition and dynamics of biological communities (Poff et al. 1997, Merritt et al. 2010). In turn, the composition and structure of riparian vegetation mediate day-to-day variation in fluvial conditions such as water temperature and turbidity as well as the formation and destruction of fluvial forms (Naiman et al. 2005, Sandercock et al. 2007, Merritt 2012).

The spread of trees and shrubs in the introduced genus *Tamarix* (commonly referred to as tamarisk or saltcedar) has provided an opportunity to increase our understanding of these relationships between plants and fluvial processes. Native to Eurasia, *Tamarix* was initially planted as an ornamental shrub and cost-effective means to stabilize stream banks, but spread rapidly during the 20<sup>th</sup> century, concurrent with a period of large-scale river alteration due to dam and reservoir construction (Robinson 1965, Nagler et al. 2011). Research by Ringold et al. (2008) corroborated the finding of Friedman et al. (2005) that various species of *Tamarix* are among most common woody plant across all western floodplains and are especially abundant in more xeric zones in valley bottoms. The role of *Tamarix* in western U.S. riparian ecosystems has

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prompted research on various aspects of its ecology and management including its relationship to native riparian vegetation and wildlife, how it affects recreational values, and how it influences and is influenced by water availability (Shafroth et al. 2005, 2010b, Stromberg et al. 2009).

Here, we describe hydrologic and geomorphic controls on *Tamarix* distribution and abundance as well as reciprocal effects of *Tamarix* on hydrologic and geomorphic conditions. These relationships bear on key questions for river science and management such as, “Does flow regime alteration favor *Tamarix* establishment over native taxa?” and, “How do *Tamarix* stands modify processes of channel narrowing and floodplain formation?” After an overview of the basic geomorphic and hydrologic character of rivers in the American West, we examine how this setting has facilitated the regional success of *Tamarix* and review the influence of *Tamarix* on the form and function of these systems. We conclude by discussing the relevance of a shifting climate, vegetation management and continued water resource development to the future role of *Tamarix* in these ecosystems.

## **Riparian Vegetation In Relation To Hydrogeomorphic Form And Function In Western U.S. Rivers**

Rivers in the western US progress from their headwaters, often in montane settings with high topographic relief, through intermediate-elevation foothills and valleys before reaching their terminus in a larger river, inland basin or sea. The lower gradients and wider valleys typical of many downstream (higher order) reaches permit the development of potentially extensive and topographically complex floodplains (Leopold et al. 1964). The largest riparian forests occur along reaches subject to weaker lateral geologic constraints and greater lateral hydrologic connectivity between channels and floodplains (Naiman et al. 2005, Cooper et al. 2012). Human

actions such as grazing and agricultural clearing also influence the amount and type of vegetation in riparian ecosystems, and widespread construction of dams and irrigation networks has altered patterns of discharge and sediment movement that affect riparian plants (Patten 1998, Graf 1999, Nilsson and Berggren 2000, Poff et al. 2007).

At the watershed scale, the amount, timing and form of precipitation (e.g., rain vs. snow) combine with terrestrial land-cover, lithology and human infrastructure to control the magnitude, seasonal distribution and sequence of flows reaching a particular location (Poff et al. 2006a, b). Flow variation shapes the fluvial landscape in arid and semi-arid western rivers by affecting the delivery and removal of sediment that forms bottomland surfaces such as floodplains, islands, bars, splay deposits, oxbows, and terraces (Figure 3.1, Schumm and Lichty 1963, Leopold et al. 1964, Hereford 1984, Tooth 2000). The energy available for erosion and transport of sediment changes as a function of discharge magnitude (Baker and Ritter 1975), parent material (e.g., percentage sand, clay or silt) and landscape setting (e.g., valley slope and constraint). Discharges of larger magnitudes have lower probability of occurring in any given year, which translates into a recurrence interval that describes how often, on average, particular flows will occur. In some systems, intermediate magnitude floods with recurrence intervals of less than five years may drive floodplain formation by depositing new sediment both in-channel and over banks (e.g., Miller and Friedman 2009). In contrast, the largest floods, with recurrence intervals greater than five to ten years, may be responsible for the most re-mobilization of channel and floodplain material (Wolman and Gerson 1978, Miller and Friedman 2009). Such “channel-resetting” floods act as a negative feedback on channel narrowing processes associated with increased sediment supply or decreased peak flows, maintaining wider active channels in which perennial vegetation is scarce or absent (Sigafos 1964, Dean et al. 2011).

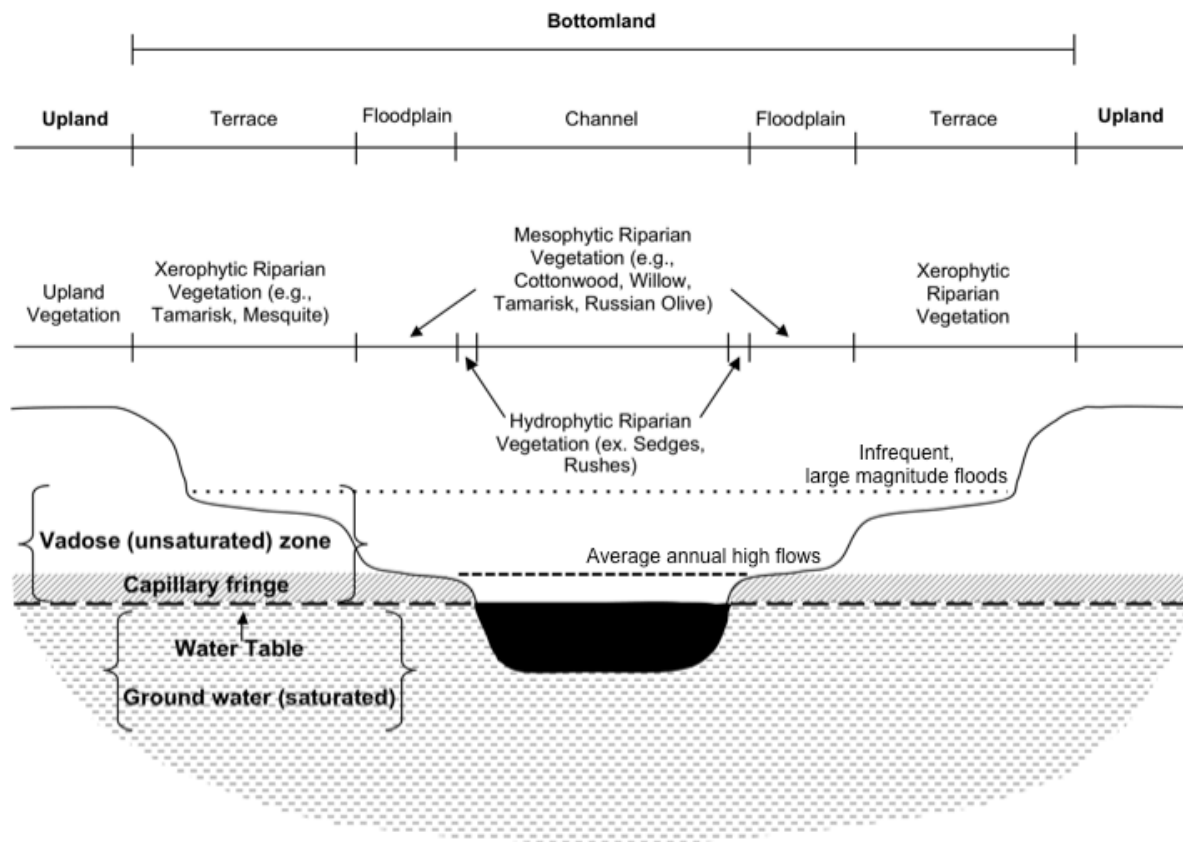


Figure 3.1: Major channel-floodplain landforms showing characteristic vegetation classes, positions where they typically grow within the bottomland, and key surface and ground water elements. Relationships are simplified for clarity and do not illustrate the complex topography, stratigraphy, hydrology, and plant community composition typical of most bottomlands. Modified from Figure 1 (p. 5) and Figure 2 (p. 37) in Shafroth et al. 2010b. Bottomlands are the areas within alluvial valleys primarily influenced by stream flow and sediment transport, and are distinguished from higher elevation uplands that do not consist of geologically recent river-affected sediment. Channels are linear depressions that contain continually or periodically flowing water and sediment. Floodplains border channels at an elevation approximately corresponding to the typical annual flood, and are constructed of river-transported sediment. Terraces are typically elongated surfaces that parallel channels above the floodplain, and are rarely inundated other than by very large magnitude floods. Ground water occurs as subsurface saturation, and its upper level is often called the water table. Above this but below ground, the capillary fringe forms a zone in which groundwater is drawn upward into interstitial spaces within sediment. More generally, the vadose zone extends from the soil surface to the water table, and is sometimes termed the unsaturated zone. Hydrophytic riparian vegetation includes plants that are well adapted to growth in saturated or very wet conditions are termed hydrophytic, whereas mesophytic riparian vegetation is better adapted to intermediate moisture levels. Xerophytic riparian vegetation consists of plants adapted to low moisture that occur within bottomlands.



These geomorphic processes and the quantity and timing of water that flows laterally over banks and below ground (as alluvial groundwater) are primary determinants of the structure and species composition of riparian plant communities (Naiman et al. 2005). Variation in physiological, morphological, and phenological (timing-related) traits causes individual riparian species to differ in their responses to flow and sediment regimes. Flows are distinguished by their magnitude, duration, frequency, timing and rate of change (i.e., the speed of transition to flood stage), and a characteristic set of flows measured an extended period constitutes a flow regime on a particular river (Poff et al. 1997). The compatibility of specific traits with site conditions (determined by flow and sediment regimes) influences establishment, growth, survival and dispersal through a variety of mechanisms (Karrenburg et al. 2002, Nilsson and Svedmark 2002, Poff et al. 2006, Renofalt et al. 2007, Merritt et al. 2010). Sediment stratigraphy and texture influence vegetation by controlling moisture availability and nutrient retention and processing (Merigiano 2005). High flows drive the formation and destruction of surfaces suitable for riparian tree seedling establishment (Scott et al. 1996, Friedman and Lee 2002). Floods also cause mortality of existing vegetation through scour, burial, or prolonged inundation. Riparian species have evolved a suite of adaptations in response to varied flows. The formation of aerenchyma (tissue with large intercellular air spaces) and active transport of oxygen to roots enable plants to tolerate flooded, submerged and anoxic (oxygen depleted) conditions (Merritt et al. 2010). Flexible stems, the ability to resprout after disturbance, and thick furrowed bark enable many riparian species to survive shear, abrasion, ice scour, and burial. Production of numerous small seeds and the ability to reproduce from branch and stem fragments enable some plants to persist in frequently disturbed river bottomlands. The interplay between these traits and the physical forces in rivers controls the spread and persistence of riparian plants such as *Tamarix*.

## **Reciprocal Feedbacks Between Hydrology, Fluvial Form And *Tamarix***

*Tamarix* possesses a set of traits that have allowed it to naturalize widely in North America (Friedman et al. 2005, Ringold et al. 2008), but the mechanisms responsible for its establishment and survival vary with position in the drainage network and with the chronology of hydrologic changes resulting from climate shifts and human modification of flow and sediment regimes (Glenn and Nagler 2005, Stromberg et al. 2007b, Merritt and Poff 2010, Mortenson and Weisberg 2010, Nagler et al. 2011). Similarly, the effect of *Tamarix* on fluvial geomorphic processes varies with factors such as local sediment supply and the history of high and low flows. These elements combine and shift through time to generate the floodplain dynamics that influence and are influenced by *Tamarix*.

### *Establishment*

The expansion of *Tamarix* through river corridors of the arid western U.S. has followed establishment opportunities created by local flow and sediment regimes, with larger scale climate shifts, land use changes and dam construction controlling proximate establishment processes. Within the riparian zone, *Tamarix* may establish across a fairly broad range of soil texture and chemistry, but seedlings require plentiful light and moisture (Shafroth et al. 1995, Cooper et al. 1999, Taylor et al. 1999, Sher et al. 2002, Sher and Marshall 2003, Glenn and Nagler 2005). Accordingly, *Tamarix* has recruited on former active channel surfaces exposed after prolonged reduction in peak flow, on bare floodplain surfaces formed by large magnitude floods, and relative to the spatiotemporal availability of alluvial groundwater (Graf 1982, Shafroth et al. 1998, Glenn and Nagler 2005, Merritt and Poff 2010).

Floods that create bars and islands through lateral and vertical accretion (gradual, layered accumulation) or deposit fresh sediment over banks within more confined valleys (Scott et al. 1996) generate bare, moist sites that provide the plentiful light and water required by germinating *Tamarix* seeds (Taylor et al. 1999, Merritt and Cooper 2000). Reduced flood magnitude can also support *Tamarix* establishment by exposing portions of the former active channel to colonization (Graf 1982). Recruitment on previously flood-mobilized surfaces was especially widespread during the early stages of *Tamarix* spread in the mid-20th century (Campbell and Dick-Peddie 1964, Graf 1978, 1982, Hereford 1984). Comparing sites on the Yampa and Upper Green Rivers below Flaming Gorge Dam, Cooper et al. (2003) described *Tamarix* recruitment on surfaces both within and peripheral to channels, relative to valley confinement (park vs. canyon) and flow regulation. The magnitude and inter-annual pattern of floods appeared to determine whether *Tamarix* established on higher elevation floodplains following high flows or on lower elevation surfaces within the active channel in association with several years of lower peak flow. *Tamarix* also increased along the Bill Williams River following completion of Alamo Dam, reaching higher cover compared to the unregulated Santa Maria River upstream from the dam (Shafroth et al. 2002). Several flow regime changes may have contributed to *Tamarix* expansion in this system, such as increased summer flows that have supported riparian vegetation in previously moisture-limited areas. The dam also reduced peak discharges and likely enabled *Tamarix* recruitment by exposing germination surfaces and reducing the frequency and magnitude of channel scouring flows (Shafroth et al. 2002). Despite such favorable effects in the period following dam construction, the width of new patches colonized by seedlings was lower along the Bill Williams after 25 years of regulation, suggesting that diminished floods could also play a role in limiting further expansion.

The timing of flood peaks and the rate of associated alluvial groundwater recession can favor or disfavor *Tamarix* germination relative to native species (Figure 3.2, Warren and Turner 1975, Graf 1982, Shafroth et al. 1998, Horton and Clark 2001, Merritt and Poff 2010, Mortenson and Weisberg 2010). Like native *Populus* and *Salix*, *Tamarix* produces abundant, small seeds widely dispersed by wind and water and able to germinate immediately. However, unlike *Populus* and *Salix* that typically disperse seed earlier in the growing season concurrently with the declining stage of spring snowmelt run-off floods, *Tamarix* releases seeds somewhat later and over a longer period of time (Figure 3.2, Stromberg 1993, 1997, Shafroth et al. 1998, Cooper et al. 1999, Sprenger et al. 2001). In some river systems, this seed release timing may allow *Tamarix* to take advantage of establishment opportunities generated by floods occurring outside of the late winter and spring, particularly in the absence of ensuing high flows or rapid groundwater declines that kill seedlings (Warren and Turner 1975, Shafroth et al. 1998, Cooper et al. 1999, Beauchamp and Stromberg 2007). A longer period of seed release could afford *Tamarix* an advantage over some native colonizers along intermittent or flashy streams where patches of bare sediment provide germination sites after late summer rainfall-driven floods, or along regulated rivers where floods occur later in the growing season (Sher et al. 2002, Beauchamp and Stromberg 2007, Mortenson and Weisberg 2010). Conversely, later seed release may disadvantage *Tamarix* if plants that establish earlier in the season have already occupied suitable sites or if subsequent floods remove *Tamarix* seedlings established at lower elevation positions on the floodplain (Stromberg 1993, 1997, Sprenger et al. 2001, Merritt and Wohl 2002).

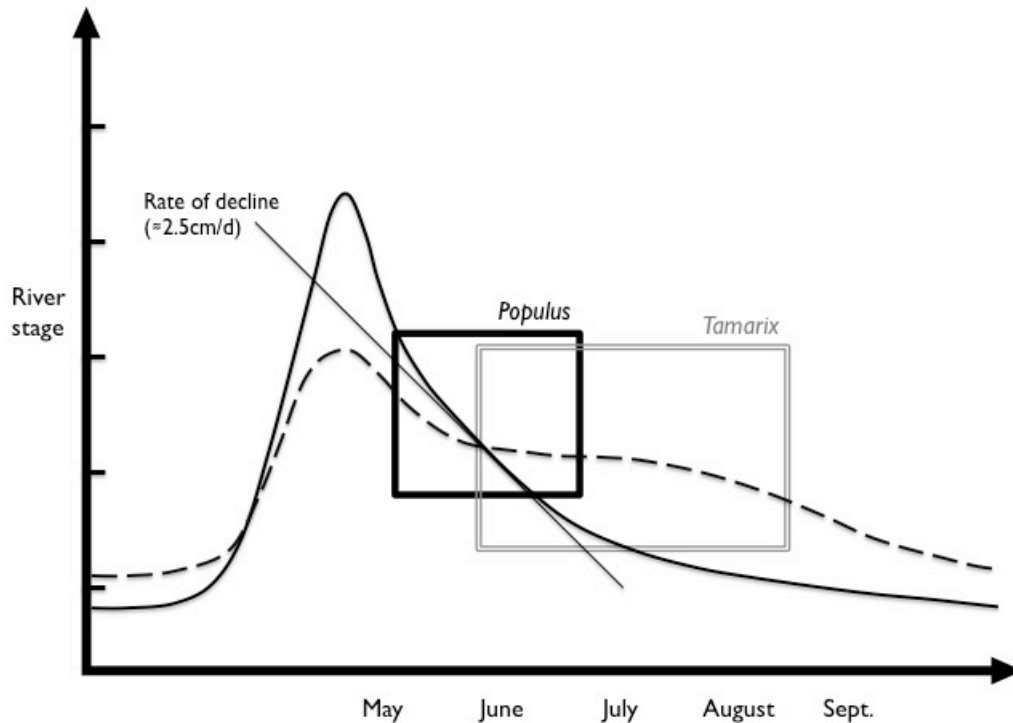


Figure 3.2: Recruitment box model comparing *Populus* and *Tamarix* establishment requirements relative to regulated and unregulated snowmelt-flood hydrographs. Both *Populus* and *Tamarix* establish on bare, moist surfaces such as those created after floods scour existing vegetation or deposit new sediment. The timing of *Populus* seed release typically coincides closely with seasonal flood recession on unregulated snowmelt rivers (solid black hydrograph), and seedling survival increases when gradual water level declines accommodate root elongation. In contrast, *Tamarix* seed release occurs somewhat later but over a longer portion of the growing season on many rivers, thereby potentially enabling it to take advantage of establishment opportunities on regulated rivers (dashed black hydrograph) to which *Populus* is not as well adapted. Note that the illustrated flow regime alteration is not representative of all regulated snowmelt rivers, and diversions for consumptive use such as agricultural irrigation may result in lowered summer flows as well as reduced peak flow magnitude and duration. Furthermore, a hydrograph that includes late season floods is not shown, but could also favor *Tamarix* establishment. See text for additional discussion. After Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – an integrative model. *Wetlands* 18:634-645.

Regulation of flood magnitude and timing has been proposed as an important driver of *Tamarix* spread (e.g., Stromberg et al. 2007a, b), although relatively few studies have closely examined how variability in flood timing and magnitude have or have not promoted the

colonization of unregulated rivers by *Tamarix*. Merritt and Poff (2010) studied current *Tamarix* establishment, abundance and dominance along both regulated and unregulated rivers relative to a composite index of flow alteration that included flood timing and magnitude. Distinguishing establishment from abundance and dominance revealed important differences in the relationship between flow alteration and the success of *Tamarix*. Contrary to the expectation that flow regulation promotes *Tamarix* establishment, this research showed equal or greater probability of recruitment along free-flowing as compared to heavily regulated reaches. The authors noted that periodic disturbance on less regulated rivers likely provides more frequent establishment opportunities than are typical of systems with reduced or eliminated floods, and contributed to the much higher probability of native *Populus* establishment at sites experiencing less regulated flows. By comparison, dominance of *Tamarix* was positively related to the intensity of alteration, and the abundance of *Tamarix* increased up to an intermediate level of flow modification before declining with maximum hydrologic alteration. Similarly, Mortenson and Weisberg (2010) found *Tamarix* canopy cover was positively related to flow alteration, but was highest at intermediate levels of hydrologic change. Furthermore, both studies indicated strong declines in *Populus* abundance and dominance (Merritt and Poff 2010) and cover (Mortenson and Weisberg 2010) with even moderate flow modification. This relationship suggested that different mechanisms limit *Tamarix* at low and high levels of regulation. Merritt and Poff (2010) proposed that overall low recruitment associated with the absence of fresh establishment surfaces may constrain *Tamarix* on intensively modified reaches, but that ecological interactions such as those between *Tamarix* and other riparian trees may play a greater role on reaches where less regulated flow conditions support recruitment of native species. Patterns of abundance and dominance are affected by growth and survival of maturing and adult individuals, and these results also

highlight the degree to which flow and sediment regimes interact with multiple life history stages to determine the local ecological significance of *Tamarix*.

### *Persistence*

In addition to influencing recruitment, flood intensity and duration affect juvenile and adult survival through inundation, scour and burial. Although *Tamarix* displays inundation tolerance (Brotherson and Field 1987), prolonged flooding can cause mortality (Gladwin and Roelle 1998, Sprenger et al. 2001, Tallent-Halsell and Walker 2002) and has been suggested as a control method, particularly if the submergence of target plants is coordinated with native seed release timing (Vandersande et al. 2001, Lesica and Miles 2004; but see Sprenger et al. 2001 for discussion of the risk to cottonwood seedlings). In a greenhouse study, Levine and Stromberg (2001) found that, relative to native species, *Tamarix* seedlings required a longer period of growth in order to reach sizes sufficient to survive sediment burial treatments. These authors proposed that restoring pre-regulation sediment regimes associated with occasional large floods might play a role in limiting the establishment and survival of *Tamarix*. On the Bill Williams River, *Tamarix* seedlings had much higher mortality rates than Goodding's willow (*Salix gooddingii*) due to both burial and scour associated with flooding (Shafroth et al. 2010a), but adult *Tamarix* in ephemeral channels in Spain displayed significant resistance to high flood velocities and shear stresses (Sandercock and Hooke 2010). Extrinsic factors such as local substrate cohesion and the density of neighboring vegetation combine with intrinsic features such as age and stem morphology to determine whether individual plants withstand the abrasive forces generated by floods (Sandercock et al. 2007). In contrast to flexible *Salix* stems and branches, the relatively dense, inelastic wood of mature *Tamarix* (Gerry 1954) tends to confer

resistance rather than resilience, either supporting continued growth after burial and scour or sustaining damage under intense flood forces (Friedman et al. 2005b).

Decreased flood frequency and magnitude may favor *Tamarix* survival over native species by reducing flows that remove plant litter from floodplains (Glenn and Nagler 2005, Stromberg et al. 2007a, Shafroth et al. 2010b). The accumulation of combustible *Tamarix* litter (leaves and dead branches), due in part to reduced rates of litter decomposition and removal by floods (Ellis et al. 1998, Molles et al. 1998, Stromberg and Chew 2002, Ellis 2001), has contributed to an increased prevalence of fire in some western riparian zones (Busch 1995). The degree to which fire favors *Tamarix* over natives remains unclear (Ellis 2001, Glenn and Nagler 2005), but in contrast to some native species, *Tamarix* resprouts readily after fire and has increased in abundance following fires in some locations (Drus et al. Chapter X, Busch 1995).

