

Linking river flow regimes to riparian plant guilds: a community-wide modeling approach

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Abstract. Modeling riparian plant dynamics along rivers is complicated by the fact that plants have different edaphic and hydrologic requirements at different life stages. With intensifying human demands for water and continued human alteration of rivers, there is a growing need for predicting responses of vegetation to flow alteration, including responses related to climate change and river flow management. We developed a coupled structured population model that combines stage-specific responses of plant guilds with specific attributes of river hydrologic regime. The model uses information on the vital rates of guilds as they relate to different hydrologic conditions (flood, drought, and baseflow), but deliberately omits biotic interactions from the structure (interaction neutral). Our intent was to (1) consolidate key vital rates concerning plant population dynamics and to incorporate these data into a quantitative framework, (2) determine whether complex plant stand dynamics, including biotic interactions, can be predicted from basic vital rates and river hydrology, and (3) project how altered flow regimes might affect riparian communities. We illustrated the approach using five flow-response guilds that encompass much of the river floodplain community: hydriplant, xeroriparian shrub, hydriplant shrub, mesoriparian meadow, and desert shrub. We also developed novel network-based tools for predicting community-wide effects of climate-driven shifts and deliberately altered flow regimes. The model recovered known patterns of hydriplant vs. xeroriparian shrub dominance, including the relative proportion of these two guilds as a function of river flow modification. By simulating flow alteration scenarios ranging from increased drought to shifts in flood timing, the model predicted that mature hydriplant forest should be most abundant near the observed natural flow regime. Multiguild sensitivity analysis identified substantial network connectivity (many connected nodes) and biotic linkage (strong pairwise connections between nodes) under natural flow regime conditions. Both connectivity and linkage were substantially reduced under drought and other flow-alteration scenarios, suggesting that community structure is destabilized under such conditions. This structured population modeling approach provides a useful tool for understanding the community-wide effects of altered flow regimes due to climate change and management actions that influence river flow regime.

Key words: coupled matrix model; flow response guild; flow regime; interaction neutral; neutral theory; riparian community; stochastic population model.

INTRODUCTION

In light of the widespread damming and regulation of most major rivers worldwide, there is a need to manage downstream flow regimes to support ecosystem integrity and functioning while concurrently meeting human water needs (Naiman et al. 2002, Nilsson et al. 2005, Poff et al. 2010, Olden et al. 2014). Flow regulation, and associated effects on water quality and sediment regimes, has induced particularly significant impacts on riverine riparian ecosystems. These include alteration of channel processes and form (Grams and Schmidt 2002, Gaeuman et al. 2005),

shifts in riparian plant community composition (Merritt et al. 2010, Stromberg et al. 2012), declines of native-dominated riparian forests (Stromberg et al. 2007, Merritt and Poff 2010), and increased abundance of nonnative and ruderal plant species along rivers (Ringold et al. 2008). In conjunction with increased extraction from rivers, climate change will likely have confounding or amplifying effects on riparian ecosystems (Palmer et al. 2009, Ström et al. 2011). In the western United States, most climate change projections suggest less winter precipitation, less snowpack, earlier snowmelt runoff, and lower total discharge under the most likely greenhouse gas emission scenarios (Seager et al. 2013). Furthermore, the frequency and severity of drought is expected to increase in already arid parts of the North America (Dai 2011), resulting in demonstrable impacts on riverine biota (Jaeger et al. 2014).

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In the western United States, the introduced Eurasian shrub tamarisk and its hybrids (primarily *Tamarix ramosissima* and *T. chinensis*) have become widespread in dryland stream riparian zones (Friedman et al. 2005). During the same time period during which tamarisk shrublands became prevalent along western North American rivers, native cottonwood (*Populus deltoides*)-dominated forests declined precipitously (Rood and Mahoney 1990). Because cottonwood-dominated riparian forests are among the most species rich riparian ecosystems in western North America, their decline is a major conservation concern (Poff et al. 2007). At present, cottonwood forests form the most extensive deciduous forests in arid parts of western North America, and empirical data and population modeling indicate that cottonwood population structure is governed by characteristics of the streamflow regime (Lytle and Merritt 2004). Even moderate alterations to streamflow regime can produce dramatic shifts in dominant riparian species and alter the physiognomy and functioning of riparian communities (Dixon and Turner 2006, Stromberg et al. 2007, Merritt and Poff 2010).

Riparian flow response guilds are non-taxonomic groups of species that have similar morphological and physiological trait syndromes and as a consequence, the species in these guilds respond to water availability and fluvial disturbance in similar ways (Merritt et al. 2010). Grouping species based upon convergent adaptations facilitates modeling and transferability of models from one system to the next (McGill et al. 2006), even across regions, enabling predictions of guild distributions under a range of possible climate scenarios and flow regimes (Rivaes et al. 2014). Using data obtained from field studies, historical aerial photos of vegetation plots, and other sources, we specify the vital rates of each guild (survivorship, growth, fecundity) as they relate to the abiotic environment (primarily floods and droughts). The guild approach allows us to leverage these site- and species-specific data sets to make inferences that are relevant to other ecological systems.

The interaction-neutral modeling approach we utilize here deliberately omits direct biotic interactions between guilds. Between-guild interactions, such as competition, are instead obtained post hoc via sensitivity and elasticity analysis. An interaction-neutral approach allows us to reveal biotic interactions (e.g., pairwise competition, keystone status) from the model structure, via the manifestation of different guild's collective life histories within a dynamic, disturbance-prone, floodplain environment. Thus, our modeling approach is neutral with respect to biotic interactions, because these are deliberately omitted, but strongly niche based with respect to autecology, because vital rates are well-specified. This interaction-neutral approach lies firmly in the middle of a continuum bounded at one end by neutral biodiversity models, which specify nothing of individual species' biology (Hubbell 2001), and at the other end by food web models that specify a priori pairwise species interactions (Williams and Martinez 2000). An advantage of the

interaction-neutral approach is that it requires little or no prior knowledge of pairwise competition or interaction coefficients. A disadvantage is that it requires a detailed empirical understanding of each species or guild's relationship to its abiotic environment as specified by vital rates.

In this paper, we first develop a general model that can be extended to any number of riparian plant species or guilds occurring on a river floodplain. We then parameterize the model for five guilds that represent a wide range of functional vegetation types present throughout western North American dryland rivers and aridland streams worldwide (Aguiar et al. 2013, Stromberg and Merritt 2015): hydrioparian tree, xeroriparian shrub, hydrioparian shrub, mesoriparian meadow, and desert shrub. We use this framework to explore flow scenarios relevant to conservation and management of riparian ecosystems. We then develop new network-based tools derived from sensitivity and elasticity analysis that can be used to identify keystone species (high number of network connections) and important interactions (strong pairwise connectivity) under a variety of environmental contexts.

METHODS

General model structure

Our model expands on a previous single-species version (Lytle and Merritt 2004) by allowing multiple guilds of species that share similar vital rates to simultaneously occupy a dynamic floodplain zone. Each guild j is described by a stage-based matrix $\mathbf{N}_j(t+1) = \mathbf{A}_j(t)\mathbf{N}_j(t)$, where $\mathbf{N}_j(t)$ is a vector containing stage abundances and $\mathbf{A}_j(t)$ is a set of transition matrices that fluctuate according to variation in the hydrograph (Caswell 2001). Thus, the population dynamics of each guild are determined primarily by how their vital rates (mortality, fecundity, self-thinning) are affected by annual cycles of flooding and drought.

