



Future forest conditions under alternative management and hydrological scenarios in the Upper Mississippi River floodplain

Matthew L. Trumper¹ · Nathan R. De Jager¹ · Molly Van Appledorn¹ · Andrew R. Meier

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Abstract

Context Floodplain forests are being transformed by multiple pressures, prompting widespread management and restoration efforts. It is uncertain how disturbances, including hydrologic change, and management actions will interact to influence the ecology of these threatened forests.

Objectives This study examined the effects of alternative management and hydrologic regimes on forest succession at an Upper Mississippi River floodplain site with a restoration project in planning.

Methods We used the spatially explicit forest landscape model, LANDIS-II, to simulate forest succession for 100 years under four hydrogeomorphic management scenarios, three forest management scenarios, and two scenarios of future hydrologic conditions. We evaluated changes in forest biomass and composition over time and assessed the relative

importance of management actions and hydrologic change on succession.

Results Forest aboveground biomass decreased in all management-hydrology scenarios, especially in the wetter hydrological scenario. Intensified hydrogeomorphic and forest management scenarios reduced the magnitude and extent of biomass declines; however, they were unable to prevent overall declines in biomass or cause large shifts in tree species composition. Silver maple (*Acer saccharinum*) was projected to decrease in biomass, while increases in biomass were projected for several late-successional species including swamp white oak (*Quercus bicolor*). Among the factors influencing variation in biomass, forest management had the largest influence in the first 50 years of our simulations, but hydrological regime became the most important factor by the end of the century.

Conclusions Our simulations indicate that management actions could play an important role in the conservation of floodplain forests, but their effectiveness will likely be limited if recent upward trends in flooding conditions in this system continue in the future. Thus, our results highlight both the potential benefits and limitations of management actions in the face of hydrologic change.

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M. L. Trumper · N. R. De Jager (✉) · M. Van Appledorn
U.S. Geological Survey, Upper Midwest Environmental
Sciences Center, La Crosse, WI, USA
e-mail: ndejager@usgs.gov

A. R. Meier
U.S. Army Corps of Engineers, St. Paul District,
Mississippi River Environmental Section, La Crosse, WI,
USA

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Introduction

Floodplain forests are being transformed worldwide by multiple stressors including shifting hydrological regimes, agricultural land conversion, and invasive species (Tockner et al. 2010). Among these stressors, altered hydrological regimes may be especially influential in shaping long-term changes in floodplain forests. Hydrology is recognized as a fundamental driver of ecological structure and function in floodplains (Junk et al. 1989; Hupp and Osterkamp 1996). For example, flooding frequency, duration, and depth are key processes that influence the distribution and growth of floodplain vegetation (Sharitz and Mitsch 1993; Toner and Keddy 1997; Townsend 2001; Wittmann et al. 2004). Anthropogenic disturbances such as river impoundment have altered flooding regimes in most of the world's river-floodplain systems (e.g., Dynesius and Nilsson 1994), leading to widespread shifts in species composition and forest decline (González et al. 2010; Mac Nally et al. 2011; Rajib et al. 2021; Rood and Mahoney 1990).

Because floodplain forests are expected to undergo further changes in coming decades, there is great interest in restoring and maintaining their natural functions and services, which include flood risk regulation, carbon sequestration, and wildlife habitat. Floodplain management and restoration practices encompass a wide range of approaches that vary in spatial scale and degree of intervention (González et al. 2015). At the catchment scale, hydrogeomorphic approaches that alter water and sediment regimes, such as levee removals and setbacks, dam removals, and controlled flow releases, have the potential to provide widespread benefits for riparian and floodplain vegetation communities (Dixon and Turner 2006; Gergel et al. 2002; Hughes and Rood 2003; Knox et al. 2022; Rood et al. 2003; Shafroth et al. 2002). However, these approaches are challenging to implement because the uncertainty surrounding ecological outcomes and the number of stakeholders needed to reach consensus both increase with spatial scale (Hughes et al. 2008). Consequently, most vegetation management practices in riparian and floodplain systems are implemented locally (e.g., site to reach scale; González et al. 2015). Management practices at the local scale include forest management treatments such as tree plantings and invasive species control to directly promote the establishment and growth of

floodplain vegetation. In addition, hydrogeomorphic modification can be used to change floodplain surface elevations in ways that alter local flooding dynamics (e.g., Forshay et al. 2022) and associated flood stress for trees. There is high uncertainty about the degree to which these local-scale management treatments can influence future forest conditions across broader landscapes, given the complex interplay of flood disturbance and natural patterns of succession in floodplains (Hodges 1997).