Decreased flooding may also reduce flushing of floodplain soils and thereby contribute to high levels of floodplain soil salinity (Jolly et al. 1993, Ohrtman et al. chapter X, Merritt and Shafroth). Numerous studies have documented the high salt tolerance of both establishing and mature *Tamarix* (Busch and Smith 1995, Shafroth et al. 1995, Glenn et al. 1998, Vandersande et al. 2001), and floodplains with high soil salinity relative to regularly flooded ones may favor *Tamarix* over *Populus* and other glycophytic (salt-intolerant) native species (Ohrtman et al. chapter X, Merritt and Shafroth *in review*). Although *Tamarix* may contribute to salinization of floodplains by exuding salt from its leaves, Merritt and Shafroth (*in review*) found that other causes of salinity (e.g., upward transport to near-surface soils due to evaporation of capillary water) overshadow the salinizing effect of *Tamarix* along the flow-regulated lower Colorado River. Further, salt concentrations in *Tamarix* dominated stands along the relatively free-flowing upper Colorado River only occasionally reached levels that would significantly affect survival of



native glycophytes, despite being elevated relative to native dominated stands (Merritt and Shafroth *in review*). Thus, presence of *Tamarix* in more saline floodplain habitats may reflect its tolerance of relatively high soil salt concentrations more than its direct modification of floodplains (Merritt and Cooper 2000, Glenn et al. *in press*).

Supplemental soil moisture provided by stream flow and alluvial ground water during dry times of year is a key factor promoting the growth of distinct riparian plant assemblages in arid and semiarid regions. Low or ephemeral flows may affect tree density and composition by exposing portions of the active channel, making them available for colonization (Scott et al. 1996) or by producing water stress that limits the extent of riparian stands away from the active channel (Graf 1978, 1982, Stromberg et al. 2007b). Among riparian trees and shrubs, *Tamarix* is well adapted to low moisture conditions (Cleverly et al. 1997, Horton and Clark 2001, Glenn and Nagler 2005). *Tamarix* tends to dominate sites with intermittent surface flows, in contrast to native cottonwood and willow species that can dominate *Tamarix* along reaches characterized by perennial surface water, relatively stable and shallow ground water tables, or high and low flows ranging within the rooting depths of these species (Busch and Smith 1995, Shafroth et al. 2000, Lite and Stromberg 2005). Functional trade-offs between drought tolerance and tolerance of inundation and disturbance constrain bottomland vegetation (Stromberg et al. 2008). *Tamarix* is well adapted to both of these limiting factors however, with traits that enable it to occupy drier sites that still experience disturbance and inundation (Pockman and Sperry 2000).

Comparing portions of the San Pedro River, Arizona that spanned a hydrologic gradient from perennial to highly intermittent flow, Stromberg (1998a) observed an increase in the relative abundance of *Tamarix* corresponding to less perennial flow and declining groundwater levels. At sites along the Bill Williams River, juvenile *Tamarix* survived greater inter-annual

groundwater declines than native saplings (Shafroth et al. 2000). At a regional scale (southern Arizona), Stromberg et al. (2007b) found more *Tamarix* patches and greater *Tamarix* basal area along reaches with intermittent surface flow and dam-altered flow regimes compared to perennial and free-flowing reaches. Despite its drought tolerance, continued groundwater declines can eventually result in decreased *Tamarix* abundance and replacement by species with even greater tolerance of xeric conditions, as noted by Graf (1982) for sections of the Salt and Gila Rivers.

### *Changes in channel form*

While flow and sediment regimes regulate *Tamarix* recruitment and survival, *Tamarix* and other floodplain plants can simultaneously affect channel form. Riparian vegetation mediates sediment erosion and deposition through surface and subsurface mechanisms. Stems and other above-ground biomass create drag that increases floodplain roughness, reduces boundary shear stress, and slows the passage of water (Griffin et al. 2005, Sandercock et al. 2007, Merritt 2012). These changes increase sediment deposition, reduce erosion relative to un-vegetated surfaces, and increase flow depth and turbulence (e.g., Griffin et al. 2005). Roots may reinforce banks, with the degree of increased cohesion depending on factors such as plant size and species, root depth and the percentages of sand and clay within banks (Pollen-Bankhead et al. 2009, Merritt 2012).

*Tamarix* is not unique in its influence on fluvial geomorphic processes (Friedman et al. 1996, Friedman et al. 2005b, Sandercock et al. 2007). Stromberg (1998b) found comparable rates of sedimentation in patches dominated by *Tamarix* and native cottonwood and willow (*Populus* and *Salix*) along the free-flowing San Pedro River. Numerical modeling suggested that flexible

stems of sandbar willow (*Salix exigua*), which may flatten against the ground at high flows, contributed to preventing significant floodplain erosion during a major flood (Griffin and Smith 2004). Intra- and inter-specific variation in stem density, diameter and rigidity likely generate differences and similarities in the hydraulic effects of riparian vegetation (Kean and Smith 2004, Griffin et al. 2005). Nonetheless, high stem density in stands of *Tamarix* may increase its influence on sediment deposition and retention relative to low density, mature cottonwood gallery forests, for instance (Hereford 1984, Pollen-Bankhead et al. 2009).

Observations of channel narrowing along western American rivers, concurrent with the spread of *Tamarix*, have prompted debate about the degree to which *Tamarix* controls or contributes to decreased width (Graf 1982, Hereford 1984, Everitt 1998). Hydrologic changes that reduce flood intensity and thereby decrease erosion and sediment transport are sufficient to produce narrowing in the absence of new stands of riparian vegetation. However, dam construction or periods of drought that generate such hydrologic change overlapped with *Tamarix* establishment on many rivers, complicating attribution of causality (Figures 3.3 and 3.4). Narrowing and dense floodplain vegetation are of particular concern when they increase hydraulic roughness, flood stage, and overbank inundation. Such patterns have been observed in association with *Tamarix* establishment along western rivers (Blackburn 1982, Graf 1982). Thus, a number of studies have sought to disentangle whether narrowing occurred largely independently of *Tamarix*, primarily because of *Tamarix* establishment, or as hydrologic changes combined with *Tamarix* establishment.

Several sections of the Green River, Utah, have been the focus of research into the relationship between changing flow regimes, fluvial geomorphology and *Tamarix*. Graf (1978) proposed that *Tamarix* cohorts established on islands, marginal bars and alluvial fans when

several years of below average peak-flow followed a flood year. He suggested that a period of climatically reduced discharge during the early 1930s likely promoted stabilization of previously dynamic channel and floodplain features by *Tamarix*, leading to subsequent sediment deposition and aggradation (Figure 3.3). The finer temporal resolution of research by Allred and Schmidt (1999) provided additional insight into the extent of narrowing that followed construction of the upstream Flaming Gorge Dam (FGD; completed in 1963). Analysis of hydrologic records combined with excavations of *Tamarix* root crowns and mapping of floodplain stratigraphy enabled these authors to associate the stabilization and vertical accretion of previously transient channel formations with increased roughness and reduced velocity surrounding *Tamarix*. In agreement with the hypothesis that *Tamarix* acted as a feedback on underlying hydrogeomorphic changes, they concluded that a large reduction in bankfull channel width (the distance encompassed by typical high flows) had occurred during the 1930s, coincident with climate-induced flow reductions and initial *Tamarix* colonization of the study area, and that dam-induced flow alteration contributed to a second phase of narrowing after 1963 when *Tamarix* was already abundant. Grams and Schmidt (2002, 2005) noted that vegetation, including *Tamarix*, played a role in the development of the post-dam landforms below FGD. They concluded that *Tamarix* had contributed to narrowing in some reaches, but peak flow reductions, sediment loads and reach-scale variation in width and sediment input (e.g., alluvial fans) ultimately moderated the type and magnitude of channel change. Also on the upper Green River below FGD, Birken and Cooper (2006) demonstrated a clear relationship between *Tamarix* recruitment and an inter-annual flow pattern consisting of a large magnitude flood followed by several years of lower peak discharge. Stratigraphic and dendrochronologic records (based on dating tree growth rings) of *Tamarix* establishment both before and after closure of FGD supported the conclusion that

*Tamarix* contributed to narrowing prior to dam-caused flow alteration. Nonetheless, these authors observed a post-dam shift in the position of *Tamarix* establishment from higher, more marginal sites to lower surfaces nearer the contemporary active channel (Birken and Cooper 2006). A fine scale dendrogeomorphic analysis of floodplains in Brown's Park and Lodore Canyon (below FGD) corroborated this observation, indicating that flow alteration by FGD promoted the formation of lower, inset deposits suitable for *Tamarix* establishment (Alexander 2008). Most of the post-FGD accretion on these surfaces resulted from controlled flood releases that have further isolated stands of established vegetation from the river rather than removing them. Consequently, Alexander (2008) attributed post-dam narrowing fundamentally to regulation of high flows, with the resulting alteration of geomorphic processes enhanced by *Tamarix*.

Studies in the Rio Grande watershed have also clarified interactions between *Tamarix* spread, hydrologic alteration, and fluvial geomorphic dynamics. Within the central Rio Grande (New Mexico and western Texas), Everitt (1998) described a series of human modifications (dams, channelization, levees, floodplain agriculture) that reduced flows and decreased sediment movement both prior to and during the initial spread of *Tamarix* in the 1930s. This chronology suggested that *Tamarix* did not play a primary role in channel narrowing and aggradation, though it did not exclude *Tamarix* as a factor in these processes. Friedman et al. (2005b) observed that *Tamarix* establishment and concurrent decreases in peak flow promoted narrowing and hindered lateral channel migration along the unregulated lower Rio Puerco, a tributary to the Rio Grande. Modeling and observation of erosion along reaches where *Tamarix* was removed have strengthened the conclusion that *Tamarix* significantly reduces the susceptibility of banks and floodplains to erosion and increases sediment deposition in this system (Griffin et al. 2005,

Vincent et al. 2009). In the Big Bend (southwestern Texas) section of the Rio Grande, recent research has analyzed how reduced peak and mean flows generated a series of changes in channel morphology that were enhanced by *Tamarix* establishment (Dean and Schmidt 2011, Dean et al. 2011). Periodic large floods historically maintained a wide sandy channel in this system, similar to other arid and semi-arid rivers (Schumm and Lichty 1963, Graf 1982, Martin and Johnson 1987). Upstream dams and diversions, however, reduced overall discharge volume as well as flood frequency during the early and mid 20<sup>th</sup> century. Subsequent channel aggradation and narrowing resulted in over-bank flooding despite diminished flows, and *Tamarix* establishment contributed to narrowing by promoting the vertical accretion of channel bars and inset surfaces (Dean and Schmidt 2011). River regulation was important to the underlying alteration of flow and sediment regimes on the Rio Grande (Dean and Schmidt 2011), but Dean et al. (2011) proposed that comparable processes might occur in unregulated rivers, particularly following a rapid climate change toward warmer and drier regimes.

Collectively, these studies support the idea that *Tamarix* and other species of riparian vegetation have acted as a positive feedback on channel narrowing processes in western rivers, building on climate and dam-induced hydrologic changes by stabilizing in-channel forms and increasing vertical accretion (Figure 3.3 and 3.4, Friedman et al. 1996, Allred and Schmidt 1999, Friedman et al. 2005b, VanLooy and Martin 2005, Sandercock et al. 2007, Dean et al. 2011a, b). As a caveat to this conclusion, these interactions vary with watershed and site-specific differences in a range of factors, including local climate, valley constraint, and human floodplain uses. Furthermore, the long-term interplay between *Tamarix* and channel form continues to develop with ongoing changes in the river environment.

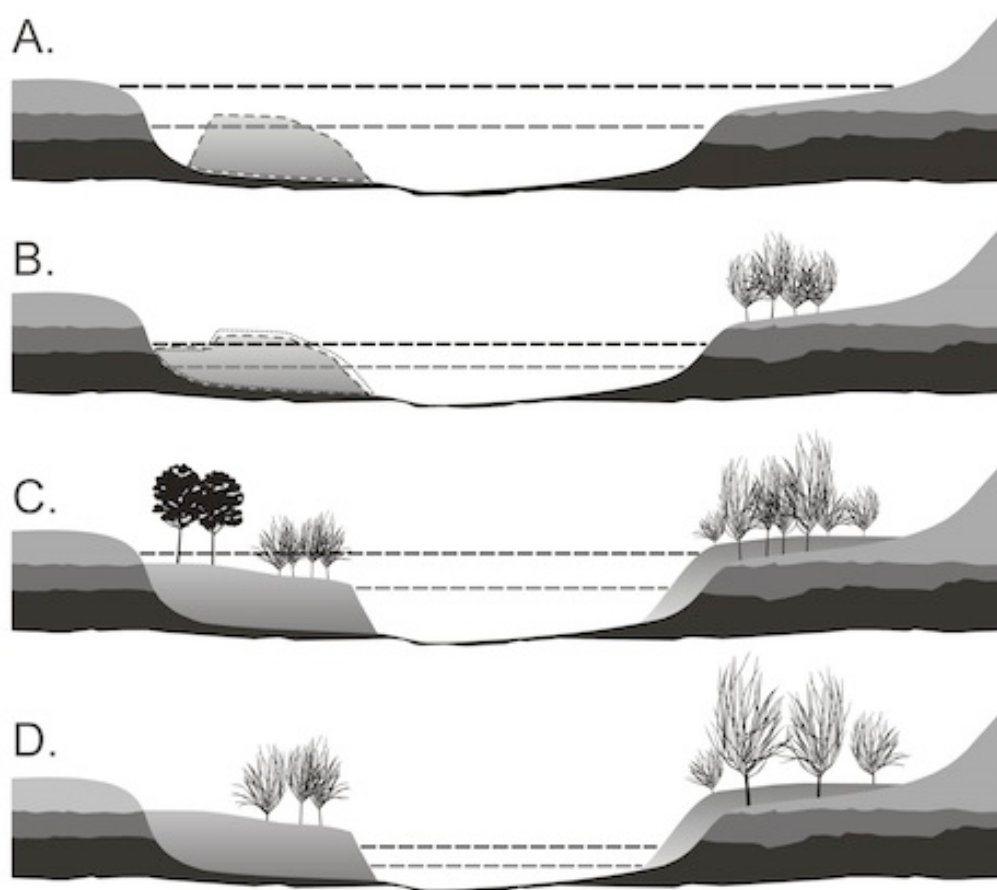
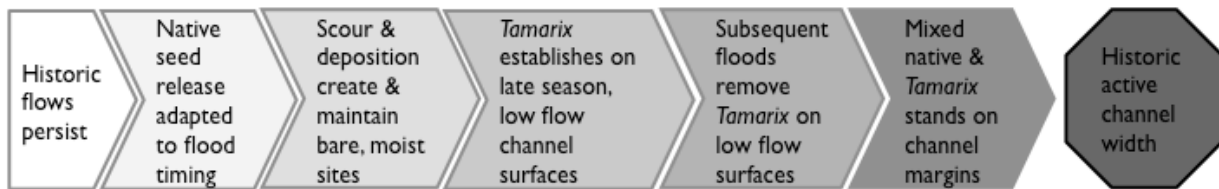
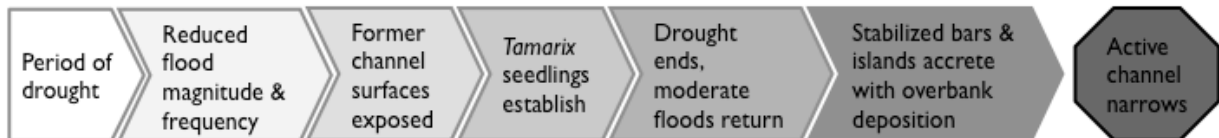


Figure 3.3: Channel form changes in response to flow alteration and *Tamarix* establishment. Shifts in form for a hypothetical river channel in the southwestern United States are illustrated over several decades, relative to a combination of reduced flooding and the establishment of riparian vegetation such as *Tamarix*. The heavy dashed lines indicate large magnitude flood flows (dark gray) and typical annual high flows (lighter gray). A) The uppermost panel illustrates a period in which occasional, very large floods mobilized sediments across a wide cross-sectional area, including transient bars and islands within the channel and at its margins (gray polygon). Riparian vegetation may occur along the river, but intense floods limit its persistence within this area. B) In the second panel, a period of drought, upstream dams, or a combination of the two reduce flood magnitudes, thereby decreasing the movement of formerly mobile surfaces and exposing previously inundated and scoured areas to colonization by riparian vegetation, such as *Populus*, *Salix*, or *Tamarix*. C) Subsequently higher flows, shown in the third panel, tend to narrow the channel width, as reduced velocity and shear stress within new stands of vegetation increase sediment deposition and reduce erosion. In addition, infilling and accretion may occur on surfaces that initially stabilized independently of vegetation establishment, with colonization by native trees and *Tamarix* extending into these areas. Riparian trees such as *Tamarix* are often partially buried by sediment over time, so that stems at the present ground surface are well above the surface on which the tree originally established. In conjunction with extensive root networks, these below-ground portions of the plant may reinforce banks and floodplains, further reducing erosion. D) The fourth panel illustrates a possible future scenario in which drought and dams eliminate any significant floods and reduce baseflow. This might result in floodplains dominated by mature *Tamarix*, possibly at lower abundance, after native trees with less tolerance of drought and lowered groundwater levels are lost.

#### Historic flow regime intact



#### Unregulated river and floodplain, flow alteration



#### Regulated river and floodplain, flow alteration

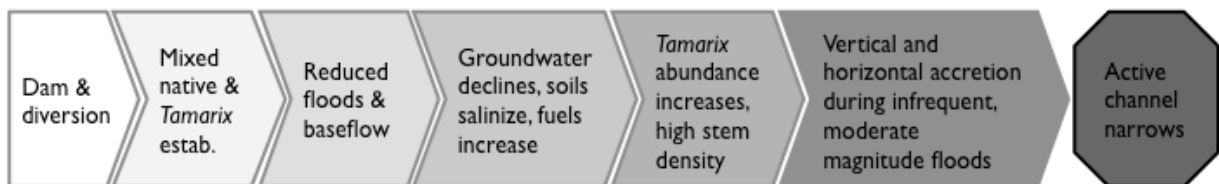


Figure 3.4: Conceptual pathways of channel alteration. In the upper scenario, persistence of the historic natural flow regime maintains abundant native vegetation and historic active channel width, with *Tamarix* present but not dominant due to its establishment primarily in lower elevation sites that are vulnerable to subsequent scour and inundation. In the middle scenario, climate shifts alter flood magnitude and frequency as well as possibly lowering late-season flow (not shown). *Tamarix* seedlings establish in areas previously subjected to higher intensity flooding, and subsequent smaller peak flows result in accelerated aggradation in *Tamarix* stands. This eventually produces higher, drier, and less connected surfaces on which *Tamarix* may persist and dominate. In the bottom scenario, flow regulation (potentially in conjunction with sediment trapping in reservoirs, not shown) reduces flood magnitudes and facilitates the establishment of *Tamarix* and native species within former active channel habitats. Over time, diminished flows favor *Tamarix* persistence but the presence of riparian vegetation reduces erosion and promotes sediment deposition during occasional high flows to enhance narrowing of the active channel.



## ***Tamarix* And Future Floodplain Dynamics**

Extensive research in varied riverine settings has led to a clearer understanding of the interacting hydrogeomorphic factors promoting *Tamarix* naturalization and the mechanisms by which *Tamarix* influences channel morphology. Such insights are critical to addressing the future of these reciprocal relationships as western river ecosystems continue to change (Auerbach et al. *in press*). In particular, ongoing climate shifts, biological interactions, and *Tamarix* control and riparian restoration efforts are likely to directly determine or indirectly mediate the role of *Tamarix*.

Changes in CO<sub>2</sub> concentration, temperature, precipitation and watershed hydrology may combine in complex ways to affect the extent and abundance of *Tamarix*, but current projections suggest that warming and altered drought frequency may facilitate further expansion throughout the western U.S. (Perry et al. *in press*). Increases in minimum winter temperatures, which currently limit *Tamarix* latitudinal and elevation extent, could enable *Tamarix* to extend its range northward or into higher elevation reaches (Sexton et al. 2002, Friedman et al. 2008). Climate change is expected to influence stream flow timing and variability as well as mean annual runoff in the western U.S. (Barnett et al. 2008, Luce et al. 2009, Perry et al. *in press*). Earlier spring snowmelt is projected to affect the timing and magnitude of peak flow, potentially resulting in earlier and smaller snowmelt runoff floods (Mote et al. 2005). Summer low flows are also expected to decrease in rivers throughout the West (Dettinger et al. 1995, Cayan et al. 2001, Luce et al. 2009). Water demands of the rapidly growing population in this region may increase the intensity of regulation on some rivers, particularly if more frequent droughts stress the existing supply infrastructure (Palmer et al. 2009, Sabo et al. 2010). Thus, increasing intermittency (Stromberg et al. 2007b), later peak flows, or reduced growing season flows

(Merritt and Poff 2010), could favor greater *Tamarix* abundance and dominance throughout the region it already occupies, while disfavoring native riparian species with earlier seed release or less drought tolerance.

Management decisions may exacerbate or mitigate such outcomes as future flow regulation affects the flow regime features that influence riparian plant community composition (Merritt et al. 2010, Auerbach et al. *in press*). For instance, the elimination of flood-caused physical disturbance and inundation may lead to more establishment opportunities for shade-tolerant species such as Russian Olive (*Elaeagnus angustifolia*) than for disturbance-adapted *Tamarix* or other pioneer trees and shrubs (Katz and Shafroth 2003, Reynolds and Cooper 2010, but see Mortenson and Weisberg 2010 for an alternative view). Alternatively, seasonal dam releases and rates of recession timed to favor cottonwood establishment may promote its recruitment along some reaches (Shafroth et al. 1998, Rood et al. 2005, Merritt and Poff 2010). The assessment and implementation of environmental flows, designed to accommodate the hydrology-related life-history requirements of species of concern, has emerged as an important frontier in river research and management (Poff et al. 2010). While it is unlikely that even very aggressive flow management would extirpate or eliminate *Tamarix* from western U.S. rivers (Merritt and Poff 2010), this strategy may substantially improve conditions for native species and thereby restrict dominance by *Tamarix* within riparian zones (Nagler et al. 2005, Stromberg et al. 2007a, Shafroth et al. 2010a).