This modeling approach can work equally well with species or guilds, but for generality to dryland riparian ecosystems worldwide, we modeled five guilds representing key life history types. The hydrioparian tree guild (typified by *Populus fremontii* in the southwestern United States) is characterized by long-lived, flood-adapted species that depend on freshly scoured bare substrates for recruitment. The xeroriparian shrub guild (e.g., *Tamarix ramosissima*, *T. chinensis*, and hybrids) is characterized by species that have a life history structure similar to hydrioparian trees but with deeper roots and shorter stems, and thus lower drought mortality rates, shorter age to maturity, and a larger time window of fecundity. Hydrioparian shrub (e.g., *Salix exigua*) is a guild that represents active-floodplain specialist shrubs and small trees that have high resilience to flooding and recruit aggressively following floods, but are prone to mortality during drought years. Mesoriparian meadow is a guild of perennial grasses and forbs, such as slender wheatgrass (*Elymus trachycaulus*), Canada wild rye

(*Elymus canadensis*), and horseweed (*Conyza canadensis*), that recruit during flood years and whose adults are moderately tolerant of flooding and drought. Desert shrub is a guild of primarily upland, drought-tolerant shrubs, such as big sage (*Artemisia tridentata*), which continue to recruit and grow during drought years but suffer high mortality from floods (Dalglish et al. 2011).

The model quantifies floodplain dynamics at the reach scale. The total potential floodplain habitat, K , represents the size of the river reach. Within K , floods, droughts, and senescence may remove individuals according to their vital rates, thereby creating space for new recruitment. The model assumes that the total floodplain habitat K remains constant across years, although river meandering changes the type and proportion of specific habitats across years. As with Lytle and Merritt (2004) the approach is not spatially explicit, in that we do not keep track of the location of individual plants. Rather, spatial structure is implicit in the manner that vital rates interact with population structure. For example, the empirically measured mortality rate of hydriparian tree seedlings due to flooding tends to be high, which is due to the fact that young hydriparian trees usually occur near the active channel on point bars that experience dynamic scouring and burial (Cooper et al. 1999, Manners et al. 2015). Older hydriparian trees experience lower mortality, partly due to their position on higher terraces away from the active channel, as active channels abandon surfaces as a result of channel migration. Importantly, we obtain vital rates empirically from field studies of existing stands observed over time (Appendix S1). Community dynamics arise directly from the interaction of each guild's vital rates with particular sequences of flooding and drought. The spatially implicit structure of our modeling approach facilitates the exploration of population dynamics generally, without depending on a particular landscape or spatial arrangement of stream channels, fluvial surfaces, or vegetation. The space occupied by any particular guild stage (K_{ij}) and its population size (N_{ij}) are proportional to each other via self-thinning rates (b_{ij}) derived from stage-specific stem densities (where i is the stage and j is the guild). This allows both the number of individuals and the floodplain area (m^2) occupied by each class to be estimated over time. See Lytle and Merritt (2004) for a detailed explanation of how spatial position in the floodplain is implicitly incorporated into this modeling approach.

Recruitment

Recruitment for hydriparian tree and xeriparian shrub conforms to the "recruitment box model" for riparian plants (Mahoney and Rood 1998). For these two guilds, recruitment takes place only in years that meet the following conditions: a scouring flood occurs, at least part of the receding limb of the hydrograph occurs during the period of seed release, and at least one seed-producing tree is present in the river reach. In years that meet these

requirements, the degree of recruitment success is determined by availability of bare substrates (created by mortality of existing vegetation during the flood), rate of hydrograph decline, and the degree to which flooding is synchronized with seed set. Because this is a multi-guild model, recruitment is potentially affected by all guilds occupying the riparian zone, so this interdependence is incorporated into the recruitment function $F_j(t)$. For a guild j , the upper limit on recruitment is determined by the total area of bare substrates that become available following the flood. This upper limit is modified by the rate of hydrograph stage decline for each guild, $g_j(h)$, and the proportion of post-flood days that occur during seed set, $p_j(h)$, so that

$$F_j(t+1) = \left(K - \sum_{j=1}^n \sum_{i=2}^m K_{ij}(t+1) \right) \times p_j(h) g_j(h) \quad (1)$$

where $K_{ij}(t+1)$ is the space that will be occupied by the i th stage of the j th guild following a flood. There is a total of n guilds each with m stages, and K is the total space available to all riparian guilds within the reach. Eq. 1 introduces generalized density dependence into the model because the recruitment success of any given guild is affected by the aggregate density of all individuals on the landscape.

We assume that reproduction is independent of the number of reproductive adults present (i.e., one reproducing individual can potentially seed the entire reach). This is achieved by assigning reproduction directly during matrix projection, conditional on at least one reproductive adult being present prior to the flood at time t . The hydrograph stage decline function, $g_j(h)$, varies between 1 (complete establishment) and 0 (complete failure) and depends on the rate of post-flood hydrograph stage decline h (cm/d). The function $g_j(h)$ is also 0 in years with no flood. The timing function $p_j(h)$ gives the proportion of all possible recruitment days (that is, days on which the hydrograph is declining post-flood) that occur in tandem with seed set. Stage decline rate for the receding limb of the hydrograph for each year of gage record was calculated by linking discharge to stage (rating curve) from two staff gages from our study site on the Yampa River. These functions allow us to examine more precisely how within-year timing of floods affects population dynamics of guilds (Stella et al. 2010). Hydriparian shrub and mesoriparian meadow reproduction only occur in flood years and depend on the total amount of unoccupied space (Eq. 1). For these guilds, we did not assume a particular dependence on the rate or timing of flood stage decline ($p = 1$, $g = 1$ in flood years and 0 otherwise), but this could be added in cases where these within-season dynamics are understood. Conversely, desert shrub recruitment occurs only in drought years in unoccupied space or space made available by mortality of other stages and guilds.

Guilds do not compete directly in the model, in the sense that they do not directly alter one another's survival

probability or fecundity. Competition occurs indirectly because each guild occupies some portion of K , the total amount of riparian habitat available to all guilds within a given reach, and K is bounded by the size of the riparian zone. Guilds may affect each other's population dynamics by occupying space that might otherwise be available for new recruitment. For example, the mature stages of one guild may experience low mortality from flooding; because of this population-dynamic inertia, space that might otherwise be scoured by floods and colonized by seedlings of other guilds is unavailable. This is a form of competition, since the recruitment of any given guild is affected by the abundances of all guilds on the landscape. It is important to note that Eq. 1 makes no assumptions about the strength or direction of pairwise biotic interactions, and only posits that bare space for recruitment is a finite quantity. This way of modeling seedling recruitment is analogous to the lottery model for reef fish recruitment (Sale 1977).

Overseeding is also permitted in our modeling approach (Eq. 1), where seedlings of multiple guilds can occupy the same space, at least initially. This assumption allows us to avoid specifying direct competition at the seedling stage, since initial seed germination in the model is strictly a function of the hydrograph and a guild's vital rates and is not affected by the presence or absence of seeds from other guilds.

Incorporating flow regime dynamics

The life cycle of each guild was divided into discrete stages (N_{ij}), with transition probabilities corresponding

to the probability of surviving within a stage (P_{ij}) or surviving to the next stage (G_{ij}) in successive years (Fig. 1). Transition probabilities varied depending on whether a given year had a flood, a drought, or neither, so that $G_{ij} = (1 - S_{ij}) \times (1 - D_{ij}) \times b_{ij} \times a_{ij}$, where S_{ij} is flood mortality given that a flood year occurs, D_{ij} is drought mortality given that a drought year occurs, b_{ij} is a self-thinning rate, and a_{ij} is the baseline probability of transitioning to the next stage apart from flood and drought mortality. Similarly, the probability of remaining in a stage class was $P_{ij} = (1 - S_{ij}) \times (1 - D_{ij}) \times (1 - a_{ij})$.