The Upper Mississippi River (UMR) is an ideal setting to evaluate the influence of alternative management and hydrological regimes on patterns of forest succession in floodplains. Within the last two centuries, the river-floodplain system has been transformed to support agricultural development and commercial navigation, including the construction of a series of locks and low-head dams (Romano 2010; Houser 2022). These anthropogenic modifications have significantly reduced floodplain forest coverage in the UMR (De Jager et al. 2013a; De Jager and Rohweder 2022; Nelson et al. 1994). De Jager et al. (2013a) found that approximately 42% (~ 136,000 ha) of the UMR floodplain from Minneapolis, Minnesota, to Cairo, Illinois, was in forest cover c.1890 and that approximately 28% (90,000 ha) remained in forest cover by 1975. Although smaller in magnitude, contemporary forest loss continues to occur across most portions of the UMR (De Jager and Rohweder 2022), and model projections show continued losses for the next century (De Jager et al. 2019, 2024). Increasing discharge (Van Appledorn 2022), as well as the expansion of insect pests, diseases, and invasive herbaceous species such as reed canarygrass (*Phalaris arundinacea* L.), are among the likely causes of increased rates of tree mortality, limited recruitment, and dominance by stands of even-aged silver maple (*Acer saccharinum* L.; De Jager et al. 2019; Knutson and Klaas 1998; Yin et al. 1997). In response to these concerns, there is considerable interest in using management practices to enhance and restore floodplain forest habitat in the UMR (Guyon et al. 2012; Romano 2010). Numerous ecosystem restoration projects led by the Upper Mississippi River Restoration program have been developed with the goal of improving forest conditions (USACE 2022a).

Models that link hydrology to ecological responses are useful for projecting changes in forest communities under alternative management and

hydrology scenarios. Several modeling approaches have been used to simulate vegetation dynamics under alternative hydrologic regimes in riparian and floodplain settings (Auble et al. 1994; Benjankar et al. 2020; Glenz 2005; Mahoney and Rood 1998). Many of these models were developed based on the assumption that floodplain vegetation communities require specific hydrologic conditions and that variables such as flood frequency and duration drive patterns of habitat suitability (Benjankar et al. 2011; Merritt et al. 2010). Additionally, some modeling approaches have integrated more mechanistic representations of spatial and temporal flood-vegetation relationships into existing forest succession models (e.g., Pearlstine et al. 1985), including on the UMR (De Jager et al. 2019). These process-based models have the advantage of incorporating a variety of additional aspects of forest succession in floodplains (e.g., seed germination, competition, insect disturbance). Forest landscape models that incorporate the effects of flooding and management practices can be used to identify plausible trajectories of change in floodplain forests and determine where management treatments may be most effective in

maintaining forest productivity and diversity (De Jager et al. 2024).

In this study, we evaluate the combined effects of forest management, local-scale hydrogeomorphic modifications, and regional hydrologic change on forest succession for an area of the UMR, referred to here as Reno Bottoms, where a forest restoration project is planned (Fig. 1). To aid the planning process, we simulated floodplain forest dynamics over the next 100 years under two different regional hydrological regimes, four different local hydrogeomorphic management scenarios, and three different forest management scenarios. We used the LANDIS-II forest landscape model (Scheller et al. 2007) to simulate forest succession under different combinations of management actions and hydrologic change. Recently, De Jager et al. (2024) applied this modeling platform to investigate trends in forest coverage at Reno Bottoms, focusing on projected regional hydrological changes and invasive species management. They found that forest loss is projected to continue across broad areas of Reno Bottoms over the next 100 years, both under flooding regimes similar to past conditions and under those characterized by an increase in flooding