A variety of other *Tamarix* control and riparian restoration efforts may also reduce the abundance of *Tamarix* within floodplains it already occupies or hinder its colonization of additional areas (Shafroth et al. 2010b, Shafroth et al., this volume), and therefore influence hydrogeomorphic feedbacks along these reaches. Herbicidal control of *Tamarix* along the Rio

Puerco in New Mexico permitted substantial lateral bank erosion during a major subsequent flood (Vincent et al. 2009). Whereas the sprayed reach experienced an 84% increase in mean width, unsprayed reaches upstream and downstream experienced little erosion. Vincent et al. (2009) proposed that the character and magnitude of this erosional response was likely related to the flashiness of flow on the mostly unregulated Rio Puerco as well as floodplain attributes such as the prevalence of sand. Reinforcing the importance of such factors, high flows produced relatively modest channel adjustments following mechanical *Tamarix* removal within Canyon de Chelly, Arizona (Jaeger and Wohl 2011). Despite the complete extraction of individual trees in some treatments, the lower flow competence likely combined with an entrenched channel and more cohesive floodplain materials to limit erosion in this system (Jaeger and Wohl 2011). By contrast, work in Dinosaur National Monument demonstrated increased survival of box elder (*Acer negundo*) under *Tamarix* canopies and the possibility of promoting desired vegetation composition without disturbing floodplain sediment (DeWine and Cooper 2010). Integrating control efforts with hydrogeomorphic regimes may affect the success of projects. For instance, the timing and magnitude of floodplain inundation after *Tamarix* removal will likely help determine the species composition of the subsequent plant community. Finally, adaptive river management requires research into the hydrogeomorphic consequences of herbivory by the rapidly spreading *Tamarix* leaf beetle (*Diorhabda spp.*; Lewis et al. 2003, Hudgeons et al. 2007). Large stands of defoliated or dead *Tamarix* now occur along numerous western rivers and streams (O'Meara et al. 2010), but how these areas will respond to flow variation or support native tree establishment remains poorly understood. Key uncertainties for beetle-colonized *Tamarix* stands include the degree to which floods will mobilize sediment by removing standing dead trees or weakening subsurface root reinforcement, the hydraulic similarity of vegetation

that replaces *Tamarix*, and how such changes might scale up to influence regional patterns of channel change. Taken together, these issues suggest the importance of planning restoration efforts within the context of intrinsic watershed attributes (e.g., drainage area, geology, land cover) and complementary management actions (e.g., dam operation, active re-vegetation) affecting the target reach (Shafroth et al. 2008).

## **Conclusion**

Flow and sediment regimes fundamentally affect riparian plant communities, and influence the recruitment, survival and dominance of *Tamarix* along western U.S. rivers. Along many of these rivers, hydrologic alteration resulting from climate shifts, land use changes, and water control infrastructure contributed to the spread of *Tamarix* and facilitated its subsequent influence on channel form and function. Nonetheless, as demonstrated by its colonization of both regulated and free-flowing rivers, *Tamarix* possesses a combination of morphological and physiological traits that are well-suited to a wide range of conditions found on contemporary Western floodplains.

Like native *Populus* and *Salix*, *Tamarix* requires bare, moist surfaces for establishment, such as those created by flood disturbance. However, the timing of flood peaks and subsequent recession may favor *Tamarix* when the availability of establishment sites matches its pattern of seed release more closely than that of native plants. In addition, reduced flooding and baseflows may favor *Tamarix* relative to native *Populus* and *Salix* due to its greater tolerance of drought, soil salinity and groundwater fluctuation. The influence of *Tamarix* on local erosional and depositional processes varies according to interactions between its biology (e.g., stem density

and size), site characteristics (e.g., valley constraint and prevailing sediment types), and flow regime (e.g., flood frequency and magnitude).

It is likely that *Tamarix* will remain an important component of riparian zones in the American West, though control efforts coupled with flow management tailored to the needs of native species may hinder its dominance of new floodplains or those it currently occupies. The introduction and spread of *Tamarix* has provided a unique opportunity to advance understanding of basic relationships between hydrologic, geomorphic and ecological processes in rivers. *Tamarix* continues to provide a focus for studies of the reciprocal relationship between riparian trees and hydrogeomorphic dynamics, as climate change and additional water development reshape river ecosystems in the American West.

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## CHAPTER 4: ASSESSING *TAMARIX* INVASION RISK RELATIVE TO CLIMATE CHANGE AND WATER MANAGEMENT

### Summary

Anticipating riparian responses to climate change amidst widespread river regulation poses a major research challenge. The spread of non-native species has affected riverine ecosystems worldwide, and hydrologic alteration due to changing temperature, precipitation, and water management is expected to influence ongoing and future biological invasions. In the western United States (U.S.), introduced woody plants in the *Tamarix* genus have naturalized along many rivers, often in conjunction with flow modification. In some cases, *Tamarix* now dominates the composition of riparian vegetation communities, modifying biodiversity and ecosystem service production. Temperature and moisture availability have been associated with the current landscape-scale distribution of *Tamarix*, and warming trends and shifts in precipitation therefore create the possibility that its range will expand. However, realized *Tamarix* population growth within newly suitable potential habitat is likely to depend on the flow regimes attributes that drive recruitment and mortality. *Tamarix* effectively colonizes riparian zones as a result of reproductive adaptations to fluvial disturbance that include rapid maturation and the release of many small seeds over a prolonged annual period, and its morphological and physiological adaptations confer greater tolerance of water stress and soil salinity than native pioneer trees and shrubs. Thus, water management in a hotter, drier future may consequently favor *Tamarix* persistence relative to native riparian vegetation, but the risk of further invasion is related to whether these altered environmental drivers also generate sufficient establishment opportunities. I applied a process-based modeling approach in an effort to characterize this



invasion risk within a basin, the Upper Green River (UGR) in southwestern Wyoming (U.S.), that is currently thermally marginal for *Tamarix* but is projected to become increasingly suitable. At a watershed scale relevant to management, this simulation framework linked climate projections, hydrologic processes informed by human water demand, fluvial geomorphic drainage network divisions, and flow-mediated changes in riparian populations. Simulated outcomes indicated the potential for interacting flow regime attributes to mediate invasion risk, and suggested that a hotter, more arid climate may not necessarily facilitate *Tamarix* spread, particularly along regulated, perennial, snowmelt-driven rivers. Wetter climate scenarios produced future annual high flows that were often on the order of the largest peaks during the historic period, and the frequency and extent of establishment opportunities for *Tamarix* could increase within the UGR if such floods suffice to mobilize sediment and disturb riparian zones. Yet, the consistently earlier timing of snowmelt floods projected across climate and management scenarios could counteract the effects of increased high flow magnitude if overbank events substantially precede the period of *Tamarix* seed availability, and river stage declines leave newly created bare patches too dry for establishment. This research demonstrated how a watershed scale, process-based modeling approach could capture important features of the hydrogeomorphic variation likely to influence the risk of non-native species spread in river corridors. Such an approach could inform assessment of the ecological impacts of climate change and water management on riparian zones.

## Introduction

The spread of non-native species threatens freshwater ecosystems globally, resulting in potentially irreversible genetic losses and costly management consequences (Dudgeon et al. 2006, Carpenter et al. 2011). Water control infrastructure such as reservoirs, canals, and levees can promote this biotic invasion by altering flow regimes, impairing and fragmenting habitat, and facilitating the movement of intentionally or inadvertently introduced organisms (Johnson et al. 2008). Furthermore, climate changes that weaken thermal constraints on cold-intolerant exotic species may exacerbate the influence of river regulation on the invasion process (Rahel and Olden 2008). The perceived likelihood of water scarcity and flood damage due to intensified drought or extreme precipitation may restrict the operational flexibility of existing dams or prompt calls for new dam construction, thereby interfering with efforts to control or prevent novel species (Figure 4.1). Introduced species spread throughout many of the highly regulated river basins of western North America during the 20th century, and the human demand for water under a warming climate is likely to influence patterns of further invasion during coming decades (Gleick 2010, Sabo et al. 2010).

In particular, important questions concern the future of riparian vegetation communities that are increasingly composed of non-native species (Friedman et al. 2005, Ringold et al. 2008, Stromberg et al. 2013). Plants at the boundary between terrestrial and aquatic systems support rich ecological assemblages, mediate in-channel conditions (e.g., stream temperatures, sediment loads and woody debris), and play a vital role in reciprocal nutrient cycling (Gregory et al. 1991, Naiman and Decamps 1997, Baxter et al. 2005). In the arid and semi-arid Western landscape, riparian trees and shrubs may constitute the only vegetation of significant stature, providing critical habitat for a range of terrestrial vertebrates and invertebrates as well as influencing

recreational and cultural benefits (Patten 1998, Loomis et al. 2000). Yet, the dynamic character of riparian zones and their capacity to act as dispersal corridors render these vegetation communities vulnerable to invasion along free-flowing rivers (Naiman and Decamps 1997, Nilsson and Svedmark 2002). Flow regulation may create additional colonization opportunities for novel species around reservoirs and in downstream reaches subject to altered stress and disturbance regimes (Nilsson and Svedmark 2002, Richardson et al. 2007). Thus, ongoing changes in the prevalence of non-native riparian vegetation along Western rivers are expected to result from the interactions between temperature increases that directly affect plant physiology and phenology, shifts in the amount and seasonality of precipitation that affect runoff, and the widespread flow alteration due to existing dams, diversions and groundwater pumping (Stromberg et al. 2010, Perry et al. 2012).

These interacting factors are of prominent interest as they relate to the pioneer trees and shrubs in the introduced genus *Tamarix*, including the species *ramosissima* Ledeb., *chinensis* Lour., and hybrids (Gaskin and Kazmer 2009, Shafroth et al. 2010). Introduced during the late 19th and early 20th century, often with the intent of reducing sediment inputs by stabilizing erosive banks, *Tamarix* initially established self-sustaining populations in the arid Southwest (Graf 1978, Everitt 1980, Graf 1982, Everitt 1998). Relative to common native riparian trees in the *Populus* and *Salix* genera, *Tamarix* displays greater tolerance of water stress and elevated soil salinity. In addition, saplings and adults effectively recover from flood disturbance by re-sprouting, and plants may rapidly reach sexual maturity to release copious, easily dispersed seeds over a relatively long annual duration (Glenn and Nagler 2005). These functional traits led to colonization of additional rivers, and a survey conducted throughout the West found *Tamarix* to

be the third most frequently occurring and second most dominant (measured as mean relative abundance) woody riparian plant by the early 2000s (Figure 4.2; Friedman et al. 2005).

This fairly rapid expansion and the formation of dense monotypic stands along some reaches prompted increasing concern regarding the undesirable effects of *Tamarix* on several management objectives (Graf 1978, Di Tomaso 1998). A number of studies initially suggested these plants were responsible for markedly high rates of water loss through evapotranspiration, and *Tamarix* was proposed to cause various impacts such as soil salinization, channel narrowing, and native *Populus* and *Salix* decline. Accordingly, removal programs involving mechanical clearing, herbicide application, and biological control were initiated, originally with the target of water “salvage” for consumptive use (Shafroth et al. 2005). However, improved testing methods have lowered estimates of water loss and revealed that impacts on riparian fauna are not uniformly negative (Stromberg et al. 2009). Additional research has supported the conclusion that *Tamarix* was well suited to take advantage of the altered riverine conditions produced by dams, climate trends, and land use changes during the 20th century, but that many of the negative patterns attributed to *Tamarix* were driven predominantly by these underlying factors rather than the plant per se (Shafroth et al. 2005, Shafroth et al. 2008, Stromberg et al. 2009, Sher and Quigley 2013). Although this refined scientific perspective has spurred recognition of the need for riparian restoration to encompass a broader set of goals than simply *Tamarix* removal (and to avoid favoring non-native herbaceous plants in freshly disturbed areas), stands dominated by *Tamarix* clearly result in different habitat attributes than mixed or fully native stands (e.g., fewer tall snags with nest cavities and less palatable leaf litter), and control efforts continue, for example prompted by diminished recreational values (Shafroth et al. 2008, Shafroth et al. 2010).

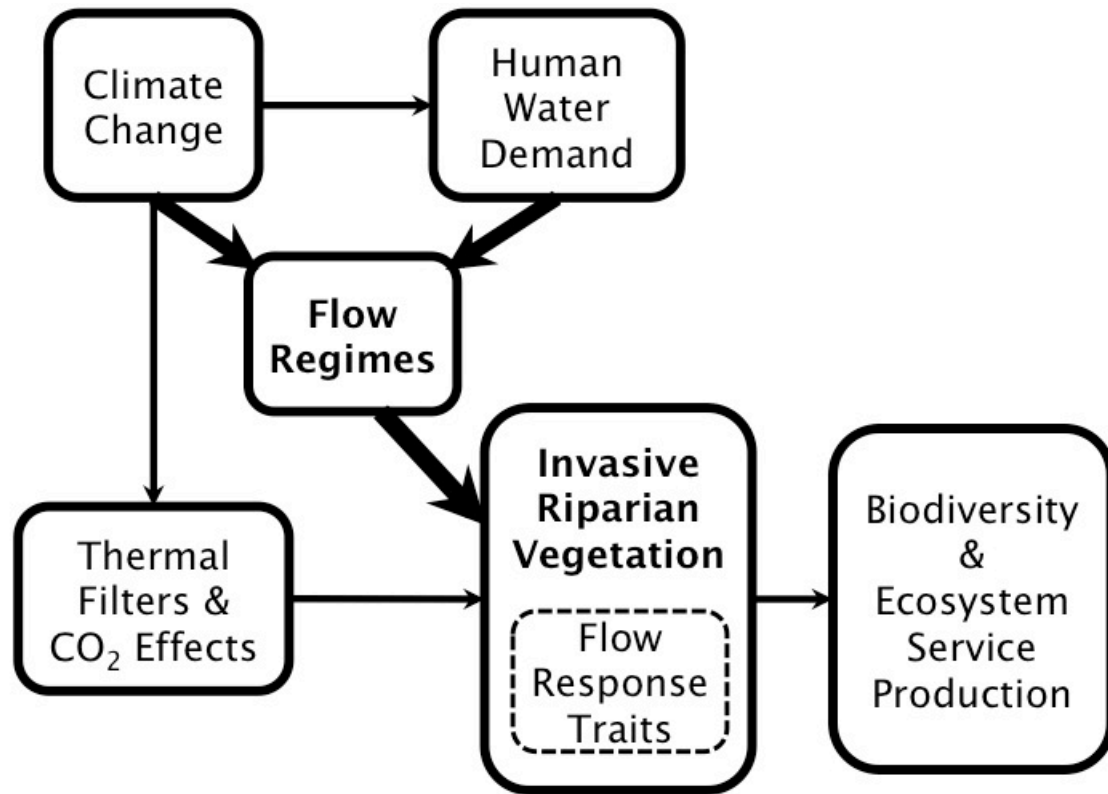


Figure 4.1: Dams and other water control infrastructure have already significantly altered flow regimes along many rivers, increasing the vulnerability of naturally dynamic riparian vegetation communities to invasion by non-native species. In addition to shifting the limitations on riparian trees and shrubs related to temperature and carbon dioxide, future climate changes will alter both the supply of and demand for water in many basins, thereby combining with existing and new infrastructure to influence the flow regimes that act as a primary control on riparian zone plant composition and abundance. Though opportunities may exist for management to mitigate undesirable changes in flow, these interacting changes in environmental drivers may increase the risk of dominance by invasive species with less desirable attributes for biodiversity or ecosystem service provision. See Perry et al. (2012) for further discussion of these interactions in the arid and semi-arid portions of western North America.

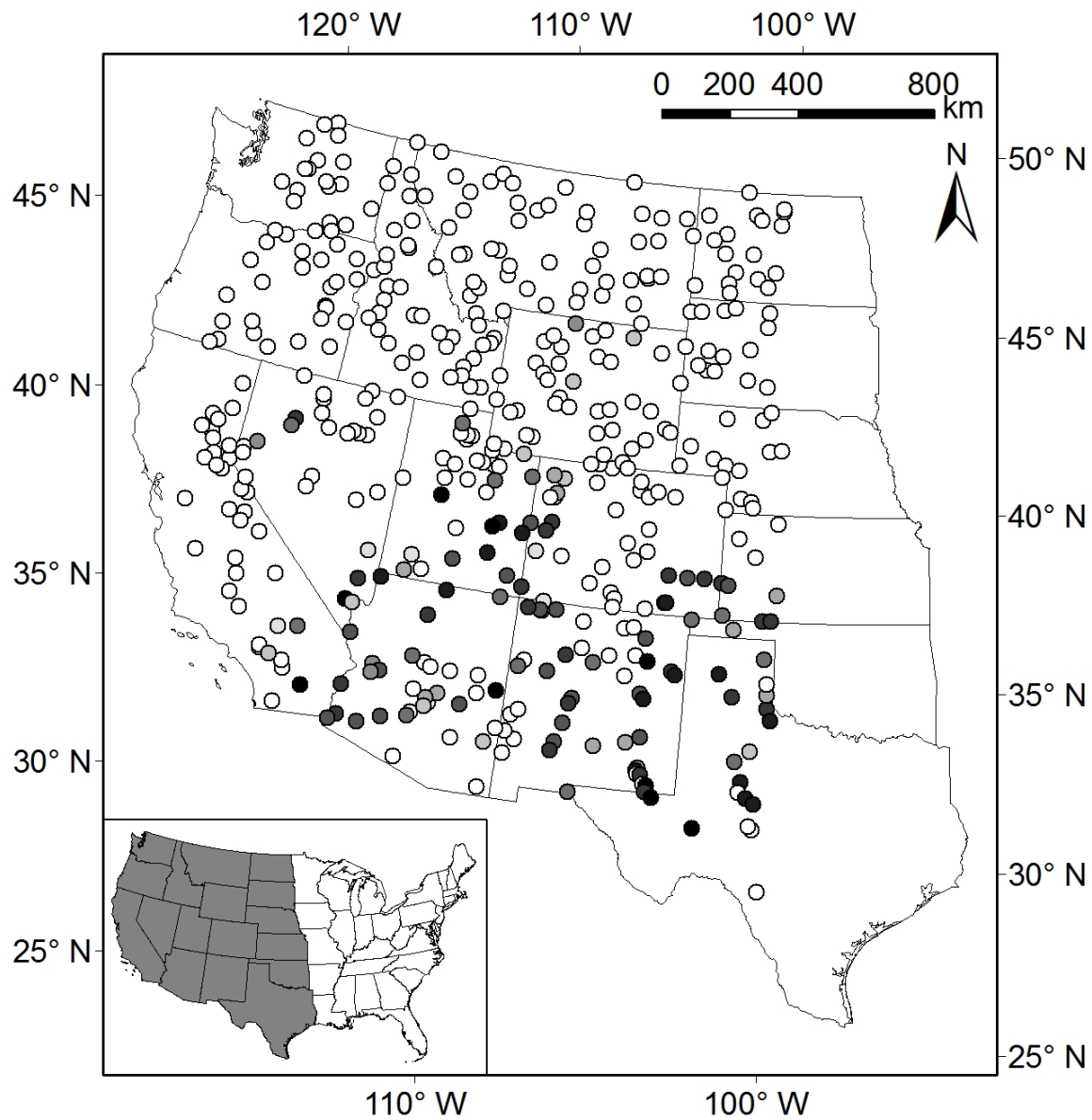


Figure 4.2: Abundance of *Tamarix* along riparian reaches associated with USGS streamflow gaging stations throughout western North America. Open circles mark sites at which *Tamarix* was not observed, and filled circles indicate its presence, with darker shading for greater abundance. Modified from Friedman et al. (2005).

Given this background of controversial and changing perceptions, research is needed into the degree to which interacting climate change and water infrastructure will enable Tamarix to expand into new territory or to reach greater dominance where it now occurs sporadically. In the context of ongoing management targeting Tamarix, this possibility raises the questions of whether and how resources should be allocated to prevent or slow encroachment within potentially suitable areas (i.e., Is further invasion likely? What efforts, if any, should be made to prevent it? How should Tamarix control efforts rank among the many priorities facing managers?). The first step to addressing this question is to characterize these areas, and this task implies the use of a modeling framework.

Distribution models relate the values of a set of environmental variables to known species occurrences, thereby offering a means to describe the suitability of other locations at which the variables can be measured (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). Large-scale species distribution models based on climate and land cover attributes have approximated Tamarix range under historically observed conditions (Morissette et al. 2006, Evangelista et al. 2008, Jarnevich et al. 2011, Nagler et al. 2011). In accordance with expectations for this arid and semi-arid riparian plant, models at the sub-continental scale have found the occurrence of Tamarix to be favored by higher growing degree-days, warmer minimum temperatures, lower precipitation, and decreased distance to surface water (Friedman et al. 2005, Jarnevich et al. 2011, Nagler et al. 2011, McShane et al. In review). A comparable set of variables informed the climate envelope model developed by (Kerns et al. 2009) for the region east of the Cascades in Oregon, Washington and Idaho. Viewed as the periphery of current Tamarix distribution, this area had received limited research attention, but these authors compiled records of Tamarix presence to generate a model from historic (1971-2000) maximum and minimum

temperature and precipitation. Extrapolated values of these variables derived from two warming scenarios then substantially increased the modeled extent of suitable habitat area. While noting the uncertainty associated with both the climate projections and the included set of environmental factors, these authors proposed that model outcomes served to highlight the possibility of increased vulnerability to *Tamarix* expansion within the study region. They noted that awareness of risk was a necessary preliminary to discussions of proactive management.

A similar conclusion of increased vulnerability is plausible over a broader geographic area in light of the current distribution of *Tamarix* (Nagler et al. 2011). Studies examining cold-hardiness (Sexton et al. 2002, Friedman et al. 2008) and drought tolerance (Cleverly et al. 1997, Horton et al. 2001, Glenn and Nagler 2005, Lite and Stromberg 2005) link the climate variables in distributional models to physiological mechanisms of growth and survival (Kearney and Porter 2009), providing support for the working hypothesis that the projected warming and aridity over much of western North America will expose watersheds to the possibility of greater *Tamarix* cover (Stromberg et al. 2010, Perry et al. 2012). Yet, within a thermally suitable region, the risk of *Tamarix* invasion will depend on the hydrogeomorphic variation that shapes river ecosystems and drives the colonization, establishment and persistence of riparian vegetation (Poff 1997, Poff et al. 1997, Naiman et al. 2005, Merritt 2013, McShane et al. In review). Though essential processes in riverine environments have not informed prior models of *Tamarix* spread under climate change, the concept of a flow niche provides a means to account for hydrogeomorphic variation and the influence of hydrologic alteration, while enabling invasion risk to be modeled at the spatial extents relevant to whole-basin management. The flow niche concept is rooted in the principle that the life history and morphology of riverine and riparian taxa are adapted to the flow regime attributes of discharge magnitude, timing, duration,



frequency and rate of change (Lytle and Poff 2004, Merritt et al. 2010). These flow niche dimensions are measured by a host of variables such as the size and seasonality of annual high flows, and the effects of particular flows are mediated by response traits such as tolerance of flood disturbance. The assumption that population change varies with the disparity between the flow response traits characterizing a species and the flow regime along a river reach then provides the conceptual basis for an assessment of invasion risk relative to the hydrogeomorphic processes governing mortality and recruitment.

A number of studies have established that the character of flooding and growing season discharge are key dimensions of the flow niche for *Tamarix*, but effects over gradients of flow magnitude are not simple (Figure 4.3, Table 4.1). Floods that scour bottomland surfaces and deposit fresh alluvial sediment create regeneration opportunities for disturbance-adapted riparian plants such as *Tamarix*, but they may also limit populations if inundation and shear forces kill new seedlings or existing trees (Scott et al. 1996, Glenn and Nagler 2005, Merritt et al. 2010). Bare, moist patches provide the plentiful light and moisture required by germinating seeds, but seedling survival depends on a rate of stage recession and soil water decline that stays proportionate to the rate of root elongation, as well as the absence of subsequent burial or shear (Shafroth et al. 1998, Sher et al. 2000). Though greater flood magnitude may increase the likelihood of disturbance leading to suitable establishment sites, reduced flows during periods of drought or following dam construction have also produced pulses of *Tamarix* recruitment along some Western rivers, as former active channel surfaces were exposed to colonization (Auerbach et al. 2013). Moreover, lower flood magnitudes that reduce disturbance mortality may permit greater *Tamarix* abundance by increasing other factors that can favor *Tamarix* over native woody pioneers, such as flow intermittency or soil salinization with loss of flushing flows (Stromberg et

al. 2007b, Merritt and Poff 2010, Stromberg et al. 2010, Nagler et al. 2011). In addition, though *Tamarix* releases seeds later into the growing season than native pioneer species with reproductive phenology specialized to spring snowmelt runoff, the within-year timing of floods can interact with high flow magnitude and frequency to determine the availability of suitable bare, moist patches relative to the presence of viable seeds (Shafroth et al. 1998, Glenn and Nagler 2005, Beauchamp and Stromberg 2007, Stromberg et al. 2007a, Stromberg et al. 2007b).