Vital rate estimation

Vital rates form the core of this modeling effort, so information was obtained from a variety of sources georeferenced to the Colorado River Basin, USA (Table 1). Hydoriparian tree and xeroriparian shrub have been well studied, so we estimated stage-specific values for flood mortality, drought mortality, baseline transition probability, self-thinning, and other rates from existing studies (Appendix S1). Vital rates for the hydoriparian shrub, mesoriparian meadow, and desert shrub guilds are less established from field studies, so we estimated relative values based on known life-history trade-offs in each group. Hydoriparian shrub is adapted to the high shear associated with flows that occur near the active river channel, but its relatively shallow rooting structure gives it a disadvantage during droughts (Douhovnikoff et al. 2005, Francis et al. 2005). Therefore, we assumed flood mortality and drought survivorship rates half those

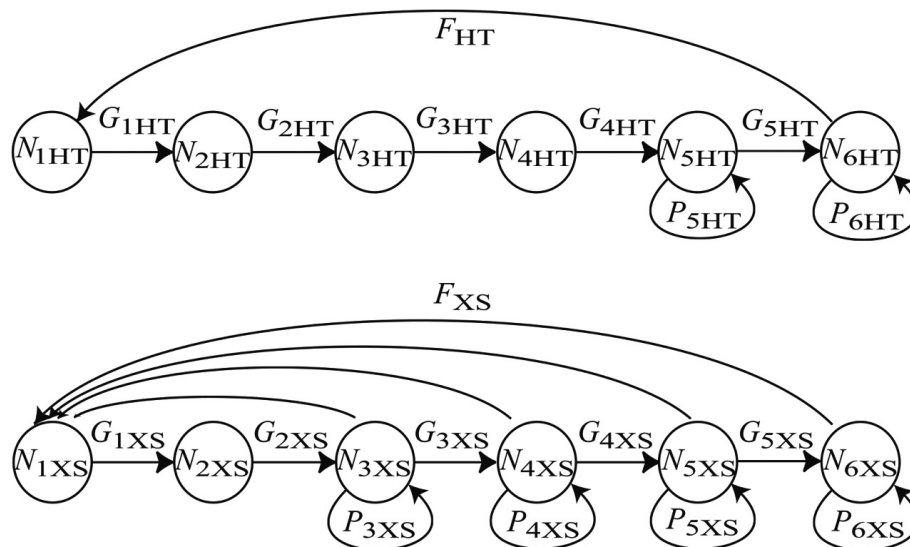


FIG. 1. Life cycle diagrams for hydoriparian tree (HT; top) and xeroriparian shrub (XS; bottom). For hydoriparian tree, stage 1 represents seedlings, stages 2 through 4 are 2–4 yr olds, respectively, stage 5 represents subadult trees (5–10 yr olds), and stage 6 represents reproductive adults. N is abundance, G is the probability of transition to the next stage, P is the probability of remaining in that stage, and F is fecundity. For xeroriparian shrub, stage 1 represents seedlings, stage 2 contains second-year plants, stage 3 represents 3–6 yr olds, stage 4 are 7–15 yr olds, stage 5 are 16–30 yr olds, and stage 6 contains all older trees. Xeroriparian shrub reproduction occurs in stages 3 through 6. General life cycle diagrams are similar for hydoriparian shrub, mesoriparian meadow, and desert shrub guilds.

TABLE 1. Stage-specific parameter values for hydroriparian tree (HT), xeroriparian shrub (XS), hydroriparian shrub (HS), mesoriparian meadow (MM), and desert shrub (DS).

Parameter	Stage					
	1	2	3	4	5	6
q_{iHT}	350	10	1.0	0.91	0.6	0.12
b_{iHT}	0.029	0.10	0.91	0.66	0.20	–
S_{iHT}	0.97	0.33	0.22	0.19	0.073	0.02
D_{iHT}	0.49	0.16	0.083	0.05	0.01	0.01
a_{iHT}	1	1	1	1	0.17	0.03
q_{iXS}	400	29	4.5	1.4	1.3	1.3
b_{iXS}	0.07	0.16	0.31	0.93	1.00	–
S_{iXS}	0.9	0.55	0.25	0.05	0.01	0.01
D_{iXS}	0.5	0.15	0.05	0.025	0.025	0.025
a_{iXS}	1	1	0.25	0.11	0.07	0.05
q_{iHS}	350	35	1	1	1	1
b_{iHS}	0.10	0.030	1	1	1	–
S_{iHS}	0.49	0.17	0.11	0.10	0.04	0.01
D_{iHS}	0.75	0.58	0.54	0.53	0.51	0.51
a_{iHS}	1	1	1	1	0.17	0.01
q_{iMM}	350	35	1	1	1	1
b_{iMM}	0.10	0.030	1	1	1	–
S_{iMM}	0.99	0.67	0.61	0.19	0.073	0.02
D_{iMM}	0.49	0.16	0.083	0.025	0.005	0.005
a_{iMM}	1	1	1	1	0.17	0.03
q_{iDS}	350	35	1	1	1	1
b_{iDS}	0.10	0.030	1	1	1	–
S_{iDS}	0.99	0.67	0.61	0.60	0.54	0.51
D_{iDS}	0.24	0.08	0.042	0.025	0.005	0.005
a_{iDS}	1	1	1	1	0.17	0.03

Notes: Parameter q is stem density (individuals/m²), b is self-thinning rate, S is flood mortality in a flood year, D is drought mortality in a drought year, a is baseline transition probability. Subscripts refer to guilds. Column headers refer to guild stages. Cells with a dash have no parameter value.

of hydroriparian tree. We also assumed that the baseline transition probability in the final stage (a_{iHS} , which can be interpreted as the senescence rate apart from flooding or drought mortality) is greater than that of hydroriparian tree to reflect a shorter lifespan, and allowed reproduction in 3-yr-olds and older. Mesoriparian meadow exhibits the opposite life-history syndrome as hydroriparian shrub. During early life stages this guild is more prone to mortality from flooding than hydroriparian tree, but exhibits some degree of drought tolerance once established. Therefore, we halved the flood survivorship of mesoriparian meadow relative to hydroriparian tree during stages 1–3 and again halved the drought mortality of hydroriparian tree during stages 4–6. Desert shrub is an upland guild that has high drought tolerance but low resistance to flooding (Schlaepfer et al. 2012), so we assigned it half the flood survivorship and drought mortality of hydroriparian tree for all stages.

Model projection

We used 83 yr of hydrograph data from the free-flowing Yampa River near Maybell, Colorado, USA (1916–1999; U.S. Geological Survey gage number 09251000). Based on

river geomorphology, years when peak discharge exceeded 280 m³/s during the timing of seedset were considered flood years, and years in which flows failed to exceed 210 m³/s were drought years (based on known thresholds for drought mortality; Cooper et al. 1999). Years falling in between these thresholds were considered non-event years, for a total of 55% flood years, 20% drought years, and 25% non-event years under natural flow regime conditions. These threshold values are specific to the Yampa River, and appropriate thresholds would need to be determined to apply the model to other rivers systems. Matrix projection was accomplished in annual time steps. To project the model forward in time, a year was drawn at random from the time series and the corresponding flow metrics were calculated for that year (flood decline rate, timing, and whether it was a flood, drought, or non-event year). In flood or drought years, all guilds would be subject to flood or drought mortality, respectively, in addition to baseline transition probabilities.

Management and climate scenarios

To simulate the effect of altered flow regimes on population dynamics, the model was projected forward under a variety of relevant hydrograph scenarios by altering the frequency of year-types in the Maybell gauge data set. Vital rates were held constant across all scenarios (i.e., our goal was to simulate ecological rather than evolutionary dynamics), but hydrograph parameters were allowed to vary across an array of flow regime scenarios. To simulate increased flood (or drought) frequency, we successively changed two of the 83 gauge years so that eventually all of them became flood (or drought) years (42 iterations in total). At each iteration, the model was projected forward a large number of years (10000 yr in most scenarios), the first 500 yr were discarded as burn-in, and population sizes were averaged over the time series. To simulate flow homogenization due to damming, we successively changed year types, starting at natural flow regime frequency, until all of them became non-event years. To simulate the effects of climate change, we iteratively changed the timing of all flood peaks to occur earlier or later in the year.