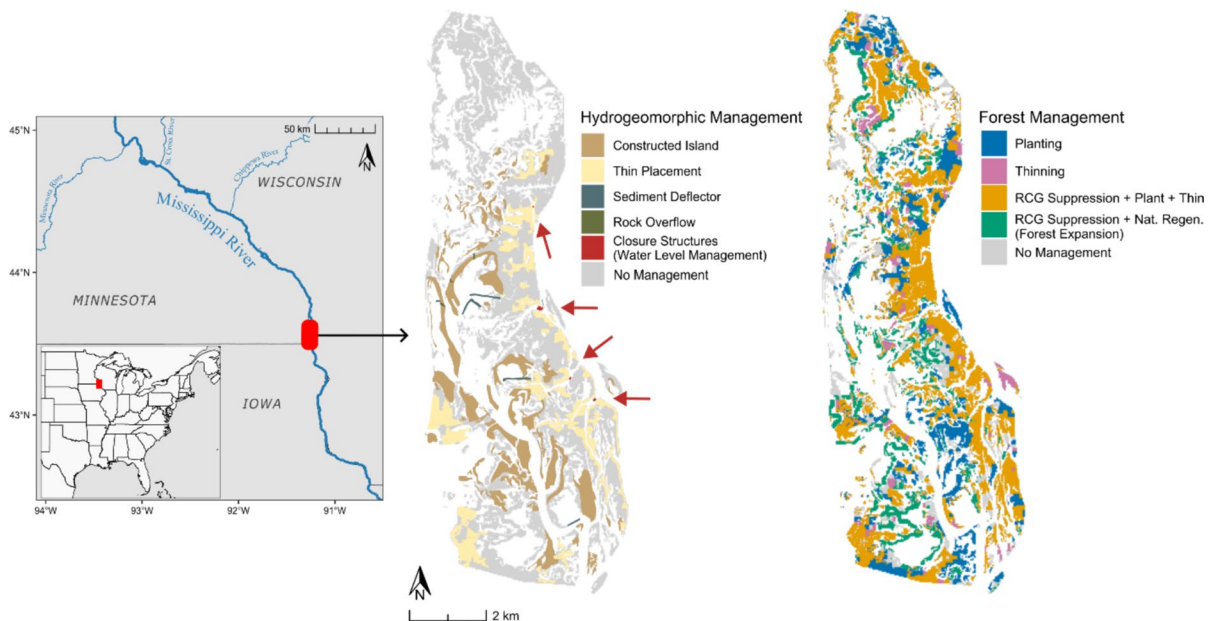


Fig. 1 Map of the Reno Bottoms study area along the Upper Mississippi River. Left: Location of Reno Bottoms on the border between Minnesota, Wisconsin, and Iowa. Right: Maps of the simulated landscape including the location of the poten-

tial hydrogeomorphic and forest management treatments. Red arrows point to the locations of closure structures. Reed canarygrass (*Phalaris arundinacea* L.) is abbreviated as RCG

conditions. Our study builds on this previous effort by incorporating several planned local-scale hydrogeomorphic management actions and by expanding the number of alternative vegetation management scenarios. Furthermore, we extended our analyses to account for trends in forest succession and community dynamics.

We aimed to evaluate the extent to which local-scale management actions could influence patterns of forest biomass and composition at both the project scale and the broader landscape scale. Thus, we used our model simulations to address three related questions:

- (1) How do patterns of floodplain inundation vary among hydrogeomorphic management and future regional hydrological scenarios?
- (2) How do management activities, applied at varying scales and degrees of intensity, influence patterns of forest biomass and composition across scales (i.e., site to landscape)?
- (3) What are the relative influences of hydrogeomorphic management, forest management, and hydrological regime on forest biomass across spatial and temporal scales?

Methods

Overview

We simulated forest succession within Reno Bottoms, located in a portion of the UMR that spans south-east Minnesota, northeast Iowa, and southwest Wisconsin. We used the same modeling framework and many of the same input files developed by De Jager et al. (2024) to aid management agencies in designing habitat restoration and enhancement plans at the site. However, De Jager et al. (2024) focused on the effects of alternative hydrological scenarios and invasive species on forest cover. Our study differs from this previous work in that we modeled the full range of management actions under consideration by management agencies at Reno Bottoms, including four alternative hydrogeomorphic regimes and three alternative forest management regimes. In addition, we examined changes in forest biomass and composition over time and across scales. Additional details related

to our modeling framework and previous applications to floodplain inundation and forest succession can be found in De Jager et al. (2019, 2024).

Study area and landscape initialization

The study area covers 2,500 ha within Reno Bottoms, which comprises a mosaic of floodplain forests, marsh wetlands, and diverse aquatic habitat. The area is within the Upper Mississippi River National Wildlife and Fish Refuge and contains high-quality forest habitat, with some areas representative of the Upper Mississippi River floodplain prior to lock and dam construction (USACE 2023). However, the floodplain forests of Reno Bottoms have undergone substantial degradation over the last century (De Jager et al. 2024; USACE 2023). Management agencies consider recent declines in forest cover across the study area to be primarily driven by increases in the duration and magnitude of high-water events. However, they also believe that floodplain forests within Reno Bottoms have been negatively affected by a variety of other natural disturbances, such as invasive herbaceous species, insect outbreaks, disease, and herbivory. Of particular concern are the declines in American elm (*Ulmus americana* L.) and green ash (*Fraxinus pennsylvanica* Marshall) populations due to Dutch Elm disease and the emerald ash borer (*Agrilus planipennis*), as well as the expansion of invasive herbaceous species such as reed canarygrass, which can colonize open forest habitat and prevent woody plant establishment. Other herbaceous species, especially a non-native subspecies of stinging nettle (*Urtica dioica* L. spp. *dioica*) and the native wood nettle (*Laportea canadensis* L. Weddell), colonize these forests and appear to inhibit regeneration. Observed forest decline at Reno Bottoms has prompted efforts to preserve and enhance high quality forest habitat, including support from the Upper Mississippi River Restoration program for a habitat restoration project.