Table 4.1: Hypothesized effects on establishment, abundance and dominance of changes in the key *Tamarix* flow niche dimensions of annual high flow magnitude and timing.

<b>Flow niche dimension</b>	<i>Tamarix</i> response		
	<b>Establishment</b>	<b>Abundance</b>	<b>Dominance</b>
Peak magnitude & variability	Decreases possibly favorable during transient colonization of former active channel surfaces, but long-term flood suppression may limit colonization opportunities	Reduced flood disturbance likely favorable due to decreased mortality	Decreased flooding potentially favorable if associated with salinizing soils that limit competitors, but potentially unfavorable relative to later-successional, shade-tolerant species
Peak timing	Later high flows potentially favorable, but floods outside of the period of seed release may limit recruitment or favor other species	Indirect effects via establishment and potential interactions with native riparian species	Follows from establishment effects

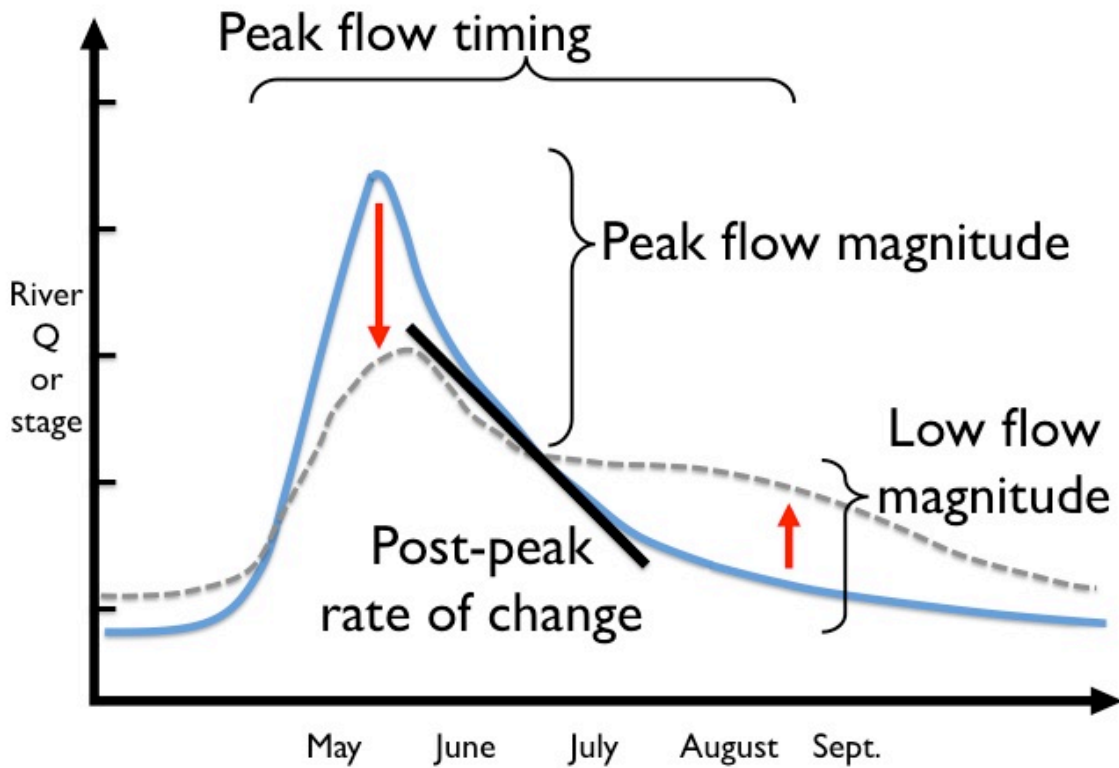


Figure 4.3: Key within-year flow niche dimensions for *Tamarix* relative to an archetypal annual hydrograph for a snowmelt river, with (grey dashed line) and without (solid blue line) typical water infrastructure effects. The magnitude and variability of annual flood peaks influences the availability of suitably bare, moist establishment sites. The timing of such peaks relative to the period of seed release and the post-flood rate of stage recession influence whether sediments contain adequate moisture for germination and root elongation. The magnitude and variability of low flows may also influence the water stress under which seedlings must grow. See (Shafroth et al. 1998) and (Braatne et al. 2007) for discussions of the general applicability of these “extended Recruitment Box” concepts to pioneer riparian vegetation. Dam storage and irrigation demands may alter the natural pattern of a regular spring peak, a gradual post-flood recession and a summer low flow period by reducing peak flows and potentially elevating low flows (also the result of some trans-basin diversions). Though the ecological effects of these changes vary considerably with local fluvial geomorphic conditions and may include a pulse of *Tamarix* recruitment on former active channel surfaces, stabilized flood peaks may disfavor the long-term regeneration of disturbance adapted riparian plants such as *Tamarix*, while potentially increasing the abundance of later successional trees with shade-tolerant recruitment. In addition to within-year patterns, the year-to-year sequence of these factors is also likely to influence *Tamarix* invasion by determining whether germinating seeds reach reproductive status. Colonization has been positively associated with a pattern of several smaller flood years following a larger one. Simulations described in this chapter emphasize the between-year magnitude and within-year timing of annual high flows.

Though abundant *Tamarix* may follow from alternative pathways, the size and sequence of annual high flows have been clearly associated with colonization success, and these factors are therefore important influences on invasion risk (Cooper et al. 2003). For example, corroborating previous findings for the importance of both single-year peaks and interannual flow sequences (Cooper et al. 2003), Birken and Cooper (2006) found that the establishment dates of mature *Tamarix* individuals along reaches of the Green River below Flaming Gorge Dam (UT, USA) were significantly related to a multi-year pattern of a large magnitude annual peak followed by a smaller high flow that favored survival of prior-year seedlings. Comparably, Reynolds et al. (2012) associated *Tamarix* establishment in Canyon de Chelly (AZ, USA) with several above-average precipitation years in the 1980s (presumed to produce substantial floods) that were followed by lower flows, channel narrowing and incision that greatly reduced overbank disturbance and resulting mortality of immature plants. Along the highly regulated Grand Canyon of the Colorado River (AZ, USA), reach-scale geomorphic variation and fluctuating water levels associated with seasonal hydropower production demands have promoted ongoing *Tamarix* recruitment (Mortenson et al. 2012). Nonetheless, Mortenson et al. (2012) reported a strongly negative effect of increasing summer precipitation in the year following establishment (thought to erode poorly rooted seedlings) and measured a positive relationship between *Tamarix* establishment during 1984-2006 and the annual peak flow magnitude, driven by the large floods of the unusually wet mid-1980s and the 2000 intentional flood release. Significantly, these floods occurred at times that were favorable relative to the window of *Tamarix* seed release, unlike the short duration intentional floods of March 1996 and November 2004 that were associated with much less *Tamarix* establishment. Early spring or winter high flows that leave floodplain sediments dry by the time *Tamarix* seeds arrive may limit successful germination (Beauchamp

and Stromberg 2007), leading Mortenson et al. (2012) to recommend planned floods in March or early April and to propose that native clonal shrubs (e.g., *Salix exigua*, *Pluchea sericea*) could benefit relative to *Tamarix* from advanced flood timing under climate change.

Comparative studies of multiple rivers have provided further insight into *Tamarix* recruitment and abundance in relation to flow alteration by dams. Sampling 64 perennial reaches on 13 rivers throughout the southwestern U.S., Merritt and Poff (2010) found that ongoing *Tamarix* recruitment was high along free-flowing rivers but declined slightly with increasing regulation. These authors postulated that the fluvial disturbance more common along less regulated reaches likely generates suitable establishment sites for *Tamarix*, whereas long-term flood suppression might eventually limit regeneration and ultimately abundance (as for other native pioneers). However, high seedling establishment along less-modified reaches did not necessarily correspond to high adult abundance, and the latter was positively associated with increasing flow modification. Noting that Stromberg et al. (2007b) had also observed the greater success of native riparian pioneer species under perennial, relatively free-flowing conditions, Merritt and Poff (2010) suggested the likely importance of post-germination competitive interactions as a limiting influence on *Tamarix* relative abundance in the absence of river regulation. Along 20 perennial river sections in this region, Mortenson and Weisberg (2010) also observed a decline in native cover and a positive association of *Tamarix* with flow regulation, while simultaneously noting the potential for abundant *Tamarix* along free-flowing reaches. As Merritt and Poff (2010) therefore concluded, flow modification has promoted the spread and dominance of *Tamarix* in the West, but the hydroclimate and natural patterns of flood disturbance on many Western rivers were also suited to the traits possessed by *Tamarix* and susceptible to invasion.

Thus, the interaction of Tamarix flow response traits with the hydrologic alteration resulting from climate change and water control infrastructure is likely to strongly influence the risk of greater Tamarix abundance within watersheds expected to become thermally tolerable. In order to examine this risk more closely, I simulated the change through time in Tamarix cover relative to the future annual peak discharge magnitude and timing modeled for the Upper Green River basin. Drawing on the literature describing Tamarix and other pioneer woody riparian vegetation, I developed a stage-structured, discrete time population model incorporating flood disturbance as a source of mortality and a control on establishment. A model of watershed hydrology subject to human water demand generated the necessary input sequences for simulation, and this hydrologic model was in turn forced by downscaled climate model projections and integrated with a geomorphic classification of the drainage network.

Though Tamarix may colonize a wide variety of fluvial geomorphic settings, and small stands can occur throughout a river network, its occurrence and abundance have been positively related to lower elevation reaches of greater drainage area (Ringold et al. 2008, Merritt and Poff 2010, Mortenson and Weisberg 2010). Accordingly, I emphasized modeling risk for river sections with low channel gradient and wide valleys that may provide extensive floodplains capable of supporting the largest Tamarix populations (Nagler et al. 2011). Climate models consistently indicate that temperatures will increase throughout western North America during the 21st century, but differences in projected precipitation across General Circulation Models (GCM) and differences in hydrologic model structure have resulted in substantially varying estimates of surface runoff and seasonal flow patterns (Subhrendu and Pruitt 2011, Perry et al. 2012). Seeking to capture high and low boundaries of this variation, I compared four climate input scenarios at the extremes of a distribution of projected temperature and precipitation

anomalies. Finally, in order to gain insight into whether water management will exacerbate or mitigate the ecological consequences of climate-driven flow alteration (Palmer et al. 2009), I examined a scenario of ‘naturalized’ flows alongside the baseline ‘business-as-usual’ hydrologic model configuration that retained the historic dam operations and irrigation withdrawals.

I used this exploratory modeling platform to test the hypothesis, based on the principle that *Tamarix* establishment requires periodic floods during the window of seed release, that invasion risk would be greatest under the hottest, wettest climate scenario, given continuation of the management status quo. After describing the modeling approach, I present the results of this attempt to characterize riparian invasion risk relative to projected hydrologic change, and discuss implications for further research and management application.

## **Methods**

### *Study area*

The Upper Green River (UGR), above Flaming Gorge reservoir in southwestern Wyoming (USA), forms the main Upper Basin tributary to the Colorado River and therefore provides a critical component of the water supply to millions of residents of downstream states. The sparsely settled basin consists of harsh, high desert terrain surrounded by the mountains of the Wind River and Wyoming Ranges. These mountains produce the majority of annual water yield as snowmelt runoff. Agricultural land uses predominate (primarily ranching and irrigated alfalfa and grass hay), but a surge in energy production (i.e., natural gas from the Pinedale Anticline and Jonah Field) has recently begun to alter local communities and the regional economy.

Numerous smaller reservoirs store the flows of headwater and tributary reaches to meet local irrigation demand. For example, the Eden Project infrastructure, including the Big Sandy

Dam and a system of canals, supplies water to irrigate approximately 69 km<sup>2</sup> of cropland (<http://www.usbr.gov/projects/>, accessed May 2013). In addition, the larger Fontenelle Dam and reservoir (completed in 1964; capacity approximately 0.426 km<sup>3</sup>) generates hydropower and is operated for storage in conjunction with downstream dams. Trends in local agricultural, municipal and industrial water needs are not well described, but are likely to depend on the interplay between municipal population growth (i.e., Pinedale and Green River, WY), energy sector use and the adoption of more efficient irrigation practices. However, the basin yields much of the supply for Flaming Gorge reservoir, a key element of the infrastructure that delivers water to downstream stakeholders. Demand scenarios under the hotter, more arid conditions expected for the Lower Colorado Basin suggest a growing likelihood of regional shortages (Reclamation 2012), and raise the possibility that decisions regarding the interconnected Colorado water system will propagate up through the network to further alter flows in the UGR.

Isolated individual *Tamarix* and small stands are currently sporadically present in the lower portion of the UGR (D. Auerbach, *personal observation*), and a recent survey of riparian habitat along the Green River below Fontenelle Dam found only small *Tamarix* (<1m) present in a few locations (Fortin et al. 2010). The species is common along the Lower Green River and tributaries to the south (Figure 4.2), and locally abundant populations occur elsewhere in Wyoming and to the north in Montana, particularly around reservoir margins (Lesica and Miles 2004, Lehnhoff et al. 2011). Thus, dispersal limitation does not appear to prevent the spread of *Tamarix* in the study area, as existing populations are close enough to provide sources of its copious, wind and water transported seeds (Friedman et al. 2005, Auble et al. 2012). However, *Tamarix* has not yet had an appreciable ecological impact, as in some other northern locations (Lehnhoff et al. 2012).



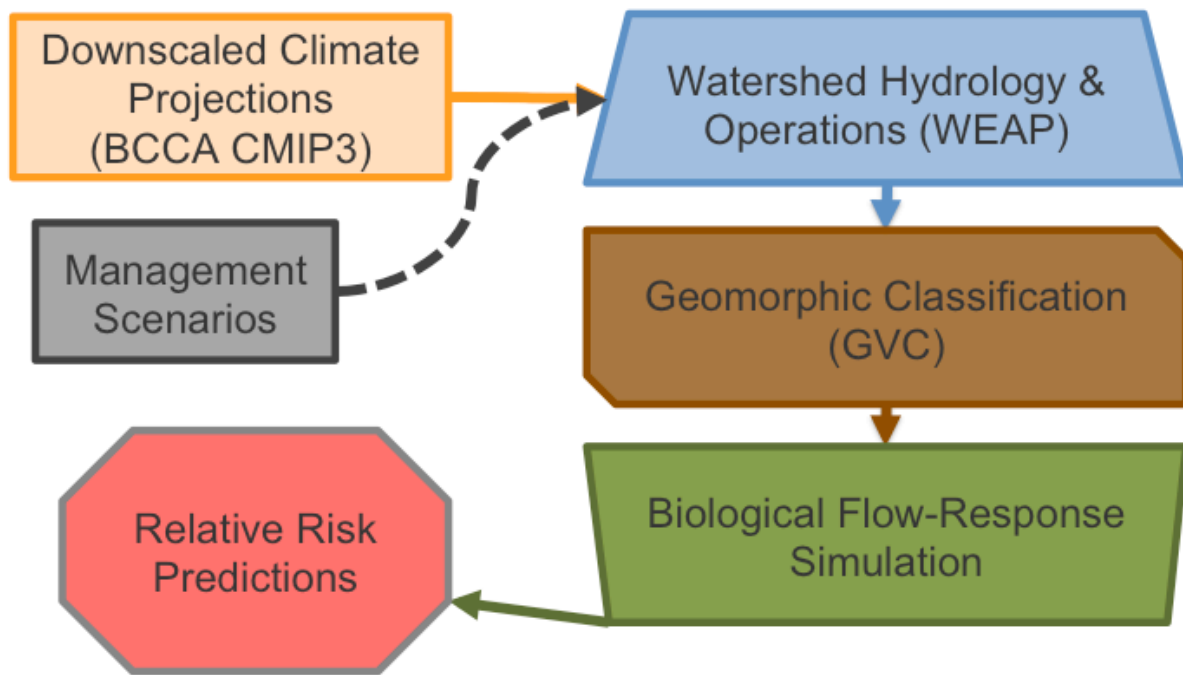


Figure 4.4: Conceptual overview of the linked model framework. Statistically downscaled temperature and precipitation projections generated by alternative GCMs served as forcing for the WEAP model. This representation of watershed hydrology combined human demand and water control infrastructure (e.g., dams and diversions) with rainfall-runoff and snow accumulation/melt calculations to route flows through the UGR. The WEAP flow network was integrated with the GVC classification routines, which distinguished the valley form of network units according to longitudinal slope, lateral constraint and hillslope coupling. Modeled discharge records associated with GVC units then served as forcing for a stage-structured model of *Tamarix* population growth relative to annual high flows.

#### *Hydrologic and geomorphic model platform*

As determinants of stream power, and thereby shear stress and disturbance intensity, reach slope and confinement are fundamental controls on the ecological effects of a particular discharge. Though individual plants may occur at sites subject to a fairly broad range of stream power, *Tamarix* stand size is positively associated with the lower gradients and wider valleys of high order reaches (Merritt and Poff 2010, Mortenson and Weisberg 2010). In order to consistently distinguish the river sections most suited to supporting large *Tamarix* populations within the UGR, a semi-automated spatial analysis was conducted on a 10 m<sup>2</sup> digital elevation

model (DEM) of the watershed extent (Carlson 2009, Bledsoe et al. *in preparation*). This Geomorphic Valley Classification process (GVC; consisting of Python scripts for ArcGIS 9.3) involved 1) generating a river network from a flow accumulation layer, 2) disaggregating network segments according to slope thresholds (“Low energy” segments were classified as slope < 0.1%), 3) determining the per-segment valley bottom extent according to segment-averaged estimates of the 100 year flood depth and the lateral “break in slope”, 4) calculating the steepness of surrounding hillslopes, and 5) classifying the resulting reach-valley segments into one of the 8 categories present in the basin as a function of downstream gradient, valley confinement, and hillslope coupling. The entire basin-wide set of valley polygons (3000+ units in all eight classes) was trimmed to the 471 units overlapping the flow network of the hydrologic model (Figure 4.5). Classes of the GVC units retained along the ‘sparse’ hydrologic model flow network were appropriately representative of the classes of surrounding units for which it was not possible to represent flow (i.e., units in the retained set were of the same land form as most nearby clipped units from the ‘dense’ DEM-based network). Data and processing constraints necessitated this approach, but the loss of drainage network locations with potentially distinct hydrology constituted a model limitation, particularly with regard to the possibility that flow was intermittent (and thereby potentially favorable to *Tamarix*) within GVC units not captured by the hydrologic flow network.

Stockholm Environmental Institute personnel implemented and calibrated the semi-distributed Watershed Evaluation and Planning hydrologic model (WEAP) for the UGR (Young et al. 2009). Many distributed, process-based hydrologic models represent basin yield or ‘supply’ in the absence of human ‘demand’ influences such as dams, withdrawals and returns. However, the WEAP platform integrates a representation of the water demand infrastructure within a basin

with precipitation-infiltration-runoff calculations (including snow accumulation and melt) for watershed sub-catchments distinguished by land cover, soils, and elevation. This provides the capacity to evaluate climate change impacts in the context of water management, and WEAP has recently been used to explore the scope for management adaptations to mitigate negative climate-hydrology changes affecting threatened salmon populations in California (Thompson et al. 2011). Within the 19,080 km<sup>2</sup> drainage extent of the UGR, the area of modeled sub-catchments ranged from 0.17 km<sup>2</sup> to 1434 km<sup>2</sup>, with a median of 45.6 km<sup>2</sup>.

Climate forcing inputs to WEAP (temperature, precipitation and wind speed) generated continuous modeled discharge at a weekly time-step for 143 nodes throughout the UGR that were linked to at least one unique GVC segment. The simulations described here were restricted to the WEAP nodes associated with GVC valley segments in the ‘Low Energy Floodplain’ (LEF) and ‘Medium Energy Open’ (MEO) classes hypothesized as most likely to support substantial *Tamarix* populations (Figure 4.5). Units in these classes were similar, but MEO sections had slightly higher gradients and were more common in the upper portion of the drainage and along tributaries to the main channel of the Green River (Table 4.2).

Table 4.2: Attributes of the two GVC classes included in the analysis. Low Energy Floodplain (LEF) and Medium Energy Open (MEO) classes were present throughout the basin, but the latter was more common at higher drainage network positions associated with slightly steeper gradients. The assigned *kflood* value refers to the biological response model; see text for details.

	<b>Unit Length (km)</b>	<b>Mean Unit Gradient</b>	<b>Base Elevation (m)</b>	<b>Drainage Area (km<sup>2</sup>)</b>	<b>Associated WEAP Nodes</b>	<b>Assigned <i>kflood</i> Value</b>
MEO (n=118)					N=58	3
Minimum	0.205	0.0001	1186	10		
Median	1.511	0.0068	2188	211		
Mean	2.602	0.0079	2225	803		
Maximum	13.46	0.0378	2956	17980		
LEF					N=106	5
Minimum	0.071	0.0001	1848	11		
Median	2.268	0.0022	2099	1103		
Mean	3.054	0.0027	2102	4231		
Maximum	19.42	0.0145	2928	19080		

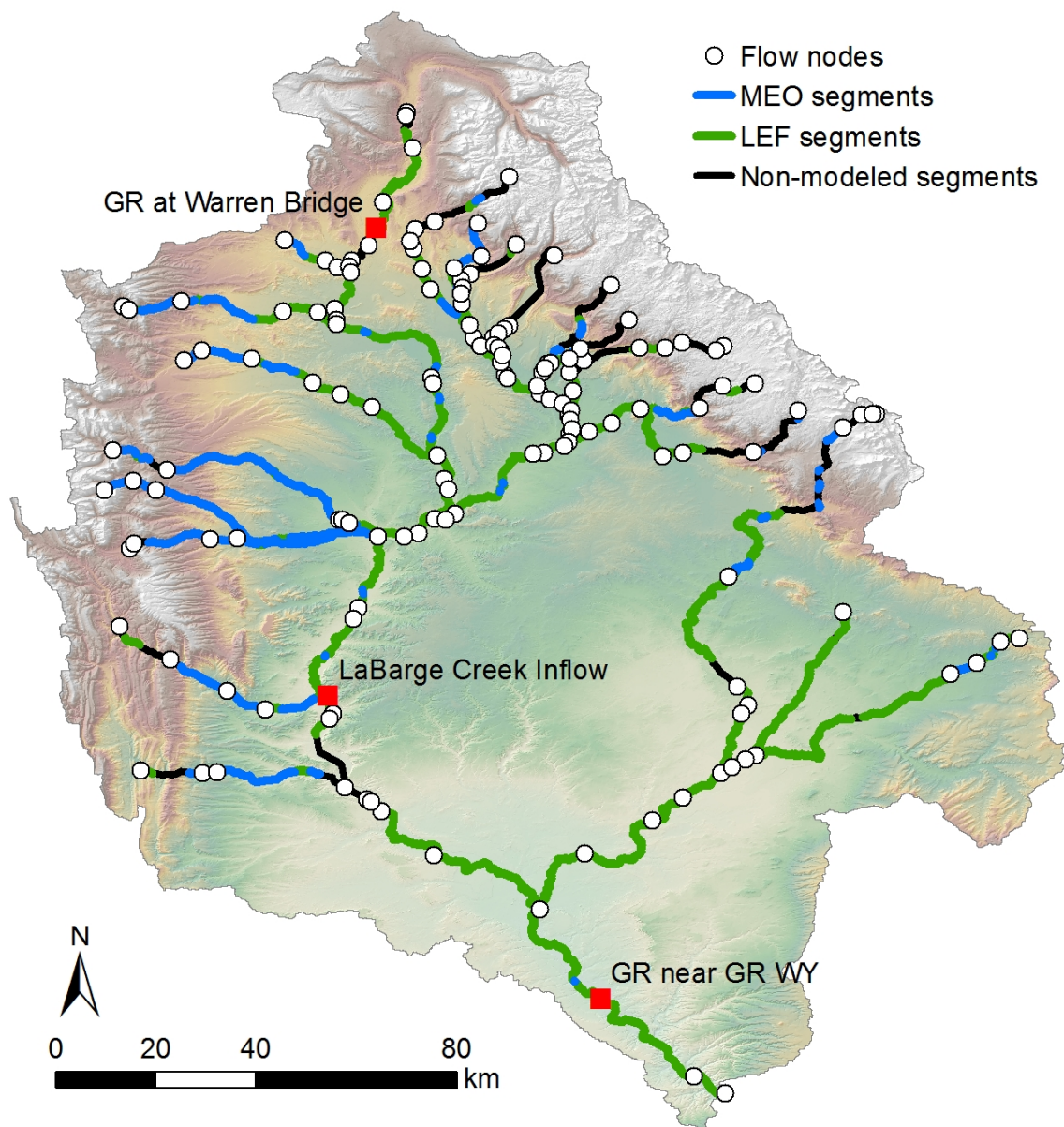


Figure 4.5: The Upper Green River basin extent included within the WEAP model (19,080 km<sup>2</sup>), showing the GVC valley segments associated with WEAP flow nodes. Nodes represent the discharge calculated from sub-catchments distinguished by land cover and elevation as well as the effects of diversions, return flow and dam storage. The red squares mark focal upper, middle and lower-network nodes illustrated in subsequent figures. The ‘Green River at Warren Bridge’ node is located above most water management, the ‘LaBarge Creek Inflow’ node is above Fontenelle dam and reservoir but is affected by upstream water diversion, and the ‘Green River near Green River, WY’ node is subject to both Fontenelle and infrastructure along the Big Sandy River (the lowermost major tributary entering from the East). Valley sections in the Moderate Energy Open (MEO, blue) and Low Energy Floodplain (LEF, green) classes constituted the majority of the basin and were assumed to have the greatest potential to support extensive *Tamarix* stands. Black sections are GVC units that were not included in biological simulations.