Model performance

We evaluated model performance by analyzing the sensitivity and elasticity of individual vital rates to perturbations, and by comparing our modeled results to empirical field data. Sensitivities and elasticities were estimated using the iterated sensitivity and elasticity analysis described in Lytle and Merritt (2004). For this computationally intensive exercise, we changed a given vital rate by increments of 0.01 in the vicinity of its actual value, projected the model forward, and recorded population sizes at each increment. At each increment, this was repeated independently up to 1000 times to achieve stable convergence on mean values. Sensitivity was calculated as the slope of the average population size (N_{ij}) regressed

against the vital rate, which is analogous to taking the partial derivative of population size with respect to the vital rate of interest (Lytle and Merritt 2004). Elasticity was also calculated as the slope of this regression on a logarithmic scale. Only sensitivities and elasticities with $R^2 > 0.3$ were retained for further analysis and interpretation. Because this is a multi-guild model, we also calculated cross-guild sensitivities and elasticities, which quantify how changing any single vital rate in a particular guild affects the population dynamics of all other guilds in the system. Furthermore, as sensitivities and elasticities can change in the context of different hydrologic regimes, we repeated this entire exercise using the natural flow regime hydrograph (20% drought years) as well as an increased-drought hydrograph (75% drought years). We used these cross-guild sensitivities to create sensitivity networks, which can be used to quantify the effect of one guild on the entire community within the context of any given flow regime. We compared our modeled results to empirical data reported by Merritt and Poff (2010), which examined the relative dominance of established cottonwood vs. tamarisk stems across 13 western U.S. rivers that differed in degree of flow modification. To keep results parallel with the original study, which focused on established cottonwood and tamarisk stems in the active floodplain, we made the comparison with established hydriparian tree and xeroriparian shrub stems (5–10 and 7–15 yr olds, respectively).

RESULTS

Our model recovered some well-documented riparian dynamics and also produced some less intuitive and more informative findings. Despite the fact that competitive interactions were not defined in our model parameterization, the trade-offs between life history attributes and relationships to flow implicitly captured a spectrum of community dynamics. Model projections were ergodic under all flow regime scenarios tested, with populations fluctuating about a quasi-equilibrium after only 30–50 yr regardless of initial population sizes. All populations followed strong boom-bust dynamics driven by sequences of flood or drought year types. This was especially evident in seedling stages, which often experienced large pulses in recruitment followed by high mortality in subsequent years.

Simulations of increasing drought frequency demonstrated strong effects on the relative dominance of the five flow-response guilds (Fig. 2). Hydriparian shrub and hydriparian tree were the two most dominant guilds on the landscape under natural flow regime conditions (drought frequency = 0.2), but hydriparian shrub abundance declined in direct proportion to increasing drought. Hydriparian tree, xeroriparian shrub, and mesoriparian meadow were each negatively correlated with hydriparian shrub abundance, with slight increases in area occupied as the drought frequency approached approximately 0.5. At higher

drought frequencies (>0.8) hydriparian shrub and mesoriparian meadow were absent from the floodplain, which became increasingly dominated by desert shrub and a higher percentage of bare, unvegetated ground. Rates of change also differed by guild. While hydriparian shrub showed a near-linear decrease in abundance with increasing drought, desert shrub increased exponentially. Both hydriparian tree and xeroriparian shrub exhibited a threshold response, with abundances constant or slightly increasing until high drought frequencies were reached, in which case abundances of both guilds decreased sharply.

The model accurately represented some well-documented patterns of xeroriparian shrub and hydriparian tree abundance, which have somewhat similar life histories and vital rates, particularly in early life-stages. In a flow homogenization scenario, where we increased the frequency of non-event years (no drought or flood), the model predicted an increase in the relative dominance of xeroriparian shrub over hydriparian tree (Fig. 3). This modeling result parallels empirical results obtained by Merritt and Poff (2010) from 13 rivers in the western United States that differed in their degrees of flow modification. The model also demonstrated an increase in the relative coverage of xeroriparian shrub vs. hydriparian tree with increasing drought frequency. Thus, the model appears able to parlay differences in measured vital rates between these two guilds into meaningful predictions about abundances on the landscape.

Under a climate-change scenario representing altered flood timing, average coverage of hydriparian tree increased with earlier floods, and then demonstrated a decline (Fig. 4). Xeroriparian shrub illustrated the opposite effect, with earlier floods causing a reduction in abundance and later floods producing an increase. The relative difference between the two was maximized under flow regimes occurring approximately 20 d earlier than current natural flow regime conditions.

Multi-guild sensitivity analysis revealed that population dynamics were strongly dependent on vital rates both within a single guild and across the entire community (Fig. 5). All guilds except desert shrub showed negative within-guild responses to changes in vital rates, reflecting the fact that increased susceptibility to any given source of mortality should produce a reduction in population size. Changes in one guild's vital rates also produced significant positive responses across the community. For example, changing hydriparian tree's susceptibility to flooding (S_{HT} , left column in Fig. 5) produced a marked increase in xeroriparian shrub, hydriparian shrub, and mesoriparian meadow populations. Thus, even though pairwise guild interactions were not specified in the model, apparent biotic interactions such as competitive release arose from the interaction of individual guild's vital rates with the abiotic environment. These community-wide effects were most strongly apparent in hydriparian tree, but xeroriparian shrub, hydriparian shrub, and mesoriparian meadow also had

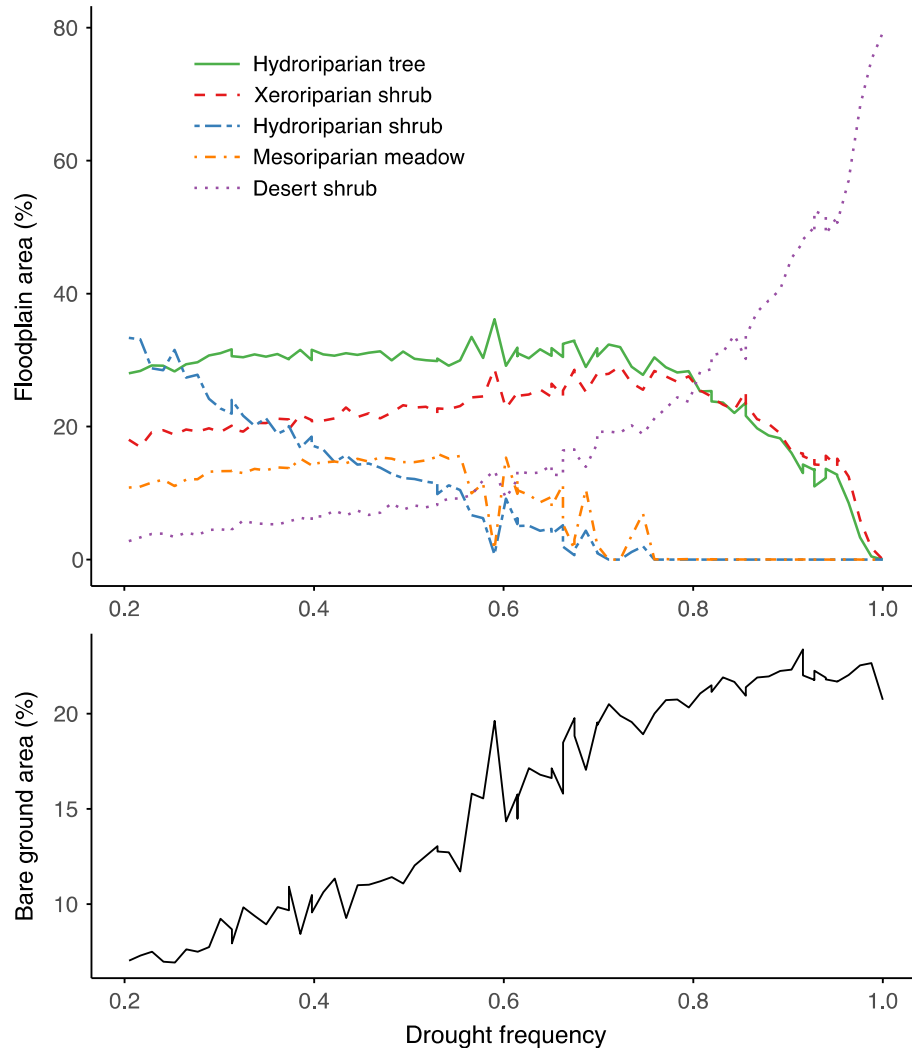


FIG. 2. Effect of increasing drought frequency (proportion of years experiencing drought) on abundances of the five vegetation guilds (top panel) and bare substrates (bottom panel), starting at natural flow regime drought frequency (0.20).