We created an initial map of vegetation species-age composition for the study area using forest inventory data (USACE 2022b). Overstory tree data were collected using variable radius plots using a 10 ft² ac⁻¹ (2.3 m² ha⁻¹) basal area factor sampling tool, while herbaceous vegetation data were collected within ~5 m fixed radius plots (area of 1/50 ac or 1/124 ha) at the same location. Plots were placed at an approximate density of 1 plot per 2.5 acres (1 ha).

The areas that are currently forested within Reno Bottoms are heavily dominated by silver maple, with 65.4% of the 2,005 total inventory plots classified as silver maple dominated. The second most common forest type was maple/ash/elm, which comprises 16.8% of the plots and includes silver maple, green ash, and American elm. Higher diversity mixed forest types including swamp white oak (*Quercus bicolor* Willd.) were concentrated in the northern and north-east portion of the study area near the main channel and comprised roughly 7% of the plots. Other prominent species included eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), willow (*Salix* L.), river birch (*Betula nigra* L.), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), boxelder (*Acer negundo* L.), and hackberry (*Celtis occidentalis* L.). Forest inventory plots also included data regarding vegetation in the forest understory. The plot data indicated a general lack of regeneration of tree species across the study area. Additionally, the presence, absence, and dominance of reed canarygrass was noted and mapped.

Inundation model and scenarios

To evaluate the effects of flood-related mortality on succession, we developed annual maps of the number of days the floodplain was inundated (under water) during each growing season (April 1–September 30) from 1972 to 2019. This process involved several steps. First, a terrain surface was developed by combining data from a light detection and ranging (LiDAR)-derived digital elevation model and bathymetric surveys completed from 2018 to 2019. Next, we used output from a two-dimensional (2-D) Adaptive Hydraulics (AdH) model developed by the U.S. Army Corps of Engineers (USACE 2023) to generate 13 water surface elevation maps, which collectively represent a broad range of discharge conditions experienced at the site. We then developed maps of water depth by subtracting terrain elevation from each water surface elevation map, resulting in a total of 13 depth maps (one for each discharge condition). To predict a daily time series of water depths for each pixel in the study area for the period of record (1972–2019), we linearly interpolated between sequential AdH-derived water depths across the modeled discharge conditions. Next, we summed the number of days that each pixel was inundated during the growing season in

each year, resulting in 48 annual inundation duration maps for the study area. Finally, we created inundation duration classes (10-day intervals of total growing season days inundated) for the annual inundation maps. These inundation maps were at 30-m resolution. Additional details about the inundation modeling are available in USACE (2023) and De Jager et al. (2024).

We used two 100-year scenarios of future hydrologic change developed by De Jager et al. (2024) to better understand successional trajectories under plausible alternative hydrologic regimes. The scenarios both represent a period from 2020 to 2119. These future hydrology scenarios were developed based on the annual inundation duration maps described above. Briefly, the historical daily time series of water depth was used to calculate the number of growing season days for which water levels exceeded bank full stage (20% exceedance stage) across the study area from 1972 to 2019. A future 100-year scenario was developed by randomly selecting annual inundation maps from the observed record such that the future inundation scenario maintained the same average number of days above bank full stage as observed from 1972 to 2019 (random scenario). A second 100-year hydrological scenario was developed by fitting a linear trend model to the historical average number of days above bank full stage and projecting the observed upward trend forward for 100 years (trending scenario). The two scenarios share the same level of interannual variability in floodplain inundation, but the trending scenario projects increasingly wet conditions that are in line with recent analyses showing significant positive trends in discharge across much of the UMR over the same period (Van Appledorn 2022).