As input to WEAP, time series of climate forcing variables downscaled via the bias-corrected constructed analog method (BCCA) were obtained from the World Climate Research Programme's (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset ([http://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/](http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/)). Mean basin temperature and precipitation were calculated during the 'historic' years 1970-1999 and the 'future' years 2030-2059 for each of 112 potential GCM runs subject to the Intergovernmental Panel on Climate Change's (IPCC) "b1", "a1b" and "a2" emissions storylines (Figure 4.6). The difference between future and historic means was then taken as  $\Delta T$  and  $\Delta P$  values per-GCM, and used to ordinate the pool of runs. Two runs at the extremes of precipitation change ('dry', a decline in mean precipitation and 'wet', an increase) were selected at each of the interquartile increases in temperature ( $+1.5^{\circ}\text{C}$  or 'warm' and  $2.5^{\circ}\text{C}$  or 'hot'; Figure 4.6). For ease of reference, the selected GCM/IPCC runs were designated 'dry, warm' (*a2.mri\_cgcm2\_3\_2a.3*), 'dry, hot' (*a2.miroc3\_2\_medres.2*), 'wet, warm' (*a1b.ncar\_pcm1.2*), and 'wet, hot' (*a2.ipsl\_cm4.1*). Mean weekly flows resulting from each of these forcing inputs were calculated during the historic and future periods, with future discharge examined under both a 'business-as-usual' configuration of WEAP with operational rules identical to the historic period, and a 'natural flow restored' configuration, in which water withdrawals and reservoir storage were prevented. While such a 'natural' scenario is logistically and politically improbable, it provided an informative contrast with projections under the current level of water management.

Unlike an event-based model calibrated to instantaneous discharge, this implementation of WEAP calculated flow on a weekly time step (i.e., as a function of the cumulative weekly precipitation and average weekly temperature). Model error associated with WEAP (and all other hydrologic models) was unavoidable, and the downscaled GCM outputs each carried additional

unknown structural biases. In order to keep these uncertainties consistent among simulations and to accommodate modeled high flows on a different scale than observed measures, the scaled annual peak flow required by the biological response model was calculated as a relative quantity from a model-to-model comparison. For each year during the historic and future periods, I extracted the magnitude of the maximum weekly flow during an extended growing season between the first week of April and the first week of September (weeks 14 to 35), as well as the week in which this largest flow occurred. These values were calculated individually at each node for each GCM under both management configurations. I divided the series of future values by the median of the historic distribution of this annual high flow measure in order to produce sequences of scaled magnitude representing years in which high flows were overbank (values  $>1$ ) or did not have the capability of causing flood disturbance mortality and generating suitable establishment sites for *Tamarix* (values  $<1$ ). The median of the historic annual high flow was effectively the peak with a 2 year recurrence interval in the 30-year historic sample, and may have represented a conservative threshold relative to the common assumption of bankfull discharge at  $Q_{1.5}$  (note the *sample* flow with exceedance probability = 0.5 is not necessarily identical to the  $Q_2$  that would be calculated from fitting a flood frequency distribution). I further assumed that the intensity of disturbance for a given scaled discharge was slightly greater for the MEO units relative to the LEF sections ( $k_{flood} = 3$  and 5 respectively, see next section).

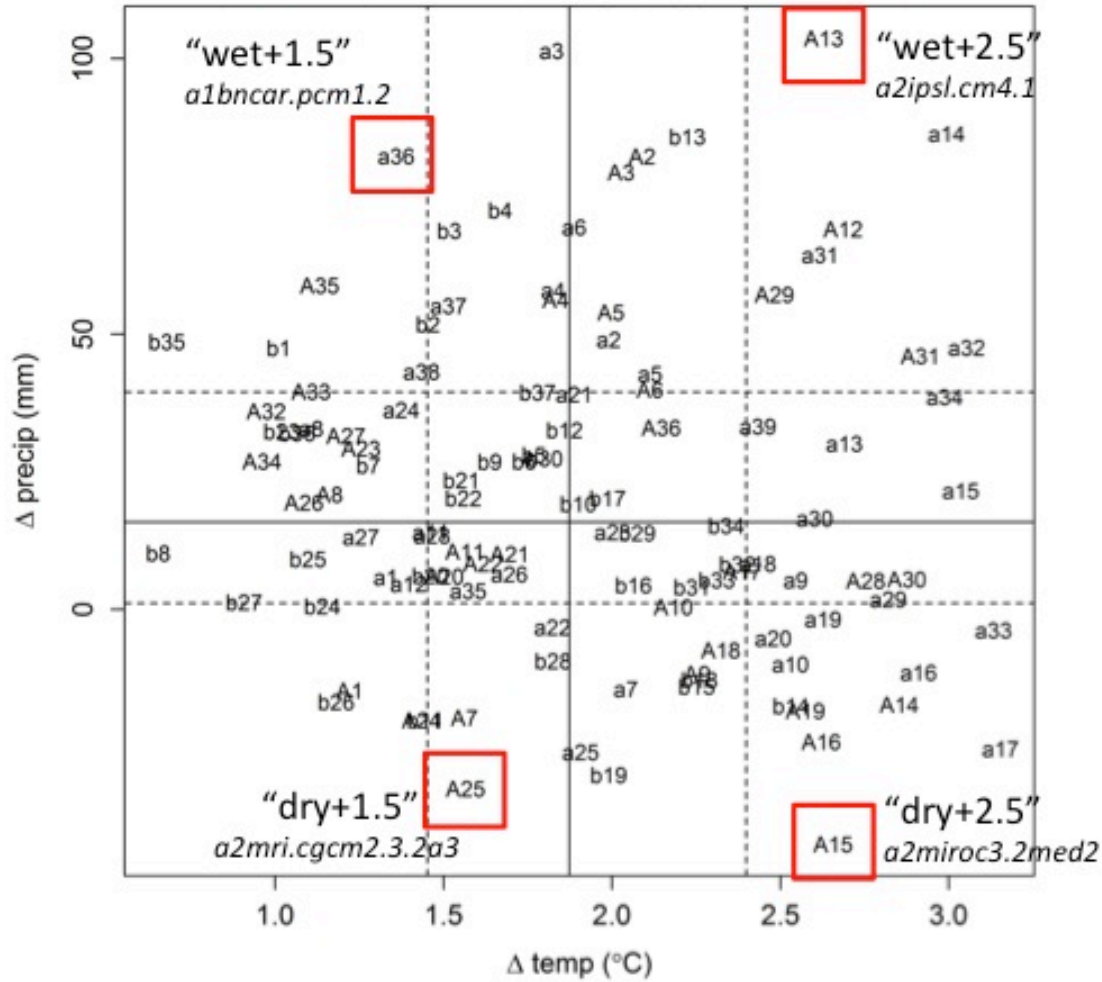


Figure 4.6: 112 candidate GCM forcing input series ordinated by the change in mean temperature and precipitation between the historic (1970-1999) and future (2030-2059) periods. The designations ‘warm’ and ‘hot’ refer to average temperature increases of 1.5 and 2.5 degrees Celsius, and the ‘wet’ and ‘dry’ labels indicate substantial projected increases in precipitation versus decreases from historic levels. Italicized model names refer to CMIP downscaling designations, and dashed lines represent the interquartile range for each measure. The selected model inputs (red boxes) were chosen to capture the largest changes in precipitation at the 25<sup>th</sup> and 75<sup>th</sup> percentiles of increased temperature, with the expectation that these differences would serve to bound the potential hydrologic outcomes, and therefore represent much of the range of potential *Tamarix* responses.

### *Biological response model*

I used this hydrogeomorphic platform as the basis on which to apply a version of the generalized model of stage-structured woody riparian vegetation presented in Chapter 2. This exploratory approach permitted the simulation of change through time in *Tamarix* cover area as an indicator of invasion risk. Here, I briefly describe the model structure and several key assumptions before presenting examples of model behavior subject to synthesized forcing sequences.

Along a finite length of riparian zone regularly affected by overbank discharge, the model updated the spatially implicit cover area of seedling, juvenile, adult and dead stages as state variables in a system of difference equations forced by scaled yearly high flows (designated  $Q_t$  and calculated as described in the previous section as the annual maximum during each future year divided by the median of the historic annual maxima). Each within-year model cycle consisted of potential flood disturbance mortality, maturation between stages, and establishment of new seedling cover, a sequence relevant to snowmelt rivers in arid and semi-arid western North American that exhibit a seasonal flood pulse. I assumed that *Tamarix* seedlings established on unoccupied, flood-affected area, and that sufficient seeds arrived for colonization to occur even in the absence of adult cover (i.e., an open system without dispersal limitation). I represented flow response trait differences between stages by assigning parameter values that conferred progressively greater tolerance of flood disturbance mortality with maturation. In addition, I assumed a relatively high loss of *Tamarix* seedling cover prior to the juvenile stage due to implicit non-flood factors (e.g., ice scour, water stress, fire, herbivory, etc.), but a relatively rapid maturation from the juvenile to adult stages, and a relatively low conversion of adult to standing dead cover.



I implicitly represented the numerous factors governing flood disturbance intensity relative to discharge magnitude (e.g., bed and bank substrate, suspended sediment load, longitudinal gradient, cross-sectional profile, etc.) as a simple function of the scaled peak forcing, modified by a single parameter controlling the rate at which flood effects rose then saturated:

$$F_t = F(Q_t) = \begin{cases} 0, & Q_t \leq 1, \text{ below bank} \\ \frac{Q_t - 1}{k_{flood} + Q_t - 1}, & Q_t > 1, \text{ over bank} \end{cases}$$

$$k_{flood} > 0, \quad F_t \in [0,1]$$

Larger values of the *kflood* parameter correspond to medium and lower energy settings in which disturbance intensity (designated  $F_t$ ) might rise relatively gradually with larger magnitude flows (in contrast to steeper, more confined reaches where small multiples of bankfull could potentially produce appreciable disturbance). Accordingly, I assigned *kflood* values of 3 and 5 to MEO and LEF units respectively (e.g., yielding  $F_t = 0.5$  and  $F_t = 0.375$  for  $Q_t = 4$ ; Figure 2.2c). I assumed that fluvial geomorphic conditions were in dynamic equilibrium, so that the total riparian zone area (i.e., the potentially occupied area) and the relationship between scaled discharge magnitude and flood disturbance remained constant through model runs.

Thus, for a vector  $\mathbf{v}$  of *Tamarix* indexed by stage ( $s, j, a, d$ ) and time step  $t$ , the system of updating functions forced by  $F_t$  was written:

$$\text{seedling: } v_{t+1,s} = \text{estab}_t \left( 1 - \sum_i v_{t,i} \right) F_{t+1}$$

$$\text{juvenile: } v_{t+1,j} = (1 - ja) v_{t,j} (1 - F_{t+1}^{jftol}) + sj * v_{t,s} (1 - F_{t+1}^{sftol})$$

$$\text{adult: } v_{t+1,a} = (1 - ad) v_{t,a} (1 - F_{t+1}^{aftol}) + ja * v_{t,j} (1 - F_{t+1}^{jftol})$$

$$\text{dead: } v_{t+1,d} = v_{t,d} (1 - F_{t+1}^{dftol}) + ad * v_{t,a} (1 - F_{t+1}^{aftol})$$

These equations state that, during each model cycle, the prior cover of each stage survived according to the level of flood disturbance affecting the riparian zone, as modified by a tolerance parameter that reduced cover loss (e.g., for the adult stage:  $v_t(1-F_{t+1}^{aftol})$ ;  $0 \leq v_t \leq 1$ ,  $0 \leq F_{t+1} \leq 1$ ; assigned values were  $sftol = 1$ ,  $jftol = 2$ ,  $aftol = dftol = 3$ ). Cover that survived flooding then matured or persisted in its current stage relative to parameters controlling seedling loss unrelated to flooding ( $0 \leq sj \leq 1$ ;  $sj = 0.25$ ), the rate of transition to the adult stage ( $0 \leq ja \leq 1$ ;  $ja = 0.25$ ), and adult mortality not due to flood disturbance (e.g., drought or disease;  $0 \leq ad \leq 1$ ;  $ad = 0.01$ ). Flooding allocated the unoccupied area from the prior time step ( $1 - \sum_i v_{t,i}$ ) into suitable establishment area, which allowed formation of new seedling cover according to a parameter controlling establishment success ( $0 \leq estab_t \leq 1$ ). I examined two alternative model formulations for this parameter: a system in which  $estab_t$  was fixed at 0.5 such that establishment success was independent of annual peak timing, and a system in which  $estab_t$  varied with the week of the yearly high flow according to a simple threshold function:

$$estab_t = \begin{cases} 0 & week \leq 20 \\ \min\left(\frac{c}{5}week - 4c, c\right) & week > 20 \end{cases}$$

This function produced a linear increase in *Tamarix* establishment success from 0, if the scaled annual peak preceded mid-May (week 20), to a maximum constant  $c$  by mid-June (week 25;  $c = 0.5$ ). This latter model configuration represented the assumption that suitable sites would be too dry for successful establishment if high flows occurred prior to a period of *Tamarix* seed release observed to begin in late May or early June at northern latitudes (Sexton et al. 2002, Sexton et al. 2006). For both the timing-independent and timing-sensitive systems, I simulated the increase in *Tamarix* abundance following initialization at zero cover of all stages in response

to the flow sequences generated by WEAP under each climate and management scenario (model development and all simulations were performed in R 3.0.0 (R Core Team 2013)). However, before presenting the results of these runs, I illustrate the effects of parameter variation on the behavior of the timing-independent model configuration, subject to fixed forcing sequences of scaled peak flows comparable in magnitude to those produced by WEAP for the UGR.

For a given forcing sequence, the model converged to a quasi-equilibrium determined by the contrasting effects of floods as a requirement for seedling establishment and as a source of disturbance mortality that cleared vegetation cover. A pattern of fewer, smaller overbank flows produced a lower level of new seedling cover relative to one that involved larger floods, but the loss of existing vegetation was simultaneously reduced. As a result, if the flood tolerance parameter values were small, then the quasi-stable adult abundance was greater under a lower disturbance regime relative to one with larger high flows (Figure 4.7; compare solid green trace of adult cover in the left and right panels of the upper row). In contrast, more intense disturbance resulted in greater average adult cover when tolerance values were sufficiently high and large establishment opportunities compensated for cover losses (Figure 4.7; lower row). In addition, the total vegetated cover imposed a limit on establishment (i.e., a form of negative density dependence), as area was allocated to the juvenile, adult and dead stages and became unavailable to seedlings (Figure 4.7; present in all runs but most apparent in lower panels with greater adult and dead abundance). The size and frequency of the simulated floods also influenced the rate to convergence under fixed sequences, with higher disturbance levels producing more initial establishment and requiring fewer cycles to reach a quasi-stable stage distribution.

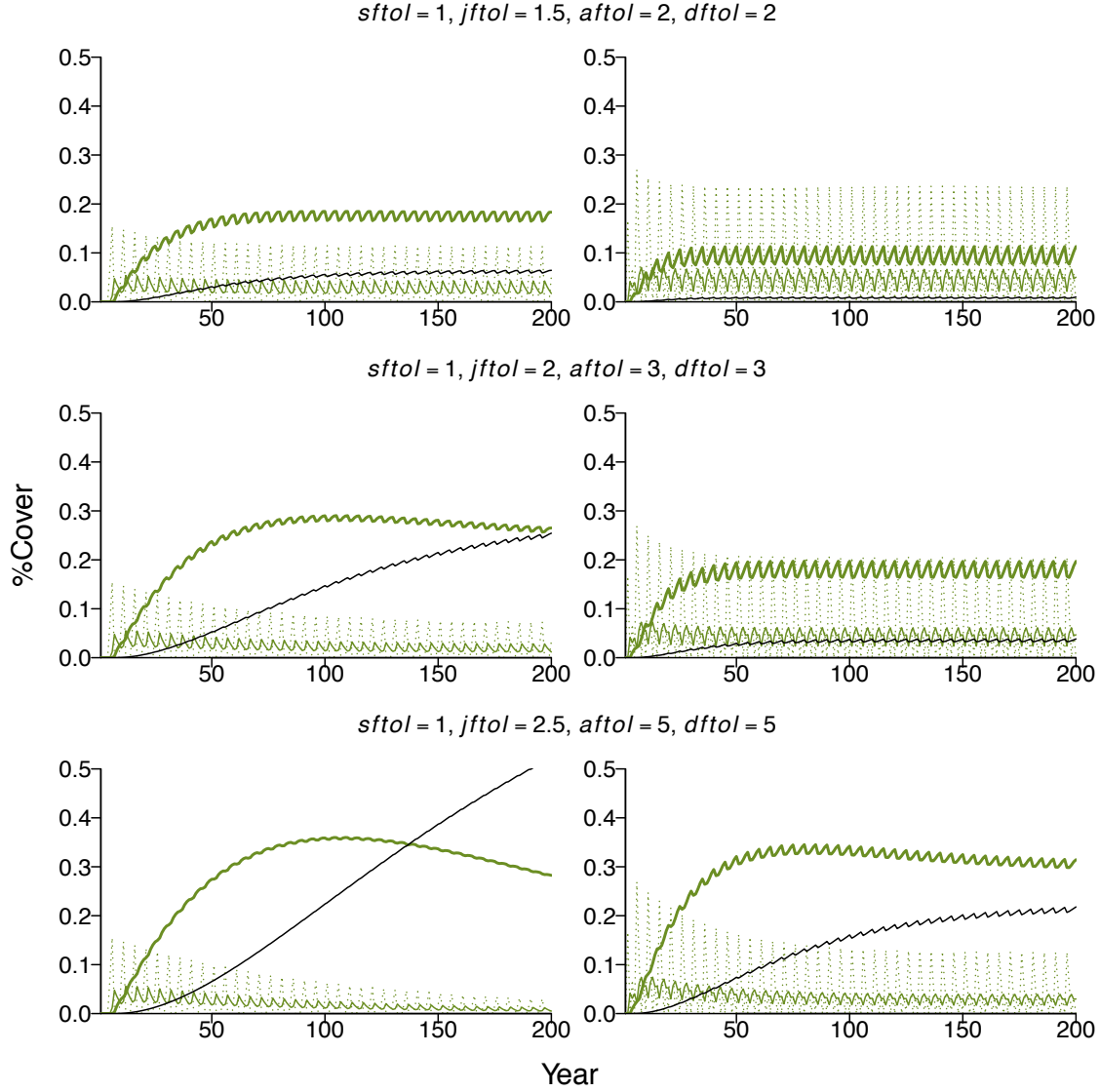


Figure 4.7: Model behavior for relative to synthetic forcing sequences of lower (left column,  $Q_t = \{2.5, 1, 1, 1, 1.5\}$ ) and higher disturbance frequency and intensity (right column,  $Q_t = \{5, 2.5, 1, 1.5, 1\}$ ). Simulated *Tamarix* seedling (dashed green), juvenile (light solid green), adult (heavy solid green), and dead (black) cover are illustrated under low (upper row), intermediate (middle row), and high (lower row) values for the flood tolerance parameters controlling the reduction in disturbance mortality. Though smaller floods produced less seedling cover, adult abundance was higher for the low disturbance forcing when tolerance was also low (i.e., due to greater mortality and loss of cover despite greater establishment under the high disturbance forcing). Intuitively, greater flood tolerance produced a higher quasi-stable level of adult cover under both disturbance regimes. However, the higher disturbance regime more effectively cleared standing dead cover, diminishing self-limitation, and afforded larger establishment opportunities to result in higher quasi-stable adult abundance relative to the low disturbance regime (lower row). Remaining parameter values were  $sj = ja = 0.25$ ,  $estab = 0.5$ , and  $ad = 0.01$ . These and the intermediate  $ftol$  values were assigned in all simulations conducted with WEAP forcing.