significant effects on other guilds in the community. Desert shrub was the only guild that did not appear to directly affect the population dynamics of other members of the riparian community.

We used sensitivity networks to visualize these complex guild interactions arising from the model. Sensitivity networks depict the direction and strength of each interaction in graphical format. Here, we show two such networks, one produced by calculating sensitivities under natural flow regime conditions (i.e., years drawn at random from the USGS streamflow gauge data, which has a drought-year frequency of 20%) and another depicting a drought scenario, where the number of drought years was increased to 75% (Fig. 6). Each node corresponds to a particular life stage within each guild, and the size of the node depicts the relative dominance (areal coverage as a percentage of the floodplain) on the landscape. The thickness of the line connecting two nodes

depicts the strength of interaction. There were strong linkages among life stages within each guild (lines along outer circle), reflecting the fact that a change to a vital rate in one stage had strong effects on abundances of other stages. More importantly, there were many linkages that crossed from one guild to another, demonstrating that a change in a vital rate had a strong impact on the abundance of other guild life stages. This was most evident under natural flow regime conditions, where the overall graph density (ratio of number of linkages to total number of possible linkages) was 0.27. In this scenario, mature hydroriparian tree (stage 6) exhibited the highest dominance on the landscape, and also had a strong keystone effect on other guilds due to its high connectance to other guilds (26 nodes). Hydroriparian tree also had a strong pairwise interaction with hydroriparian shrub populations, particularly hydroriparian shrub seedlings and stage 5 individuals.

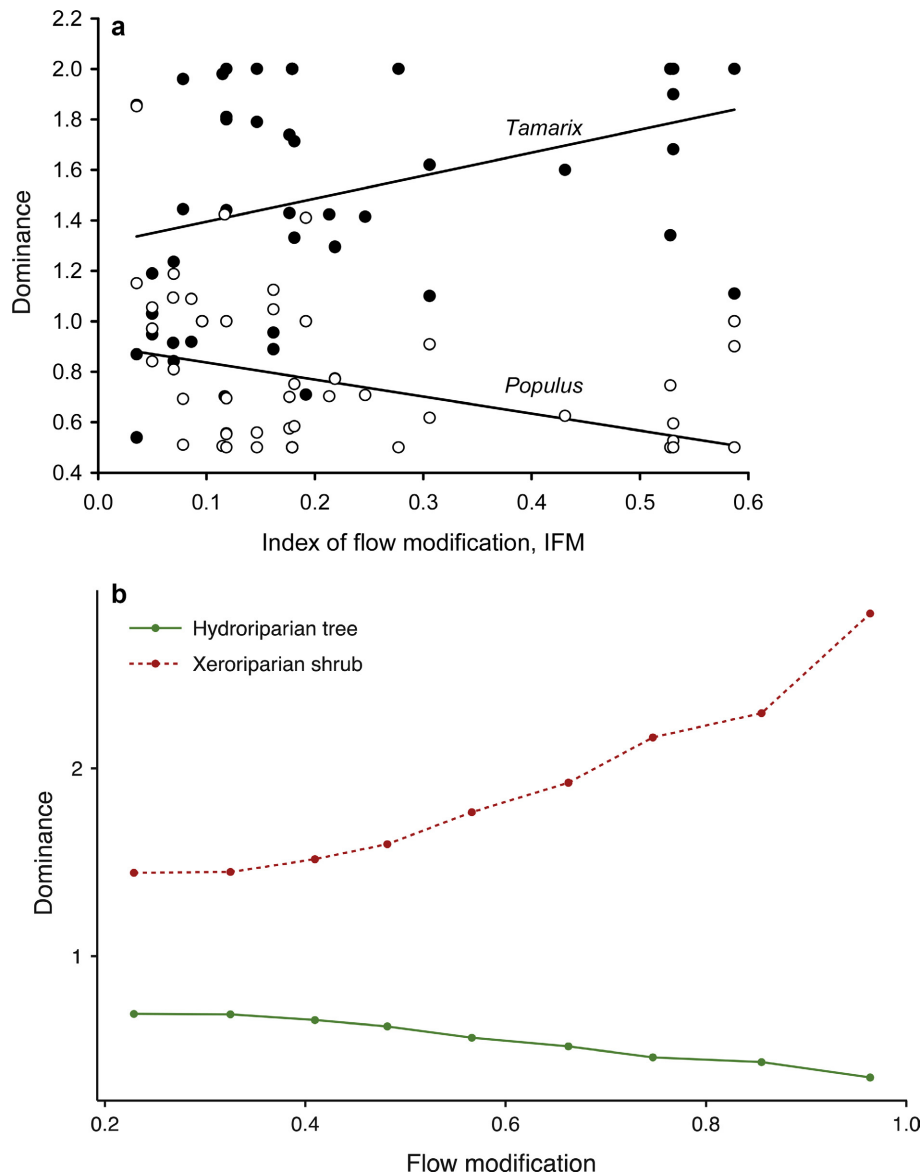


FIG. 3. (a) Figure from Merritt and Poff (2010) showing the relative dominance (measured as relative abundance) of hydriparian tree vs. xeroriparian shrub in 13 western USA rivers experiencing varying degrees of flow modification. The *Tamarix* line shows the ratio of established xeroriparian shrub/hydriparian tree, while the *Populus* line shows the reciprocal (hydriparian tree/xeroriparian shrub). (b) Model output showing relative dominance of established hydriparian tree and xeroriparian shrub stems (5–10 and 7–15 yr olds, respectively) under increasing degrees of flow homogenization (elimination of floods and droughts to increase the frequency of non-event years).

By contrast, the drought-affected community network exhibited much sparser connectivity and weaker pairwise interactions (Fig. 6b). The graph density was only 0.14, and many life stages did not have any significant connectivity to the network at all (nodes with no connections were excluded from Fig. 6). Although adult hydriparian tree still retained dominance under this altered flow scenario (connectance out = 9), hydriparian shrub and mesoriparian meadow were effectively absent from the community and xeroriparian shrub increased in relative dominance. The strength of most pairwise

interactions (e.g., between HT6 and XS6) was also substantially reduced.

DISCUSSION

Floods and droughts exert an influence on both mortality and fecundity in riparian plant communities. Floods and the hydraulics associated with high flows govern shear stress, scouring, and sediment transport and deposition, all of which can cause mortality to varying degrees especially in the vulnerable seedling stages (Kui

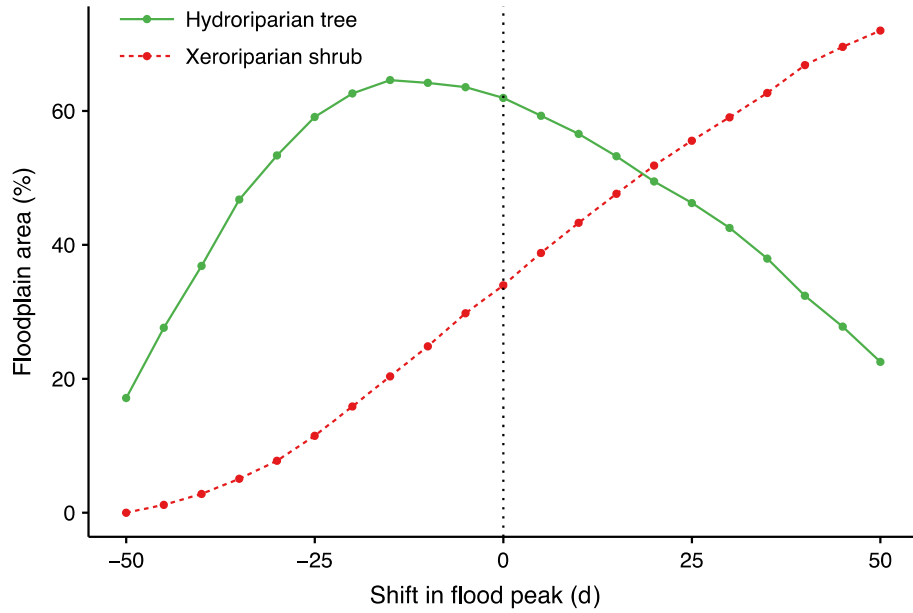


FIG. 4. Effect of flood timing on hydriparian tree and xeriparian shrub dominance on the floodplain. Negative numbers indicate a shift to earlier flood peaks, positive numbers to later flood peaks. Hydriparian tree was more abundant with slightly earlier flood peaks, but all other shifts in flood timing favored xeriparian shrub.

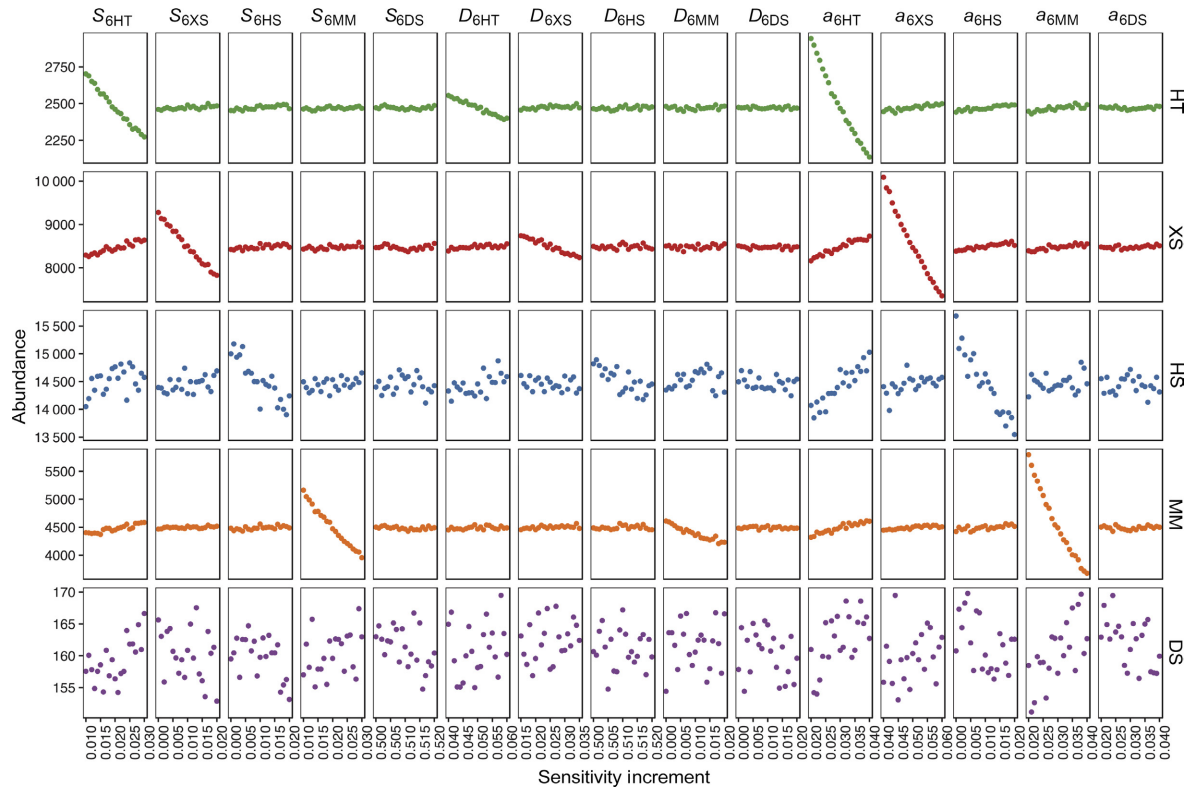


FIG. 5. Multi-guild sensitivity analysis showing the community-wide effects of changing vital rates for flood mortality, drought mortality, and baseline transition probability. Column headers depict the relevant vital rate, and guild responses (total individuals occupying the river reach K) are shown in the row margins. Only responses of stage 6 of each guild are shown here for brevity. Guilds are hydriparian tree (HT), xeriparian shrub (XS), hydriparian shrub (HS), mesoriparian meadow (MM), and desert shrub (DS).

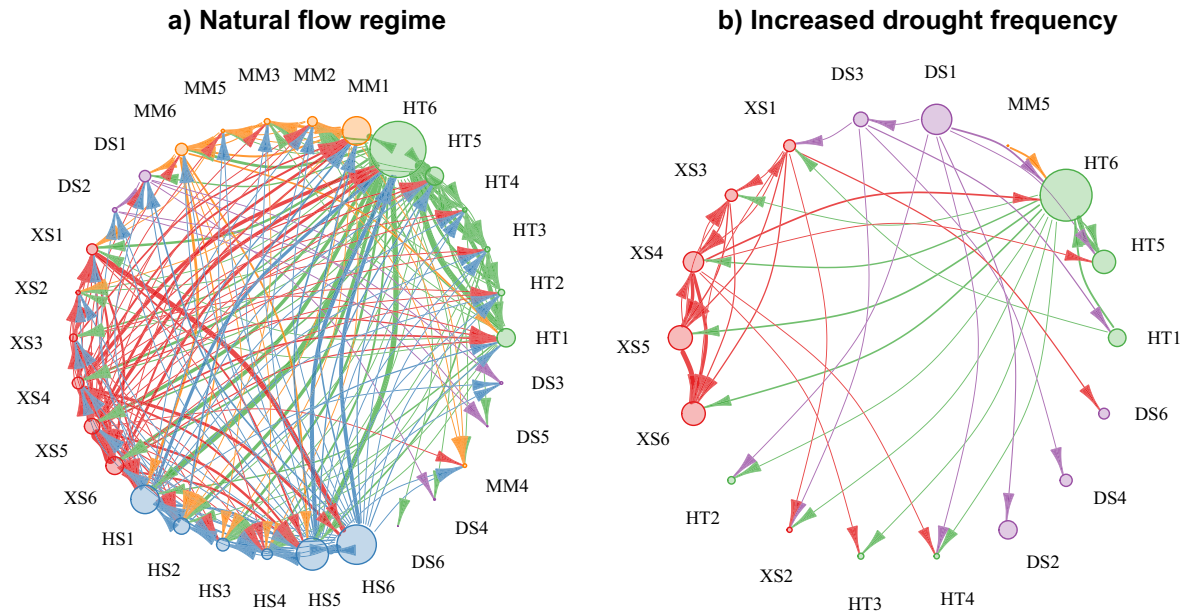


FIG. 6. Sensitivity networks depicting the community-wide effects of altering flood susceptibility (S_{ij}) under (a) natural flow regime conditions and (b) a 75% increase in drought frequency. Circle diameter depicts the areal dominance of each guild stage class and line thickness denotes strength of correlation (only linkages with $R^2 > 0.3$ are shown). Under natural flow regime conditions, the community network was saturated with linkages, and mature hydrioparian tree and hydrioparian shrub were dominant keystone guilds with high connectivity. Under the drought scenario the community network was sparse, and although hydrioparian tree retained some presence on the landscape, xeriparian shrub and desert shrub had increased in dominance.