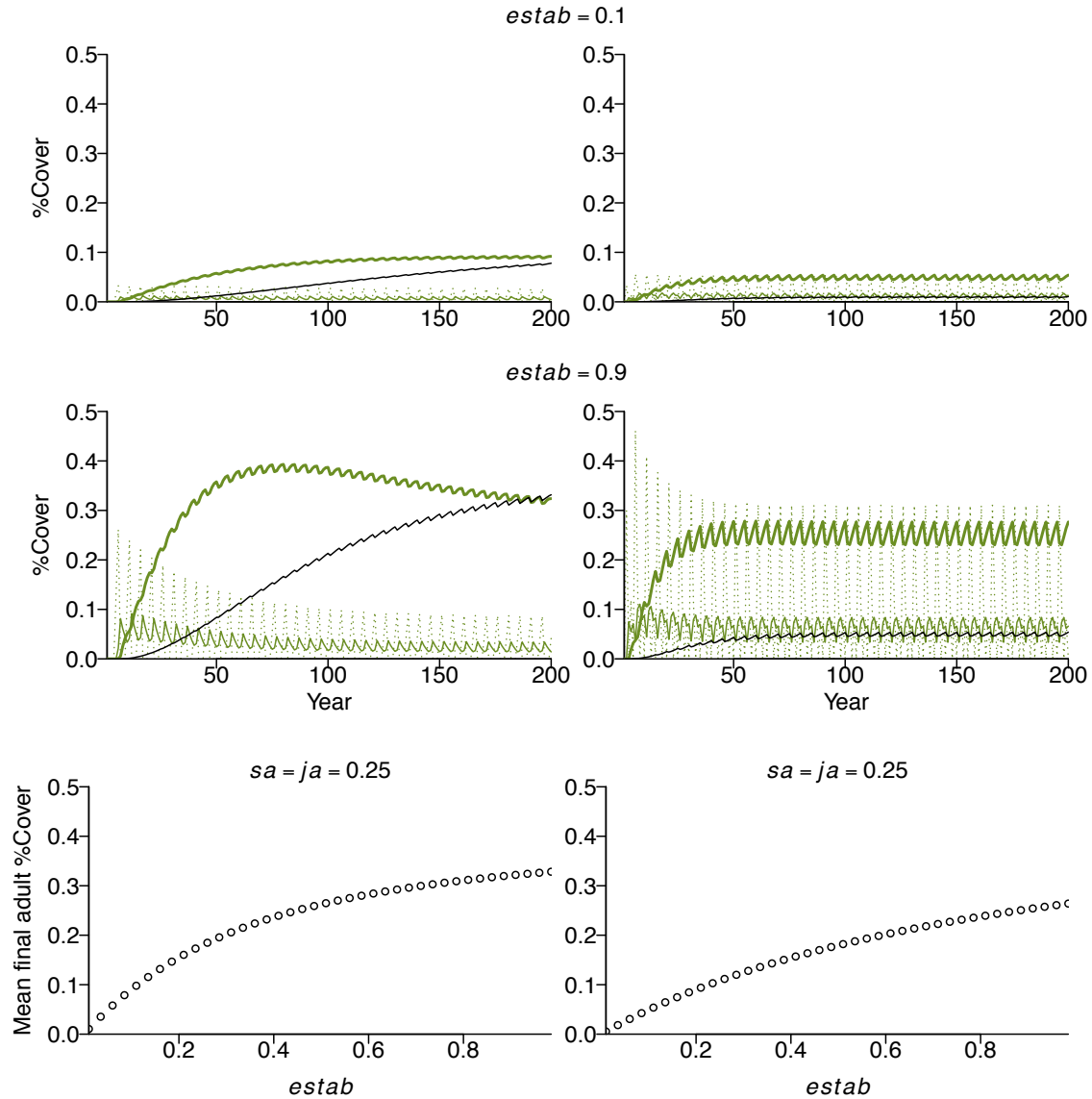


Figure 4.8: Effects of varying the *estab* parameter controlling the portion of suitable establishment area allocated to seedling cover under lower (left column) and higher (right column) synthetic disturbance regimes. Simulated *Tamarix* seedling (dashed green), juvenile (light solid green), adult (heavy solid green), and dead (black) cover are illustrated for low (upper row) and high (middle row) establishment success, and the mean adult cover during the final 10 years of runs is illustrated across the full range of parameter values (lower row). As expected, increasing establishment success yielded higher adult cover, but the combination of adult and standing cover that persisted under lower disturbance imposed greater self limitation and yielded a modest saturation in the adult cover increase relative to incremental change in the *estab* value. Remaining parameter values were as assigned in WEAP simulations (*sj* = *ja* = 0.25, *ad* = 0.01, *sftol* = 1, *jftol* = 2, *aftol* = *dftol* = 3).

Varying the parameters controlling establishment success and maturation had fairly intuitive effects on model behavior. Larger values of *estab* yielded greater stable cover under either disturbance scenario, as more of the flooded, unoccupied area was allocated to seedling cover during cycles with overbank scaled peaks (Figure 4.8). However, the effect of increasing *estab* values diminished somewhat under the lower disturbance scenario, as higher adult and dead cover areas imposed progressively greater restriction on the availability of suitable, unoccupied area and therefore the generation of new seedling cover (i.e., bare space was less limiting at the lower quasi-stable abundances associated with the lower range of *estab* values, such that an incremental *estab* increase yielded a greater proportional effect). Increasing the *sj* value also produced greater quasi-stable adult cover area under both disturbance scenarios, as seedling losses unrelated to flood mortality were reduced and more cover reached mature stages (Figures 4.9 and 4.10). However, the model was somewhat more sensitive to an increase in values of the *ja* parameter under the higher disturbance intensity scenario, as faster maturation into the more tolerant adult stage was more beneficial in the context of greater ongoing flood mortality.

Collectively, this behavior illustrated that the model captured key patterns relevant to *Tamarix* invasion. Pulsed seedling recruitment followed flood disturbance, and adult cover increased if smaller high flows in the following year allowed maturation (e.g., Shafroth et al. 2002, Cooper et al. 2003, Birken and Cooper 2006, Merritt and Poff 2010, Mortenson et al. 2012). With ongoing overbank flows to clear existing vegetation, the interaction between trait parameter values and the pattern of disturbance frequency and intensity determined the specific quasi-equilibrium distribution of cover by stage. However, the model was stably attracted to a non-zero adult abundance due to the assumptions that: 1) suitable establishment area was

available during the period of seed release, that 2) no seed limitation occurred, and that 3) none of the various non-flood factors potentially limiting *Tamarix* entirely prevented maturation of the seedling and juvenile stages (i.e., *estab*, *sj* and *ja* all  $> 0$ ). These assumptions might be considered valid, for example, along an unregulated reach where competition with native pioneer species does not fully suppress *Tamarix*, or along a regulated reach where some ongoing flood disturbance maintained establishment opportunities. Conversely, model outcomes might be thought to represent a fairly conservative over-estimate of invasion risk if conditions in a currently un-invaded but newly thermally suitable watershed invalidated these assumptions (i.e., risk might be lower if these assumptions were unmet). Seeking to maintain this precautionary perspective in the context of the uncertainty surrounding both process and parameter specification, I therefore classified categorical invasion risk for the UGR relative to the range of quasi-equilibrium adult cover values produced by artificial disturbance sequences under the assigned parameter values ( $\approx 15\text{-}35\%$ ). I calculated the mean adult cover during the last 5 years of simulated futures forced by 30-year flow sequences generated by WEAP, and I divided this measure into the categories of high (cover  $> 15\%$ ), moderate ( $15\% > \text{cover} > 5\%$ ), low ( $5\% > \text{cover} > 1\%$ ) and very low (cover  $< 1\%$ ) invasion risk. I stress that these relative risk categories represent plausible, qualitatively distinct outcomes, but should not be interpreted as quantitatively precise estimates of absolute abundance.

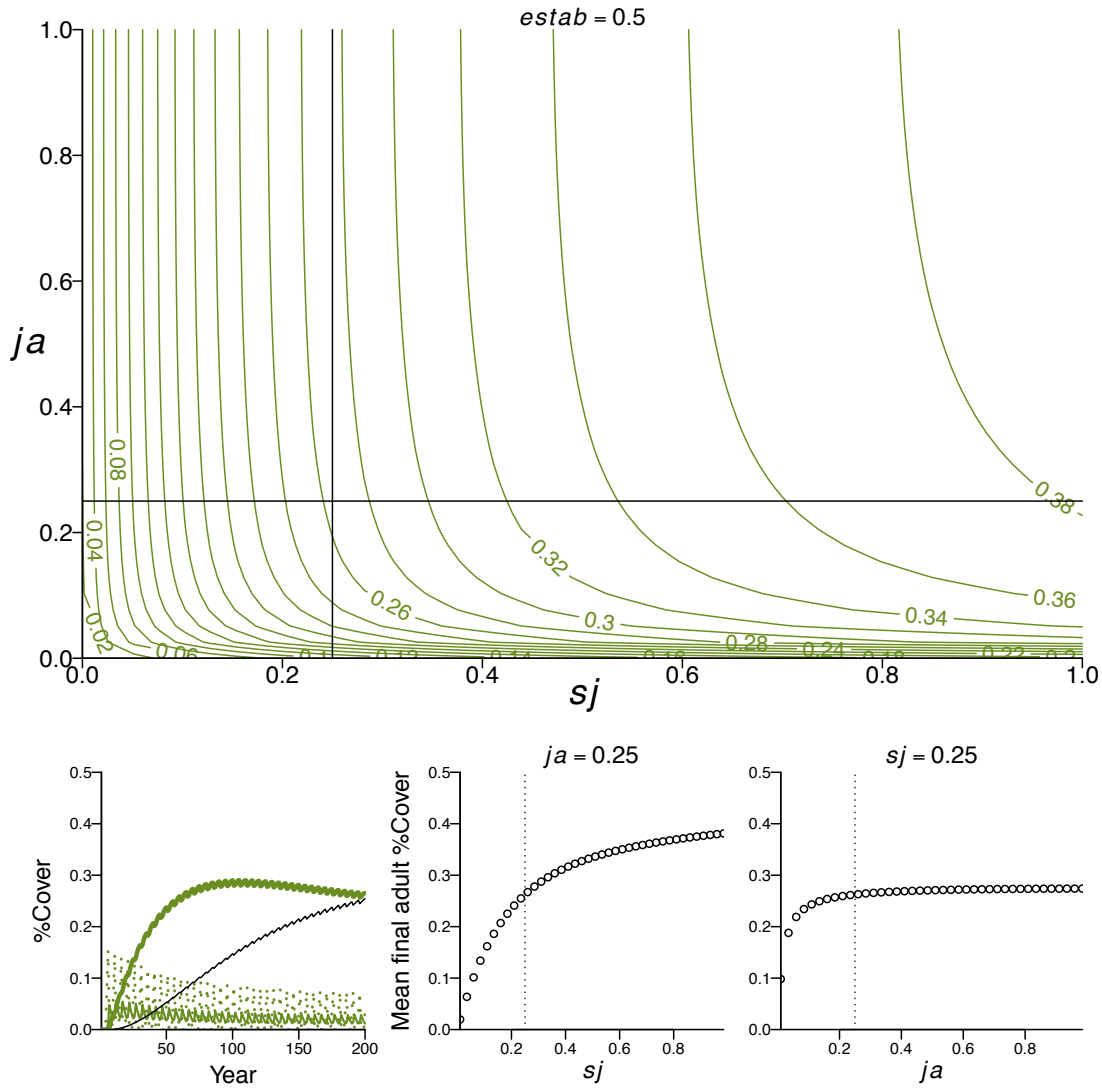


Figure 4.9: The effect of varying maturation parameters under the lower disturbance intensity forcing scenario (see Figure 4.7 for sequence of  $Q_t$  values). The upper contour plot illustrates the average adult cover during the final 10 time steps of 200 year model runs initialized from zero and with all remaining parameters assigned values used in subsequent simulations ( $estab = 0.5$ ,  $ad = 0.01$ ,  $sftol = 1$ ,  $jftol = 2$ ,  $aftol = dftol = 3$ ). The lower left panel shows the trace of all stages through time at these values ( $sj = ja = 0.25$ ; indicated by the solid black intersecting lines on the contour plot), and the middle and right panels indicate the model behavior when the  $ja$  and  $sj$  values were fixed (respectively indicated by the horizontal and vertical solid black lines on the contour plot). The model was relatively insensitive to values of  $ja > \approx 0.2$  when the low rate of disturbance mortality meant that a faster transition into the more tolerant adult stage was less important. In addition, as for the  $estab$  parameter, the saturating effect of increasing  $sj$  reflected a comparable shift toward greater self-limitation of suitable establishment space (i.e., due to higher levels of adult and dead cover).



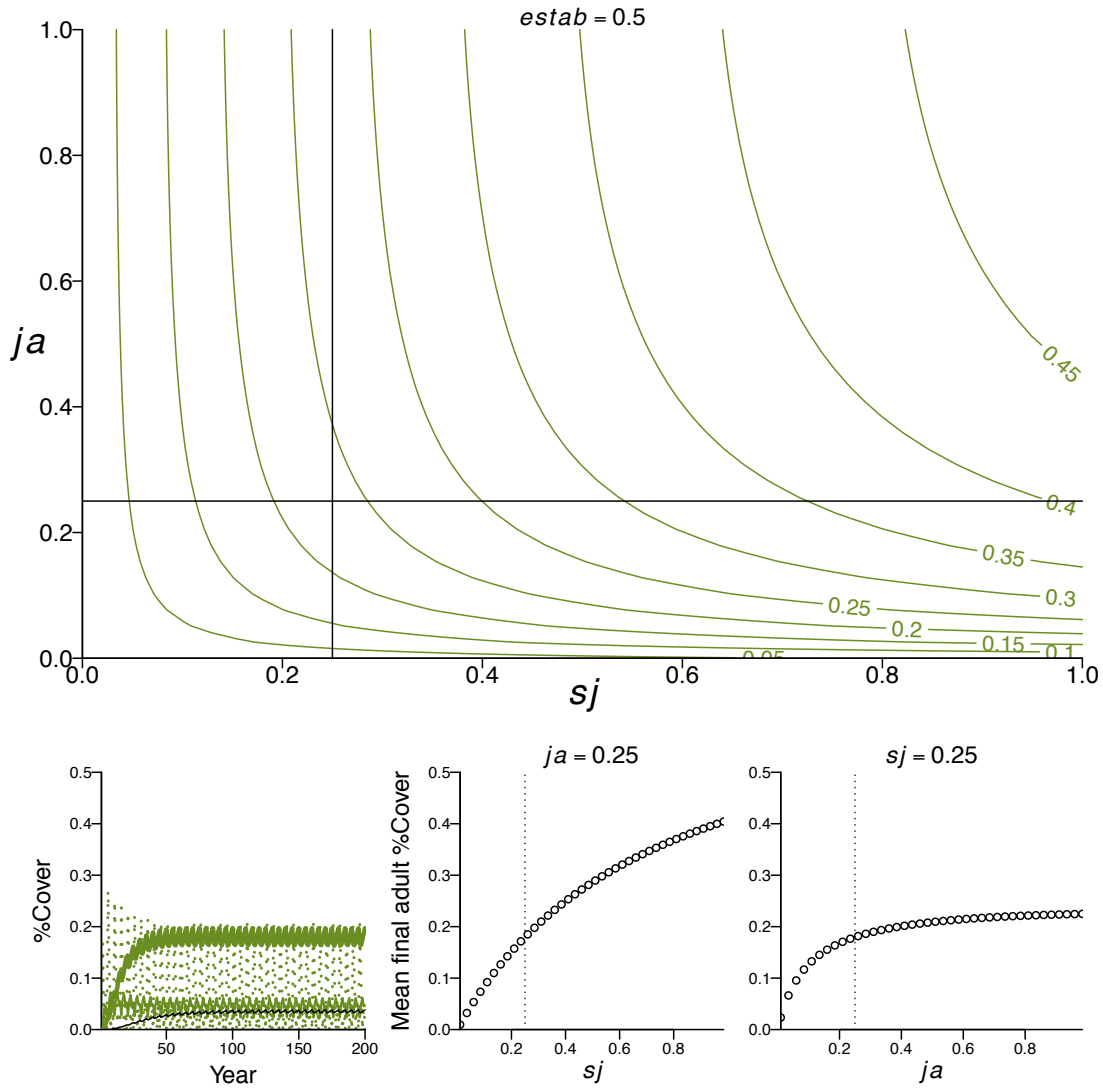


Figure 4.10: The effect of varying maturation parameters under the higher disturbance intensity forcing scenario. Panel conventions follow Figure 4.9, with the contour plot illustrating mean final adult cover (remaining parameters:  $estab = 0.5$ ,  $ad = 0.01$ ,  $sftol = 1$ ,  $jftol = 2$ ,  $aftol = dftol = 3$ ), the lower left showing a trace of stages through time, and the effects of varying each parameter individually shown at the lower middle and right. In contrast to the lower disturbance intensity scenario, adult cover was proportionally more effected by increases in each parameter over a larger range of values. The greater ongoing flood mortality meant that quasi-stable adult cover imposed less of a restriction on the available establishment space (for  $sj$ ) and faster maturation allowed more cover to ‘escape’ into the more tolerant adult stage (for  $ja$ ).

## Results

### *Hydrologic changes*

The ‘wet’ and ‘dry’ inputs yielded the expected increases and decreases in overall stream flow. Time series of projected discharge over the full future record indicated that the historically characteristic pattern of annual snowmelt peaks declining to summer lows was maintained for each of the GCM forcing scenarios under both the ‘business-as-usual’ and ‘natural-flow-restored’ WEAP configurations (Figure 4.11). Despite clear differences among GCMs in the specific years of predicted high flow, the climate model inputs all generated year-to-year variation in the magnitude of modeled annual peaks. The ‘hot, wet’ scenario generated the largest peaks relative to the historic distribution, whereas the ‘hot, dry’ GCM resulted in annual high flows that were only occasionally larger than the historic median at many locations (Figure 4.12). These differences among GCMs were reflected in Wilcoxon rank sum tests comparing the historic and future distributions ( $N = 30$ ) of the magnitude of annual high flow. Tests supported the alternative hypothesis that future peaks were larger at  $P < 0.05$  for 70% and 97% of nodes under the ‘warm, wet’ and ‘hot, wet’ scenarios respectively. A slight interaction was evident with management for the ‘dry’ scenarios, with less than 1% of nodes exhibiting significantly larger peaks under the ‘business-as-usual’ configuration, but the ‘natural-flow-restored’ scenario yielding 13% and 10% of nodes with significantly larger annual high flow magnitudes for the ‘warm, dry’ and ‘hot, dry’ configurations.

All forcing scenarios advanced the within-year timing of these high flows under both WEAP configurations, with earlier runoff somewhat more pronounced for the two hotter GCMs, consistent with expectations regarding faster melt of the snow pack (Figure 4.12). This shift was highly significant for most locations: Wilcoxon rank sum tests comparing the historic and future

distributions ( $N = 30$ ) of the week of annual high flow supported the alternative hypothesis that future peaks were earlier at  $P < 0.05$  for 81%, 95%, 90%, and 99% of nodes under the ‘warm, dry’, ‘hot, dry’, ‘warm, wet’, and ‘hot, wet’ scenarios and the ‘business-as-usual’ configuration (percentages were similar or greater with ‘natural flow restored’). Annual peak discharge during the extended growing season generally arrived 1 to 2 weeks earlier for the modeled years 2030-2059 relative to the 1970-1999 period. For the dry scenarios in particular, mid-network and downstream nodes subject to the accumulating effects of water withdrawal and storage exhibited earlier peak timing under the ‘natural’ relative to the ‘business-as-usual scenario’, as flow was not withheld to meet storage requirements.

The flow regime attributes of a consistently earlier annual peak and between-year variation in high flow magnitude held throughout the drainage network at nodes subject to different levels of water management (Figure 4.12). However, though the ‘natural’ configuration did reveal the effects of water diversion on mid-network reaches and dams above lower reaches that reduced and elevated summer low flows respectively (discussed below; Figure 4.17).

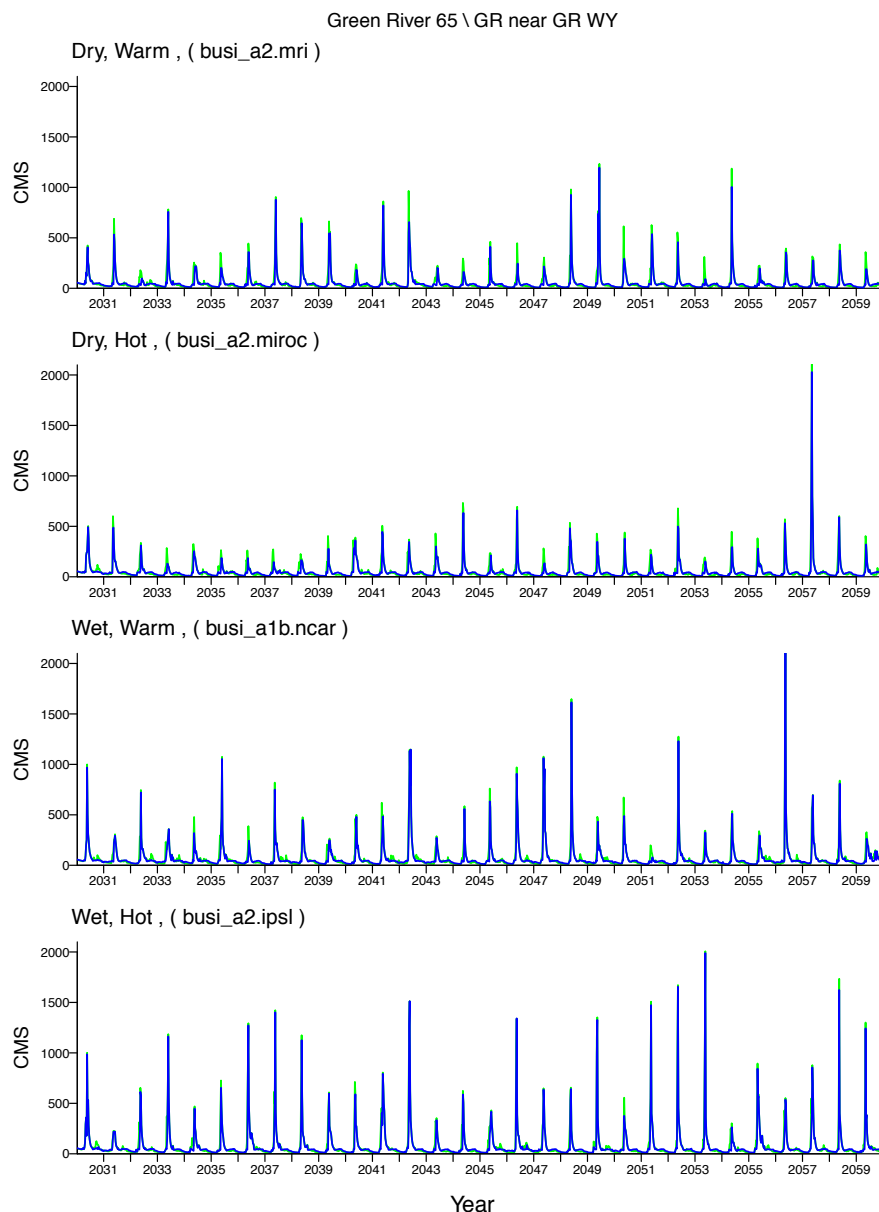


Figure 4.11: Modeled future weekly discharge at the focal lower network node “Green River near Green River, WY” under the 4 alternative climate scenarios and the ‘business-as-usual’ (blue) and ‘natural-flow-restored’ (green) WEAP configurations. As expected, decreases or increases in precipitation resulted in a clear division in flows between the ‘wet’ and ‘dry’ models, particularly evident in a comparison of the peaks resulting from the two ‘hot’ scenarios (second and fourth rows), but the characteristic annual snowmelt hydrograph was maintained for each of the downscaled temperature and precipitation projections. Though differences in climate model specification resulted in sharply diverging flow projections for any particular year, all of the GCMs yielded year-to-year variation in the sequence of high flow magnitude, with occasional very large peaks years followed by much smaller maxima (i.e., inter-annual stochasticity leading to favorable establishment patterns was present in the modeled discharge). The ‘natural-flow-restored’ configuration did not substantially alter annual high flow magnitude.

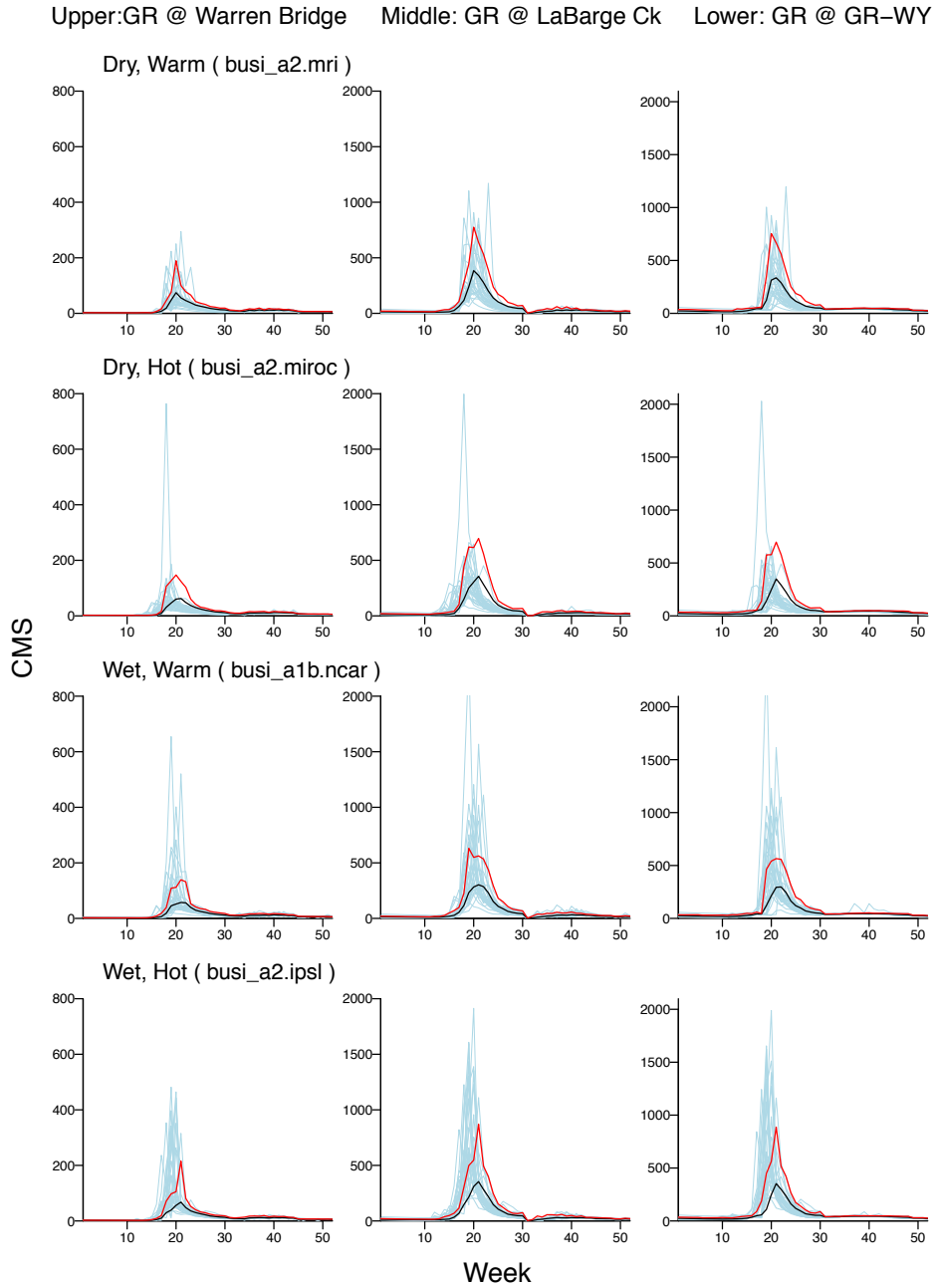


Figure 4.12: Projected future weekly discharge at different network positions (columns) under the ‘business-as-usual’ configuration. Flow during each future year (light blue) is overlaid on the median (black) and 95<sup>th</sup> percentile (red) of flow during each week in the historic period, calculated individually for each climate forcing (rows). The wet scenarios consistently generated high flows greater than the per-week, historic 95<sup>th</sup> percentile, while the dry scenarios only infrequently exceeded this threshold. This within-year perspective also reveals that the timing of the spring runoff peak was consistently advanced across years and nodes for all of the 4 GCMs.

## *Invasion Risk*

Simulation results supported the hypothesis that invasion risk would be greatest under the hottest, wettest climate scenario, given continuation of the management status quo, but this finding was contingent on the treatment of annual high flow timing. In the biological response model, the magnitude of projected annual high flows controlled the availability of suitable establishment area and the intensity of flood disturbance mortality relative to the overbank threshold defined by the median historic annual peak. Years in which high flows exceeded this magnitude thereby generated *Tamarix* seedling cover, and subsequent lower flow years led to increased adult abundance as younger stages matured.

However, the potential for such colonization was strongly dependent on whether the establishment success parameter was held constant or made a function of the week in which the annual high flow occurred (Figure 4.13). For example, in timing-independent simulations, adult *Tamarix* cover increased to the level designating high invasion risk under the regularly large floods produced by the ‘hot, wet’ climate scenario, and invasion risk was moderate for the 3 remaining GCMs at LEF units associated with the focal lower network node (Figure 4.13a, ‘Green River Near Green River, WY’ below Fontenelle Dam and the confluence of the Big Sandy River). In stark contrast, the relatively small and significantly earlier peak sequence of the ‘hot, dry’ scenario yielded no establishment opportunities at this location in a timing-sensitive simulation, and the inclusion of timing effects on *Tamarix* regeneration virtually eliminated the otherwise high invasion risk for the ‘hot, wet’ scenario (Figure 4.13b).

For timing-independent simulations, the invasion risk class for the ‘hot, wet’ scenario was reduced to moderate in upper-network, MEO settings, where disturbance intensity was assumed to be slightly greater than LEF units relative to the magnitude of overbank scaled

discharge (Figure 4.14a). However, this shift reflected a decrease in mean adult cover due to higher flood-driven mortality rather than diminished susceptibility to *Tamarix*, as seedling establishment simultaneously increased with the larger floods (e.g., as illustrated in the right panel of the middle row of Figure 4.7).

The effect of flood timing on model behavior was consistent across the two geomorphic settings and throughout the drainage network (Figure 4.15 and 4.16). For LEF units in timing-independent simulations, the highest risk was associated with the ‘hot, wet’ GCM that produced the greatest increases in yearly high flow magnitude, but all of the climate scenarios resulted in moderate to high mean adult cover (Figure 4.15). Yet the two hot scenarios showed the sharpest decline in adult cover for timing-sensitive simulations, as their warmer temperatures resulted in the earliest snowmelt runoff peaks. The spatial distribution of simulated *Tamarix* abundance largely followed from the assumption of differential flood disturbance intensities in LEF and MEO units, with the latter somewhat more common along tributaries in the upper network (Figure 4.16).

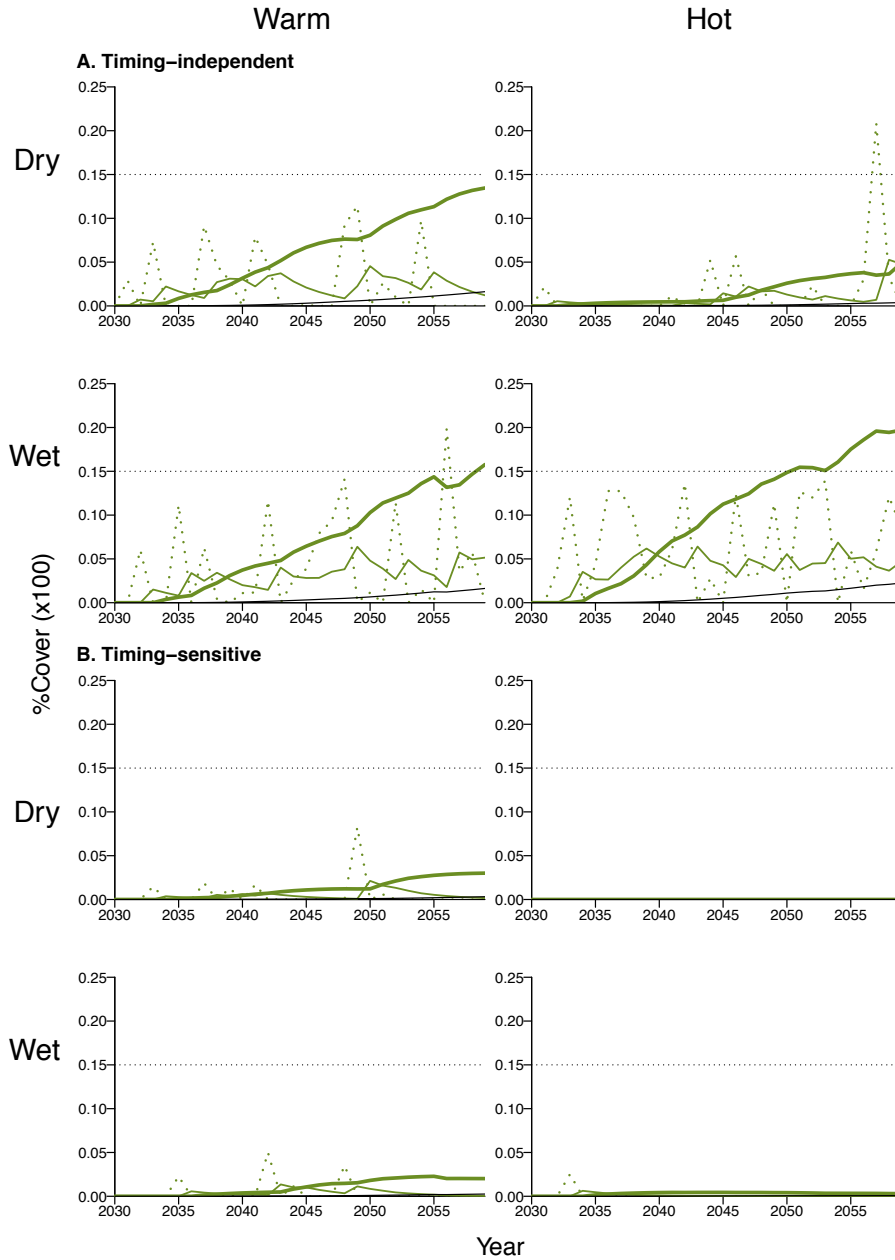


Figure 4.13: Simulated *Tamarix* abundance for a ‘Low Energy Floodplain’ (LEO) river unit at the focal lower network node “Green River near Green River, WY” under the 4 alternative climate scenarios and the ‘business-as-usual’ WEAP configuration. Panels illustrate the change through time of the seedling (dotted green), juvenile (light solid green), adult (heavy solid green) and dead (solid black) stages relative to the threshold designating high invasion risk (horizontal dotted line). A) Simulation runs with timing-independent establishment ( $estab_i = 0.5$ ) permitted *Tamarix* recruitment following yearly peaks greater than the historic median annual high flow. B) In contrast, the assumption that *Tamarix* establishment success was a function of the week in which high flow occurred entirely prevented colonization for the ‘hot, dry’ scenario and greatly reduced the adult cover present under the remaining climate forcing inputs.



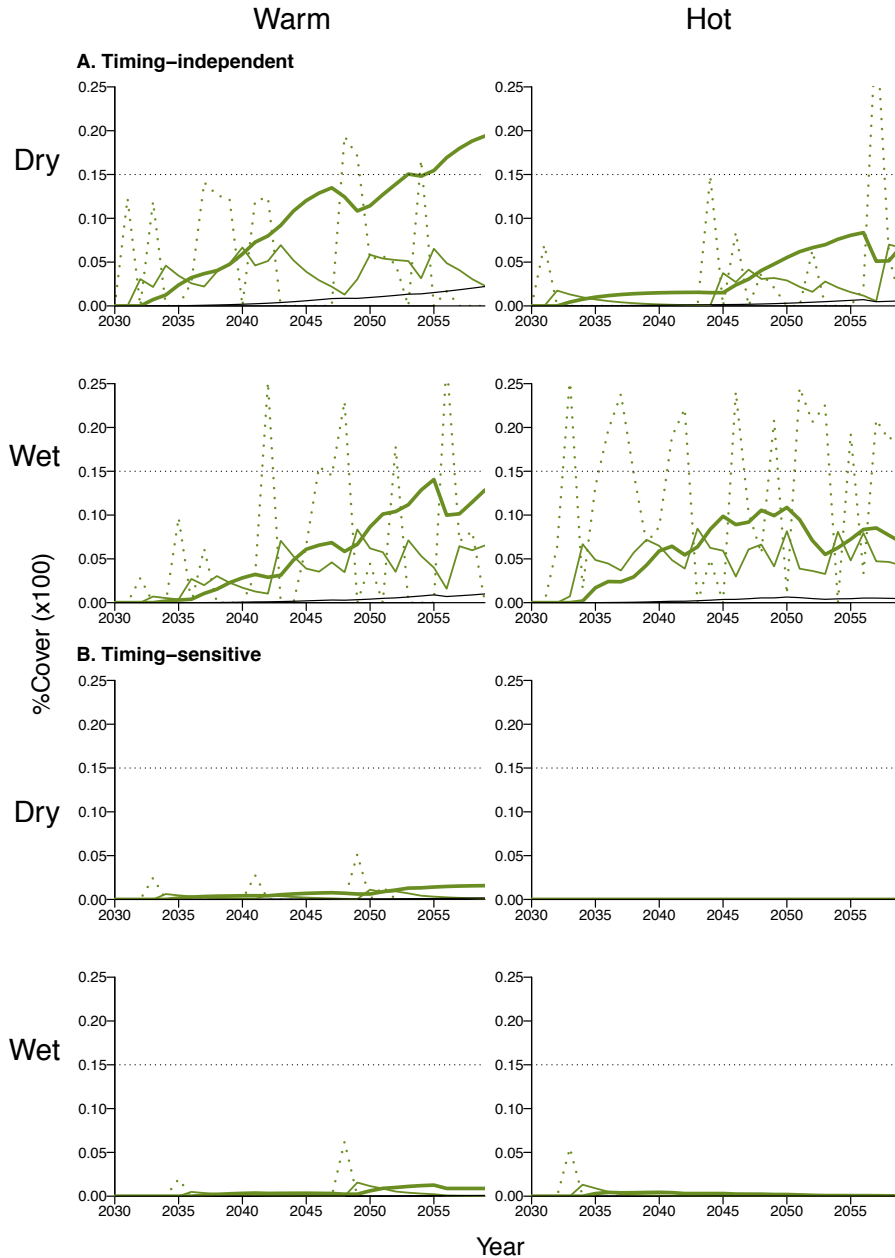


Figure 4.14: Simulated *Tamarix* abundance for a ‘Moderate Energy Open’ river unit at the focal upper network node “Green River near Warren Bridge” under the 4 alternative climate scenarios and the ‘business-as-usual’ WEAP configuration. Panel conventions follow Figure 4.13. As was the case for the lower energy, lower network node, the inclusion of peak flow timing as an influence on *Tamarix* establishment success dramatically reduced the simulated invasion risk. However, the assumption of slightly greater disturbance intensity relative to the scaled discharge magnitude in this setting altered the relationship among the climate scenarios for timing-independent simulations. Though the larger flood magnitudes of the ‘hot, wet’ scenario again led to the greatest establishment opportunities, the concomitantly higher disturbance mortality acted to limit adult cover and reduce the invasion risk class. Conversely, the increase in establishing seedling area for the ‘warm, dry’ scenario more than compensated for additional flood mortality, resulting in a shift from the ‘moderate’ to ‘high’ risk class.

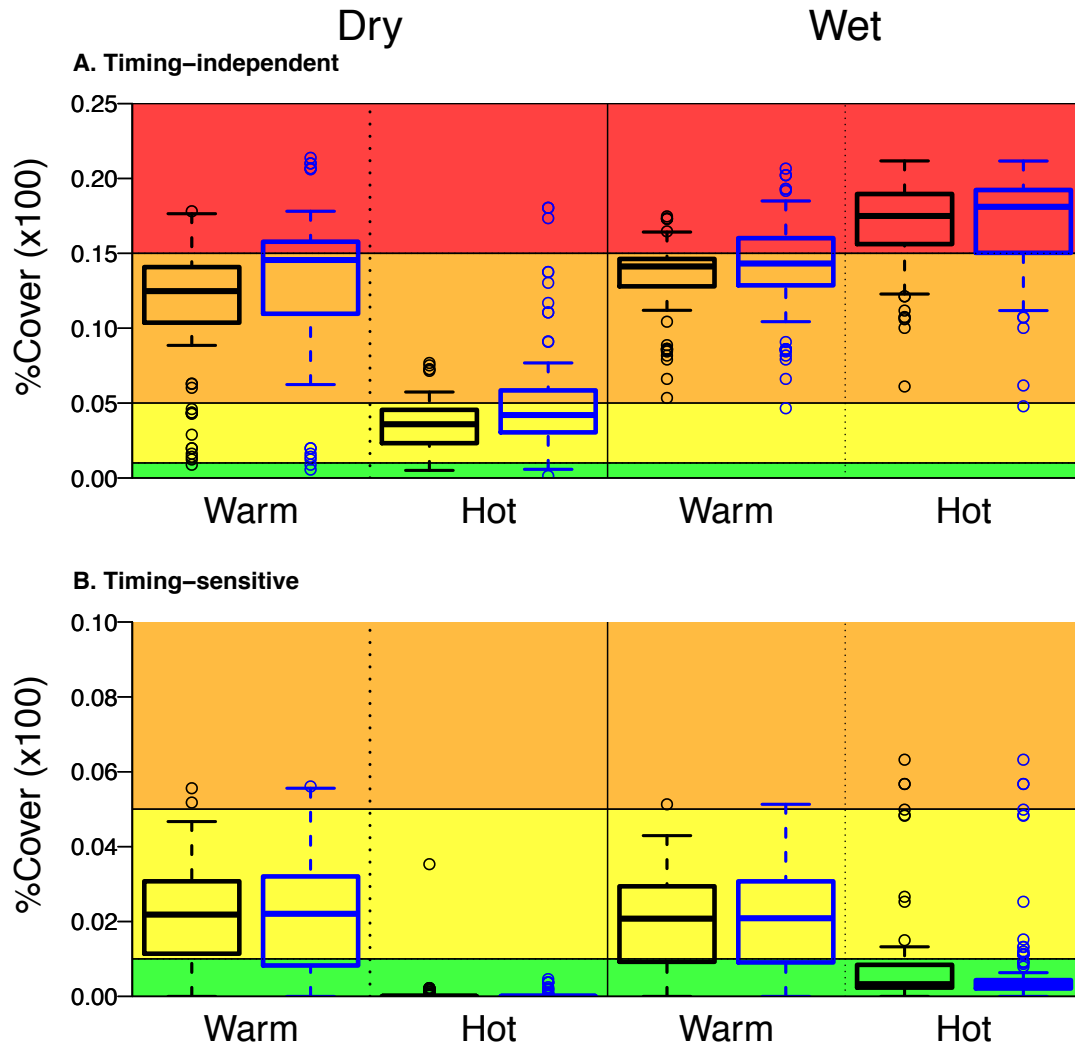


Figure 4.15: Simulated mean adult cover of *Tamarix* for all 'Low Energy Floodplain' units under the 4 climate forcing scenarios and 2 management configurations for timing-independent (A) and timing-sensitive (B) runs. Though the larger annual high flows of the 'hot, wet' GCM led to the highest risk for timing-independent model runs, this scenario also experienced the greatest decline in risk for timing-sensitive model runs due to earlier snowmelt runoff peaks. In addition, the combination of earlier and smaller peaks under the 'hot, dry' scenario nearly eliminated *Tamarix* establishment opportunities in timing-sensitive simulations. High flows under the 'natural-flows-restored' (blue) configuration were slightly larger than those under the 'business-as-usual' (black) simulations resulting in a minor trend toward greater *Tamarix* invasion risk for timing-independent runs (i.e., flood suppression by water management slightly decreased seedling establishment). However, annual peaks also arrived even earlier at many locations in the absence of management, thereby eliminating this difference in timing-sensitive simulations.

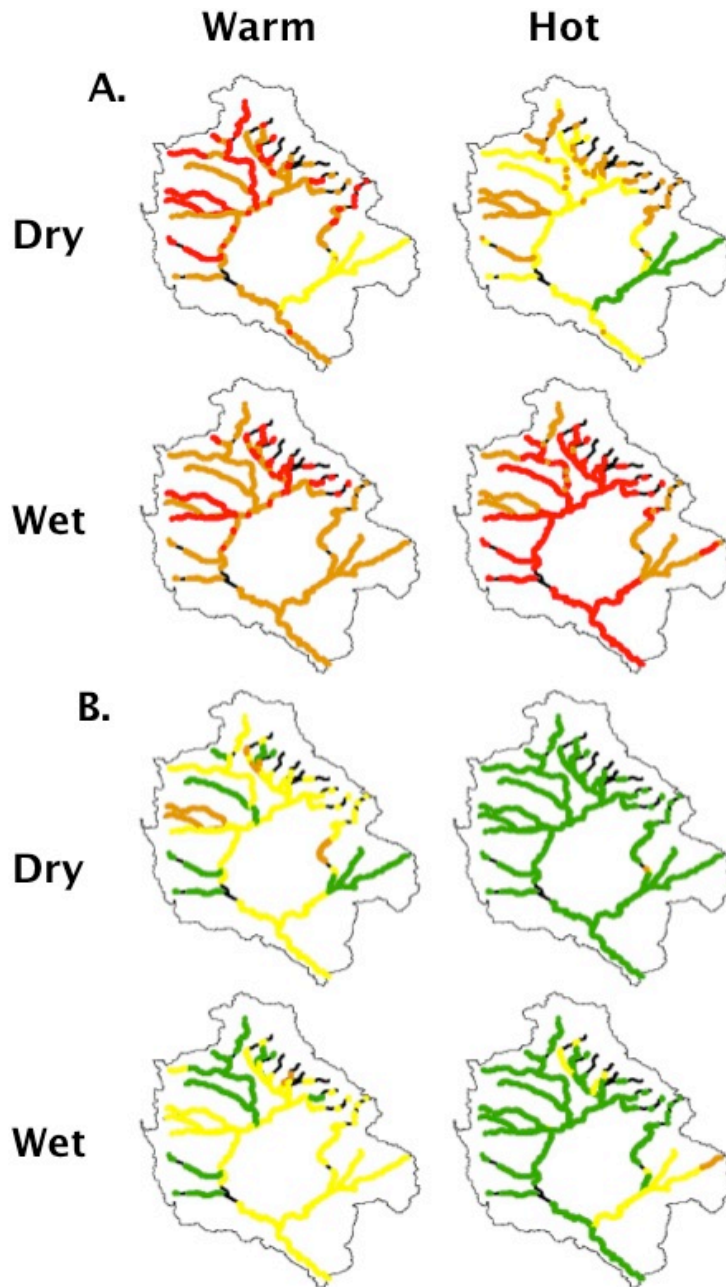


Figure 4.16: The spatial distribution of invasion risk classes measuring mean adult *Tamarix* cover during the last 5 years of model runs for each climate scenario. A) Timing-independent simulations resulted in low (yellow), moderate (orange) or high (red) relative risk for both LEF and MEO valley classes throughout the watershed, with the larger yearly floods under the ‘hot, wet’ scenario producing the most opportunities for seedling establishment. The very low (green) risk predicted for reaches along the Big Sandy River under the ‘hot, dry’ scenario reflected a paucity of recruitment opportunities as annual peak flows were seldom of greater magnitude than the historic median peak. B) Timing-sensitive simulations reduced invasion risk across scenarios and network locations, with the largest shifts evident for the hot scenarios with greater advancement in the week of annual high flow. The low risk predicted for the two ‘warm’ scenarios with the inclusion of timing reflected the conservative definition of the lower boundary of this class at 1% mean adult cover. Black sections indicate reaches that were not modeled.