and Stella 2016). Although areas nearer the channel afford resources such as moisture, these same areas are subjected to the highest frequency and intensity of disturbance, a significant trade-off for plants (Tockner and Stanford 2002, Manners et al. 2015). This was observable in the measured vital rates, where seedling flood mortality rates always exceeded those of adults, and in the strong boom-bust dynamics we observed during model runs. On the other hand, floods are a necessary driver of recruitment in all riparian guilds except desert shrub (for which recruitment is inhibited by flooding). Under extremely flood-reduced scenarios in the model, recruitment of these guilds was highly limited by the recurrence of floods. These opposing processes create highly fluctuating population dynamics that can obscure longer term trends in relative guild abundances and make it difficult to predict when large cohorts of individuals will recruit into mature stages.

In this effort we obtained stage-specific mortality rates that describe how guilds respond to flood, drought, and non-event year types. We also obtained fecundity estimates as a function of the timing and recession rate of flood events. In the context of our stochastic stage-structured model, these vital rates give us a way to understand the trajectory of population dynamics under a variety of novel flow regimes, including simulations of drought, changes in flood timing, and flow homogenization due to damming. Thus, the structured population model described here allows for a rich exploration of

information implicit in well-measured vital rates, and facilitates the exploration of how organisms interact with the environment in complex ways, resulting in landscape-level population dynamics that play out over multiple years. This full-community approach complements other riparian modeling efforts that focus on specific stage classes such as seedlings (Dixon and Turner 2006) or on the population dynamics of single species (Lytle and Merritt 2004, Harper et al. 2011).

The model recovered some patterns of riparian vegetation distribution as a function of hydrology that have been observed in other studies. By simulating the loss of flood and drought events that results from dam-induced flow homogenization (Poff et al. 2007), the model predicted an increased dominance of xeriparian shrub at the expense of hydrioparian tree abundance. This result mirrors the empirical patterns of cottonwood vs. xeriparian shrub (*Tamarix*) dominance observed in surveys of aridland rivers in the western United States, where *Tamarix* dominance increased as a function of flow modification (Merritt and Poff 2010). In this case, tamarisk possesses greater drought tolerance and longer period of seed release that allow it to increase proportionately under modified flow regimes, even though it does not entirely replace cottonwood (Glenn and Nagler 2005). The results from this kind of analysis could be used to guide flow management prescriptions where the goal is to favor a desired riparian vegetation (such as native cottonwood-dominated) over another type (such

as nonnative *Tamarix*). Our results also paralleled those of Rivaes et al. (2014), who found that future drying climate scenarios led to simplifications of the plant communities and dominance of established woodlands, mature woodlands and upland forests in sites in Spain and Portugal, with the strongest impacts on younger and more water-dependent stages. Further, higher prevalence of xeric, non-flood-adapted species in riparian areas is an indication of terrestrialization, wherein riparian areas become more similar to adjacent uplands and lose their uniquely riparian characteristics (Catford et al. 2014).

Our model also revealed riparian vegetation patterns that were less intuitive. The model predicted that a shift in flood timing toward earlier peaks, as is projected under most climate warming scenarios, might produce an initial increase in hydriparian tree abundance on the landscape. However, beyond a threshold of approximately 20 d, the model predicted a sharp decline in this vegetation type. Under these more extreme climate change scenarios, the relative abundance of xeroriparian shrubs such as tamarisk are predicted to increase with respect to hydriparian trees such as cottonwood, even though the absolute abundance of both guilds decreases. Note that although flood timing was varied in this simulation, dates of seed set were held constant. Climate change could cause these events to change as growing degree-days and the onset of spring shift earlier in the season (Parmesan 2007). It is still unknown whether climate-driven shifts in plant flowering phenology will keep pace with climate-driven shifts in peak streamflow timing, however our results suggest that if there is a temporal decoupling of seed set and peak stream flow, there will be dramatic shifts in relative abundance of important riparian plants (e.g., Stella et al. 2006). Although not specifically addressed in this analysis, it is possible to use this modeling framework to examine the simultaneous effects of multiple hydrologic stressors (shifts in flood timing, increases in drought frequency, decreases in recruitment floods) on riparian vegetation dynamics.

Our modeling approach deliberately omitted pairwise competition between guilds, yet we were able to discover important species interactions via multi-guild sensitivity analysis. In the model structure, each guild was specified as an independent matrix of vital rates, with one exception: fecundity of each guild was modeled as a function of the combined abundances of all guilds occupying the landscape. Although recruitment of all seedlings was suppressed at high aggregate densities, the model contained no assumptions about the strength or direction (with respect to guild identity) of this effect. Sensitivity analysis, however, revealed numerous strong interactions between specific guild stages that were not explicitly modeled. There were particularly strong inverse relationships between mature stage classes of hydriparian tree and all other guilds in the community; when hydriparian tree decreased due to a vital rate change, other members of the community responded by increasing

in abundance. Interestingly, these biotic interactions changed depending on the flow regime. Network analysis showed that many of the strong among-guild interactions that occurred under natural flow regime conditions were weakened under increased-drought scenarios. The lesson here is that while vital rates can be considered a fundamental attribute of a species' or guild's collective biology, species interactions may be highly context-dependent, especially in environments as dynamic and stochastic as riverine floodplains.

The ability of the model to project realistic population dynamics depends largely on the robustness of the measured vital rates. For hydriparian tree and xeroriparian shrub, vital rates were obtained from detailed analyses of aerial photographic time series, from long-term transect monitoring data, and from a wealth of edaphic and hydrologic studies pertaining to these well-studied guilds. For the hydriparian shrub, mesoriparian meadow, and desert shrub guilds, we relied largely on generalized vital rates that were specified relative to those of hydriparian tree and xeroriparian shrub. Thus, more empirical work needs to be done before we can make specific, reliable predictions for these groups. While the vital rates obtained for this study were derived largely from field studies, burial-scour experiments in artificial flumes show promise for obtaining some vital rates, at least for earlier stage classes (Kui et al. 2014). The effect of variability in vital rates, and how this affects model output, is another consideration that can be explored with methods such as global sensitivity analysis (Harper et al. 2011). It is also important to note that although we modeled these five particular guilds, the general modeling structure can incorporate other species or guilds with different life histories and degrees of tolerance to flooding or drought.

In order to generalize this modeling approach, we must also consider how it applies to other river systems. Our hydrograph data were based on the undammed Yampa River in Colorado, USA. To apply this method to other river systems, the threshold values for flood and drought would need to be determined from geomorphological data, gage records, or other information. In other river systems, it will not always be straightforward to identify the relevant flow thresholds, especially where long-term vegetation data are not available. Differences in substrate type, valley form, sources of water other than streamflow (precipitation and lateral groundwater), and other factors will affect how a given rate of discharge causes mortality. Thus, the threshold functions for what constitutes a flood or a drought need to be carefully calibrated for each system modeled. In the Yampa River, having three year-type categories (flood, drought, neither) appears sufficient for describing riparian vegetation dynamics. In other river systems, however, other mortality thresholds beyond the three used here may be needed, especially in systems that experience extreme-magnitude events that cause disproportionate mortality. Mathematically, the model can also accommodate the situation where a single

year contains both a flood and a drought (i.e., when the S_{ij} s and D_{ij} s are both non-zero). Alternatively, the special situation of a combined flood-drought year could be specified as its own year-type with corresponding vital rates particular to that situation. Rivers with highly modified floodplain geomorphologies could also present a unique modelling challenge, especially rivers that have experienced reduced channel mobility or bed incision due to damming or other human modifications, as the amount of floodplain habitat (K), could be changing over time.

Practitioners require defensible methods and actionable science for prescribing environmental flows to ensure functioning riverine ecosystems. Projections of the effects of alternative river flow management scenarios in riverscapes can serve to inform this process and facilitate cost-benefit analyses of alternative flow prescriptions. Static models that ignore stage-specific responses to river flows will tend to produce hydrographs that accommodate adults, but may fail to include flows that support recruitment, seedling establishment, and the changing flow requirements of the full complement of age classes. Our ability to balance human and ecosystem needs for fresh water requires models that reflect more than a single species or cover type, and capture interactions between multiple vegetation types across multiple life stages. The model presented here is a step towards modeling multiple guilds with shared life history traits to determine the outcomes of climate change and management scenarios on riparian forest ecosystems.

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LITERATURE CITED

- Aguiar, F. C., J. O. Cerdeira, M. J. Martins, and M. T. Ferreira. 2013. Riparian forests of Southwest Europe: are functional trait and species composition assemblages constrained by environment? *Journal of Vegetation Science* 24:628–638.
- Caswell, H., 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Catford, J. A., W. K. Morris, P. A. Vesk, C. J. Gippel, B. J. Downes, and J. Diez. 2014. Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Diversity and Distributions* 20: 1084–1096.
- Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, U.S.A. *Regulated Rivers: Research and Management* 15: 419–440.
- Dai, A. 2011. Drought under global warming: a review. *WIREs Climate Change* 2:45–65.
- Dalgleish, H. J., D. N. Koons, M. B. Hooten, C. A. Moffet, and P. B. Adler. 2011. Climate influences the demography of three dominant sagebrush steppe plants. *Ecology* 92:75–85.
- Dixon, M. D., and M. G. Turner. 2006. Simulated recruitment of riparian trees and shrubs under natural and regulated flow regimes on the Wisconsin River, USA. *River Research and Applications* 22:1057–1083.
- Douhovnikoff, V., J. R. McBride, and R. S. Dodd. 2005. *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. *Ecology* 86:446–452.
- Francis, R. A., A. M. Gurnell, G. E. Petts and P. J. Edwards. 2005. Survival and growth responses of *Populus nigra*, *Salix elaeagnos* and *Alnus incana* cuttings to varying levels of hydric stress. *Forest Ecology and Management* 210:291–301.
- Friedman, J. M., G. T. Auble, P. B. Shafroth, M. L. Scott, M. F. Merigiano, M. D. Prehling, and E. K. Griffin. 2005. Dominance of non-native riparian trees in western USA. *Biological Invasions* 7:747–751.
- Gaeuman, D., J. C. Schmidt, and P. R. Wilcock. 2005. Complex channel responses to changes in stream flow and sediment supply on the lower Duchesne River, Utah. *Geomorphology* 64:185–206.
- Glenn, E. P., and P. L. Nagler. 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western US riparian zones. *Journal of Arid Environments* 61: 419–446.
- Grams, P. E., and J. C. Schmidt. 2002. Streamflow regulation and multi-level flood plain formation: channel narrowing on the aggrading Green River in the eastern Unita Mountains, Colorado and Utah. *Geomorphology* 44:337–360.
- Harper, E. B., J. C. Stella, and A. K. Fremier. 2011. Global sensitivity analysis for complex ecological models: a case study of riparian cottonwood population dynamics. *Ecological Applications* 21:1225–1240.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences USA* 111:13894–13899.
- Kui, L., and J. C. Stella. 2016. Fluvial sediment burial increases mortality of young riparian trees but induces compensatory growth response in survivors. *Forest Ecology and Management* 366:32–40.
- Kui, L., J. C. Stella, A. Lightbody, and A. C. Wilcox. 2014. Ecogeomorphic feedbacks and flood loss of riparian tree seedlings in meandering channel experiments. *Water Resources Research* 50:9366–9384.
- Lytle, D. A., and D. M. Merritt. 2004. Hydrologic regimes and riparian forests: a structured population model for cottonwood. *Ecology* 85:2493–2503.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment-an integrative model. *Wetlands* 18:634–645.
- Manners, R. B., A. C. Wilcox, L. Kui, A. F. Lightbody, J. C. Stella, and L. S. Sklar. 2015. When do plants modify fluvial processes? Plant-hydraulic interactions under variable flow and sediment supply rates. *Journal of Geophysical Research: Earth Surface* 120:325–345.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Merritt, D. M., and N. L. Poff. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. *Ecological Applications* 20:135–152.
- Merritt, D. M., M. L. Scott, N. L. Poff, G. T. Auble, and D. A. Lytle. 2010. Theory, methods and tools for determining environmental flows for riparian vegetation: riparian

- vegetation-flow response guilds. *Freshwater Biology* 55: 206–225.
- Naiman, R. J., S. E. Bunn, C. Nilsson, G. E. Petts, G. Pinay, and L. C. Thompson. 2002. Legitimizing fluvial ecosystems as users of water: an overview. *Environmental Management* 30:455–467.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308:405–408.
- Olden, J. D., et al. 2014. Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment* 12:176–185.
- Palmer, M. A., D. P. Lettenmaier, N. L. Poff, S. L. Postel, B. Richter, and R. Warner. 2009. Climate change and river ecosystems: protection and adaptation options. *Environmental Management* 44:1053–1068.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13:1860–1872.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences USA* 104:5732–5737.
- Poff, N. L., et al. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* 55:147–170.
- Ringold, P. L., T. K. Magee, and D. V. Peck. 2008. Twelve invasive plant taxa in U.S. western riparian ecosystems. *Journal of the North American Benthological Society* 27: 949–966.
- Rivaes, R. P., P. M. Rodriguez-Gonzalez, M. T. Ferreira, A. N. Pinheiro, E. Politti, G. Egger, A. Garcia-Arias, and F. Frances. 2014. Modeling the evolution of riparian woodlands facing climate change in three European rivers with contrasting flow regimes. *PLoS ONE* 9:e110200.
- Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management* 14:451–464.
- Sale, P. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* 111:337–359.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012. Ecohydrological niche of sagebrush ecosystems. *Ecohydrology* 5:453–466.
- Seager, R., M. F. Ting, C. H. Li, N. Naik, B. Cook, J. Nakamura, and H. B. Liu. 2013. Projections of declining surface-water availability for the southwestern United States. *Nature Climate Change* 3:482–486.
- Stella, J. C., J. J. Battles, B. K. Orr, and J. R. McBride. 2006. Synchrony of seed dispersal, hydrology and local climate in a semi-arid river reach in California. *Ecosystems* 9:1200–1214.
- Stella, J. C., J. J. Battles, J. R. McBride, and B. K. Orr. 2010. Riparian seedling mortality from simulated water table recession, and the design of sustainable flow regimes on regulated rivers. *Restoration Ecology* 18:284–294.
- Ström, L., R. Jansson, C. Nilsson, M. E. Johansson, and S. Xiong. 2011. Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions. *Global Change Biology* 17:254–267.
- Stromberg, J. C., and D. M. Merritt. 2015. Riparian plant guilds of ephemeral, intermittent and perennial rivers. *Freshwater Biology* 61:1259–1275.
- Stromberg, J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrock, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography* 16:381–393.
- Stromberg, J. C., P. B. Shafroth, and A. F. Hazelton. 2012. Legacies of flood reduction on a dryland river. *River Research and Applications* 28:143–159.
- Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* 29:308–330.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 404:180–183.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1528/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in figshare <https://doi.org/10.6084/m9.figshare.4652608>