## Discussion

This analysis used projected sequences of annual high flow to develop categorical predictions of relative invasion risk on the basis of first principles regarding *Tamarix* flow-response traits (i.e., reliance on flooding for establishment and increasing tolerance of flood disturbance mortality in mature stages). Results of this exploratory modeling effort indicated the need to question the assumption that a hotter, drier climate in the Western U.S. will increase the spread and dominance of *Tamarix*. More arid future conditions may indeed favor *Tamarix* over native riparian species with lower tolerance of water stress and soil salinity (Glenn and Nagler 2005). Observations of *Tamarix* physiology support this possibility if extended droughts cause currently perennial channels to periodically dry, groundwater levels to decline, or floodplain soils to salinize with diminished flushing flows. Expanded reservoir storage and intensified groundwater pumping could further promote the non-native by exacerbating these changes. Yet, ongoing *Tamarix* dominance within riparian zones it already occupies and expansion into currently unsuitable watersheds rendered vulnerable by warming will require disturbance to create the open, moist patches necessary for successful germination and sapling growth. Accordingly, the realized extent of *Tamarix* colonization and population growth within newly suitable territory appears likely to depend on whether climate and management alter basin hydrology in ways that promote recruitment.

If sporadic but more extreme storms during the growing season produce scouring floods while *Tamarix* seeds are viable but after the period of native seed release, then *Tamarix* may establish relatively free from competition on any post-flood riparian surfaces that provide adequate soil moisture for elongating seedling roots. Artificial water bodies such as irrigation ditches and reservoir margins that are subject to regular stage fluctuations may also offer an

important source of establishment sites and support abundant *Tamarix* (Lesica and Miles 2001, Lehnhoff et al. 2011). In addition, disturbance agents other than flooding (e.g., grazing) may clear riparian vegetation and perhaps create colonization opportunities in conjunction with sufficient localized precipitation. Thus, given a pathway to recruitment in a hotter, drier future, *Tamarix* may certainly constitute a greater portion of riparian communities along rivers to the north of its current distribution.

However, along rivers with flow regimes driven primarily by snow accumulation and melt, the trends in magnitude, within-year timing, and between-year frequency of high flows will interact to determine whether sufficient establishment opportunities arise. If less winter precipitation results in annual high flows no larger than those that occurred historically, and if concerns over water scarcity prompt additional efforts to expand storage capacity and to capture more of the yearly peak flow, then the relative lack of flood disturbance may hinder *Tamarix* expansion, particularly if existing water infrastructure and vegetation have already reduced meandering or lateral erosion and stabilized channel form. A hotter, *wetter* future may not necessarily favor *Tamarix* invasion either, even if increased winter precipitation generates larger or historically comparable high flows with the competence to scour and rework bottomland surfaces. Progressively earlier arrival of these peaks, due to seasonally advanced snowmelt, may leave disturbed patches too dry when *Tamarix* seeds are released or may favor competing native species with reproductive phenology better suited to early spring floods. Yet, plants in the southern portion of the current distribution begin to release seeds prior to May (Shafroth et al. 1998), and introduced *Tamarix* has hybridized and shown the potential for rapid evolutionary change (Sexton et al. 2002, Friedman et al. 2008, Gaskin and Kazmer 2009). Sufficient gene flow across latitude could therefore enable *Tamarix* to ‘keep pace’ with shifts in flood timing and

eliminate any damping effect of early peaks on invasion. Though the timing-independent model results conceivably represent a ‘worst-case’ scenario in this regard, the relationship between flow seasonality and adaptation or plasticity of *Tamarix* seed release phenology certainly warrants further study. In the event that *Tamarix* does adapt the timing of its seed production to match earlier runoff peaks, the stochastic year-to-year sequence of high flow magnitudes will also exert an important control on whether establishing cohorts survive to maturity or are eliminated by subsequent floods {Birken, 2006 #224;Cooper, 2003 #221}. A large yearly peak followed by several smaller ones (or the comparable effect of initial filling of a storage reservoir) can favor pulsed recruitment of *Tamarix* and other woody pioneer species. Dams that store yearly snowmelt peaks for later release or withdrawal may reduce interannual variation in high flow magnitude and thereby diminish the (post-closure) probability of this pattern along regulated rivers. But how climate change will affect the periodicity of large floods and their ecological consequences also remains a question in need of more investigation.

This exploratory modeling involved a greatly simplified representation of riparian ecosystem dynamics and parameter values generalized from the literature describing the ecological attributes of *Tamarix*. However, even given precisely calibrated parameters in a more detailed and complex biological response model, considerable uncertainty surrounds the emissions scenarios used as inputs to climate models (e.g., the highest emissions scenarios may underestimate actual greenhouse gases), the consistency between past and future levels of temporal autocorrelation in driving variables (e.g., non-stationarity in multi-decadal climate processes), and the ability of climate and hydrologic models to represent future patterns of unusual climate elements with the potential for disproportionately lasting effects (e.g., the early 1980s). Options such as bootstrapping projected flow records within decades or including a large

ensemble of GCM runs could generate a sample of forcing sequences that retain long-term trends while permitting estimates of the distribution of an ecological response (e.g., population growth). Nonetheless, uncertainty at the distributional extremes and in the interannual sequence of values for key variables in the underlying physical systems presents a fundamental challenge to quantitatively accurate estimates of the abundance of riverine species with pulsed recruitment, such as *Tamarix*. Clearly, integrating dynamic models of riverine populations and communities with projected sequences of driving hydrologic variables will remain an area in need of additional research into the foreseeable future (Shenton et al. 2012).

This *Tamarix* response model emphasized annual high flow as a primary control on recruitment and persistence. Although seedling water stress could be thought to implicitly enter the stage updating functions through the parameter controlling maturation into the juvenile stage, values of this parameter were kept time-invariant and the model did not explicitly incorporate the effects of base flows. However, the magnitude and duration of annual low flow periods may exert an important influence on *Tamarix* colonization and dominance, particularly as these flow regime attributes relate to alluvial groundwater subsidies during the growing season (Graf 1982). Rapid root elongation may provide *Tamarix* seedlings with greater tolerance of declining water tables than members of the *Populus* genus (Horton and Clark 2001, Li et al. 2013), but low flows later in the growing season may also impose water stress on immature plants and reduce seedling survival. Reduced base flow magnitude, to the point of intermittency, may also favor established *Tamarix* relative to other riparian trees due to its deep taproots and high water use efficiency (Shafroth et al. 2000, Glenn and Nagler 2005, Lite and Stromberg 2005, Stromberg et al. 2007b, Stromberg et al. 2010). Nonetheless, greater *Tamarix* abundance was associated with elevated summer flows along the perennial rivers surveyed by Merritt and Poff (2010) and Mortenson and

Weisberg (2010), perhaps as a direct result of more favorable growing conditions or perhaps as a consequence of correlations with unmeasured historical factors related to regulation.

Whether or not higher growing season flows favor *Tamarix* recruitment and abundance, WEAP results indicated that base flows are likely to decrease in coming decades, notwithstanding river regulation that raises summer discharge to meet downstream demand (Figure 4.17). Climate change effects on summer low flow magnitude were apparent among the GCMs, with dry scenarios producing significant reductions relative to the median of historic yearly summer minimum discharge and wet scenarios generating values no greater than historic (Figure 4.17). Furthermore, these effects varied with network position as a result of diversions that significantly reduced flow relative to the ‘natural-flow-restored’ configuration and dams that elevated summer minimum discharge. The stark differences between low flow conditions with and without withdrawals and dam operations indicated one way in which climate-driven flow alteration will occur within the template of “serially disconnected” river networks (Ward and Stanford 1995). The modeled decrease in summer minimum flows could be viewed as amplifying the predicted invasion risk if it favors *Tamarix* relative to native species with less drought tolerant physiology, or as diminishing the chances of successful colonization if greater water stress reduces seedling survival. The natural complexity of the alluvial groundwater dynamics affecting *Tamarix* invasion risk follows from the interaction of multiple site-scale factors such as floodplain soil porosity, depth to bedrock and overall vegetation cover. How these interactions will combine with altered precipitation, runoff and flow management to promote or curtail *Tamarix* and other woody riparian vegetation also clearly demands additional research.



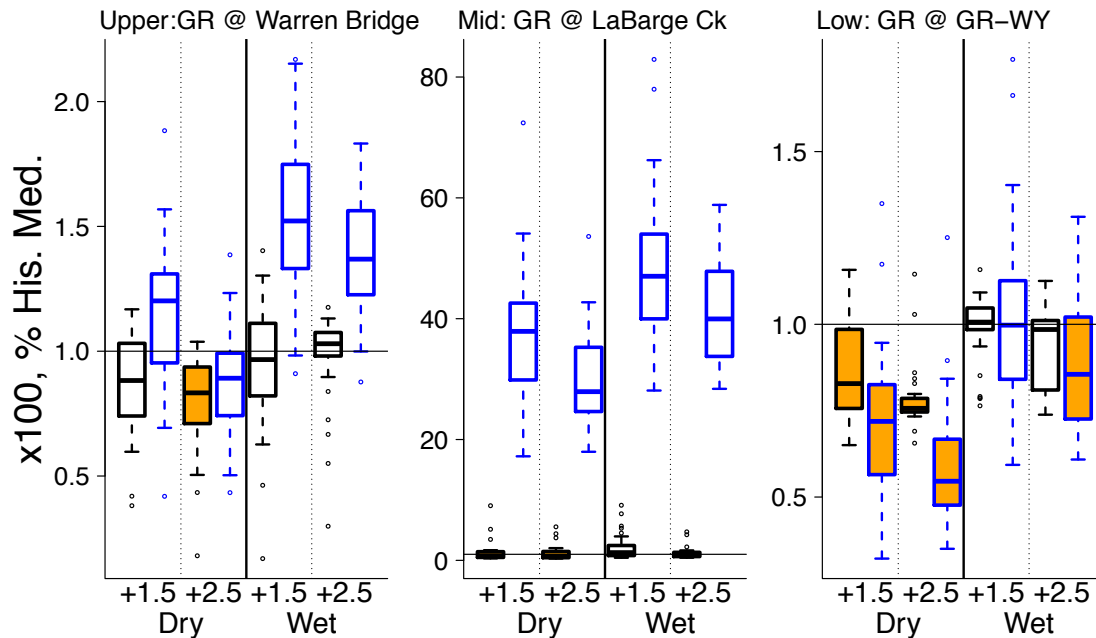


Figure 4.17: Projected future low flow magnitude as a proportion of the median historic summer minimum. The minimum weekly magnitude was measured between the first week in June and the first week of September (weeks 22 to 35) for each year of the historic and future periods per-GCM. The distribution of 30 future values divided by the historic median is shown for the four climate inputs (+1.5 and +2.5 refer to the ‘warm’ and ‘hot’ GCMs respectively), each modeled under the ‘business-as-usual’ (black) and ‘natural flow restored’ (blue) WEAP configurations. Left to right, panels illustrate upper, middle and lower network nodes, and patterns at the three focal nodes were representative of other locations at similar network positions. Boxes are colored orange if the future distribution was significantly reduced from the historic in a Wilcoxon rank sum test. The effect of removing water management was especially strong in mid-network reaches subject to diversions for irrigation and other demand, where future ‘natural’ summer minimums were 30-50 times greater than historic lows, despite overall reductions in later season flow related to increased temperatures and earlier spring runoff. In contrast, the lower ‘natural’ minimum flows at the most downstream node revealed how releases from Fontenelle dam and reservoir elevated summer base flow under the ‘business’ configuration.

Model results reinforced the value of regular monitoring programs to gauge whether temperature increases are leading to greater *Tamarix* occurrences within the Upper Green River watershed (Fortin et al. 2010). However, the plausibly low to moderate invasion risk associated with the limits to establishment imposed by earlier peak timing, possibly in conjunction with reduced peak magnitude, also suggested that actions such as promoting native tree recruitment or controlling other non-native species should receive higher priority than *Tamarix* control as

management resources are allocated to climate change adaptation. If opportunistic *Tamarix* control is deemed appropriate in the UGR or at other locations that currently provide only marginally suitable habitat, then the mechanical removal of isolated individuals will likely suffice to meet the precautionary objective of preventing mature stands that could act as localized seed sources.

Nonetheless, these results also indicated the potential scope for management designed to favor desired native species (i.e., in the *Populus* and *Salix* genera) under even the hottest, driest scenario. Along reaches above Fontenelle Dam, the large increases in summer base flows under the ‘natural-flow-restored’ scenario suggested that even moderately diminished diversions could favor the growth of any germinating seedlings and the persistence of adult stands (i.e., by increasing the availability of alluvial groundwater) by reducing water stress. Though likely to require careful negotiation, the lease or purchase of rights to currently withdrawn water for the purpose of ‘returning’ it to the channel could help to promote regeneration of native vegetation. Moreover, keeping more water in the river during the warmest portion of the year would likely benefit numerous other aquatic taxa dependent on cooler stream temperatures.

Observed annual high flows are already diminished by dam operations along much of the main channel of the Upper Green, and strongly so below Fontenelle Dam (Figure 4.18). To the extent legally possible under existing contractual obligations, the entities responsible for managing dams in the watershed might therefore attempt to ‘shape’ yearly peaks to favor native trees (Rood et al. 2003, Rood et al. 2005). In addition, managers might seek to avoid later season high flow releases when *Tamarix* seed availability is likely to be greater than that of native trees. However, managed high flows must also account for fluvial geomorphic context {Shafroth, 2010 #102}. Elevated growing season flows and diminished floods below Fontenelle may have created

conditions favorable to the survival of mature vegetation, but this flow modification may have simultaneously limited the germination of native pioneer seedlings to narrow bands within a steeper, thinner riparian zone immediately bordering the active channel (D. Auerbach, personal observation). Consequently, direct native tree re-planting in less vulnerable floodplain locations with known depths to groundwater could enable young trees to ‘escape’ the annual cycle of re-colonizing the same regularly flooded locations. Though such a strategy of ‘farming cottonwood’ in specific locations (e.g., for recreational value) may amount to conceding the improbability of deeper functional restoration such as dam removal and retiring water rights at the watershed scale (Beechie et al. 2010), it may constitute a preferable alternative to population declines under greater drought stress and limited regeneration.

In the absence of intervention, dam-altered annual peaks and water stress increased by a warming climate could also promote the non-native tree Russian olive (*Elaeagnus angustifolia*) or upland, high-desert plants within the riparian zones of the UGR (Reynolds and Cooper 2010, Nagler et al. 2011). Russian olive is already locally abundant along portions of the UGR {Fortin, 2010 #95}. Relative to *Tamarix* and native pioneer species, Russian olive produces much larger seeds that are less dependent on overbank discharge to create disturbed areas for establishment (Katz and Shafroth 2003, Nagler et al. 2011). Shade tolerant seedlings and the ability to thrive under current winter minimum temperatures may therefore enable this species to occupy much of the riparian zone area that might otherwise become vulnerable to *Tamarix* invasion. Higher magnitude floods such as those generated by the hottest, wettest climate scenario could conceivably cause appreciable Russian olive mortality, particularly for younger trees. However, existing water control infrastructure reduces the likelihood of very large scouring floods that might remove Russian olive. Furthermore, the regeneration traits of Russian olive imply less

reliance on pulses of suitable establishment area. This may render the species less sensitive to the hydrologic differences between wet and dry climate scenarios and therefore well suited to either eventuality.

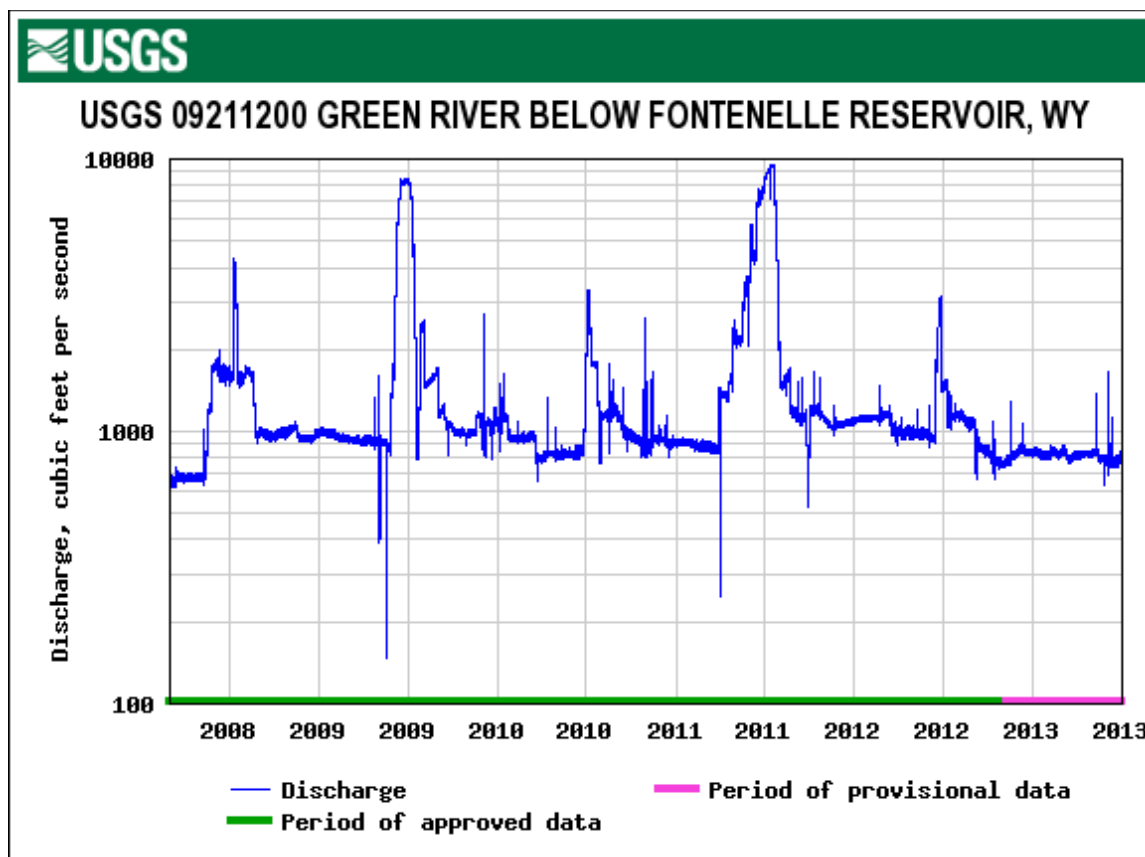


Figure 4.18: Daily flow between March 1<sup>st</sup>, 2008 and July 1<sup>st</sup>, 2013 below Fontenelle Dam and reservoir for USGS gage 09211200. As is evident from the ‘square’ 2008 high flow, dam operations strongly affect flows, and therefore riparian conditions, along the main channel of the Upper Green. Though reservoir management coordinated with the needs of municipalities in the UGR and stakeholders lower in the Colorado River basin may limit operational flexibility, opportunities to ‘naturalize’ releases from Fontenelle to benefit native riparian vegetation may exist, particularly during wetter years. For example, management of the post-peak stage decline following a future year similar to 2011 might ensure that conditions remain within the fairly well characterized Recruitment Box requirements of cottonwood. Furthermore, avoiding floods later in the year (e.g., 2010) might also reduce the risk of *Tamarix* invasion by preventing germination opportunities at times that are more likely to favor the non-native over native pioneer species. Note that the sequence of annual high flows during the 2011-2013 years might have provided the pattern of a large magnitude peak followed by smaller ones that is most likely to generate a pulse of recruitment for pioneer riparian vegetation.

In addition to competitive ecological interactions, consumer-resource effects from the widespread release and dispersal of the *Tamarix* biocontrol beetle (*Diorhabda* spp.) may also significantly affect the risk of *Tamarix* invasion, particularly relative to the ongoing spread of Russian olive. Populations of these beetles have grown and extensively defoliated *Tamarix* within portions of the Colorado River drainage downstream from the UGR, but the long-term consequences of biocontrol remain uncertain (Hultine et al. 2010, Nagler and Glenn 2013). Regardless of whether or not *Diorhabda* attacks eventually kill plants, beetle herbivory that stresses plants may have the important sub-lethal effect of reducing reproductive output, perhaps limiting the rate of spread into newly suitable habitat or reducing re-colonization of mechanically cleared areas. Additional research into these interactions is needed, particularly as the beetle also evolves in response to changing climate conditions.

Riparian ecosystems have been proposed as climate adaptation “hotspots” due to their high sensitivity to changing hydro-climatic regimes, their high potential for resilience due to historically dynamic conditions, and the high value of the benefits they deliver (Capon et al. 2013, Stromberg et al. 2013). These attributes certainly apply to riparian zones within arid and semi-arid landscapes of the western U.S., and managing for their associated benefits and biodiversity will require ongoing attention to the potential for climate warming to facilitate the expansion of introduced species such as *Tamarix*. Discussing the strategic value of *Tamarix* control and removal efforts, Nagler et al. (2011) offered a conceptual division with utility for the problem of characterizing invasion risk. These authors proposed that *Tamarix* may naturally become a sub-dominant element of riparian communities along free-flowing rivers that remain suited to the regeneration niches of native pioneer vegetation. In contrast, they suggested *Tamarix* may dominate highly regulated systems due to its adaptations to seasonally irregular

establishment opportunities, deeper groundwater, and salinized soils. Yet they acknowledged that outcomes are quite uncertain along the many rivers with flow regimes between these two ends of the spectrum of hydrologic alteration. My research demonstrates how a watershed scale modeling approach linking climate projections, hydrologic processes informed by human water demand, fluvial geomorphic drainage network divisions, and flow-mediated change in riparian populations can provide insight into invasion risk in this ‘middle ground’ of flow modification. Nonetheless, continued monitoring, modeling and analysis are required to address whether increased temperatures and precipitation changes will push these reaches toward the conditions characteristic of highly regulated systems or will result in novel regimes with larger, earlier floods and lower summer flows – or, whether ecologically-informed water management can meet human needs while preserving characteristics of the historic regime that aid desired native species.

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## CONCLUSION

The ecological integrity of rivers is vital to our long-term well-being, but society faces challenging decisions concerning the appropriate allocation of water resources to meet immediate human needs and the health of freshwater ecosystems. Riparian zones support abundant biodiversity and produce valuable ecosystem services, and the changes in their vegetation communities that may result from these water management decisions therefore require assessment. Consideration of the flow response traits that mediate plant recruitment and persistence can serve to structure process-based models of vegetation responses to hydrologic alteration, and such models can then inform our understanding of the consequences of dams and climate change. River regulation that reduces the size and frequency of flooding may decrease disturbance mortality while diminishing establishment opportunities for pioneer vegetation, with the eventual effect of favoring a shift toward greater relative abundance of upland trait types. Restoring flow variation may return functional community evenness, but the trajectory of recovery is likely to be contingent on the specific sequence of high flow events as well as the degree of dispersal limitation and the influence of fluvial geomorphic legacies of damming. Though climate changes may increase the extent of potentially suitable habitat for introduced aquatic and riparian species, the interaction of multiple flow regime attributes will govern biological invasions along river corridors. Characterizing the future colonization and persistence of introduced riparian plants such as *Tamarix* therefore requires assessment methods that account for hydrologic variation within the context of existing or planned water management practices.