Forest landscape simulation model

We simulated future succession using the LANDIS-II v6.2 forest landscape model (Scheller et al. 2007). LANDIS-II is a spatially explicit, process-based landscape simulation model designed to simulate forest dynamics over large spatial and temporal scales. The model is raster-based, with a landscape composed of interacting grid cells. We used a 30-m (0.09-ha) cell resolution in our study. Within each cell, trees are simulated as species-age cohorts rather than individual stems. Successional trajectories in LANDIS-II

are nondeterministic and emergent from ecological processes that are simulated across multiple spatial scales, including seed dispersal, tree establishment, competition, disturbance, and mortality.

We used the Biomass Succession extension (v3.2) to model successional processes of growth, competition, and mortality within LANDIS-II (Scheller and Mladenoff 2004). This extension simulates changes in the aboveground biomass of tree cohorts within each grid cell based on species life history attributes (e.g., shade tolerance, longevity, maximum growth rate). In our model, we use the same life history parameters as De Jager et al. (2019), which were developed from Burns and Honkala (1990) and forest inventory data for each species (Table S1). The probability of tree seedling establishment was calculated based on floodplain inundation classes and the presence or absence of reed canarygrass, following De Jager et al. (2024).

To simulate the effects of floodplain inundation on biomass, we used a modified version of the Land Use Plus extension (Thompson et al. 2016). This extension allows users to integrate a sequence of maps representing land use or other disturbances into simulations. Here, we supplied the 100 annual maps of inundation duration to simulate flood-related mortality. Rates of mortality were calculated probabilistically using statistical models that predict the mortality of species-age cohorts based on inundation duration (De Jager et al. 2018). Flood mortality is species and age-dependent, with the highest probability of mortality in the least flood-tolerant species and the youngest cohorts. We also simulated tree mortality due to the emerald ash borer (EAB) using the Biological Disturbance Agent extension (BDA; Sturtevant et al. 2004).

Hydrogeomorphic management scenarios

We simulated alternative hydrogeomorphic management scenarios to assess the effects of water-level management and geomorphic modification on floodplain inundation and succession (Fig. 1). These scenarios were designed by a multi-agency, multi-disciplinary team to evaluate alternative locations for hydrogeomorphic management with the goal of increasing high-quality forest habitat in the study area. Hydrogeomorphic treatments were identified based on standard habitat restoration techniques used in the UMR (USACE 2012). More specifically,

potential treatments included side channel closures intended to reduce inflows from the main channel into the study area (water-level management) and measures to increase the elevation of floodplain habitat using dredged material (e.g., thin layer placement, island construction). We refer to these latter measures hereafter as elevation enhancement. Altogether, these potential elevation enhancement measures covered ~2,400 acres (971 ha), representing approximately 39% of the 2,500-ha study area.

In total, we considered four alternative hydrogeomorphic scenarios in this study: (1) the ‘baseline’ scenario, which includes no water-level management or elevation enhancement, (2) the ‘closures’ scenario with only side channel closures, (3) the ‘elevation enhancement’ scenario with only elevation enhancement treatments, and (4) the ‘elevation enhancement and closures’ scenario, combining both elevation enhancement and side channel closures. Hydrogeomorphic treatments were implemented in our modeling framework by updating the elevation layer based on the target elevations for each treatment and rerunning the Adaptive Hydraulics model for each scenario.

Forest management scenarios

We also simulated alternative forest management scenarios that were designed to preserve and enhance floodplain forest habitat. Like the hydrogeomorphic treatments, forest treatments were identified by an interagency team and incorporated expert opinion from foresters working in the UMR floodplain. The potential forest treatments included planting, thinning, and vegetation control (Fig. 1). In the model, planting treatments were simulated by adding two-year-old tree cohorts of various species to the initial communities map. Thinning treatments were simulated by removing silver maple cohorts age 50 and 70 from the landscape; removing these cohorts best reflected the target basal area range of the UMR management community (Guyon et al. 2012). Vegetation control measures primarily involved the removal of invasive reed canarygrass. In scenarios without vegetation control, the effects of reed canarygrass were simulated by reducing woody species establishment rates (refer to De Jager et al. 2024). In scenarios that included vegetation control, it was assumed that vegetation control would eliminate reed canarygrass,

and thus woody species establishment rates were not adjusted. Further, in scenarios that included vegetation control, we allowed forest recruitment in currently non-forested areas where herbaceous species were presumably restricting forest recruitment (forest expansion zone). In total, we simulated three alternative forest management scenarios: (1) the ‘no forest management’ scenario, (2) the ‘planting’ scenario, and (3) the ‘planting and thinning’ scenario. The latter two forest management scenarios also included vegetation control treatments and forest expansion, but we use the shorter scenario names for brevity.

Model outputs and analysis

To evaluate the effects of management on floodplain inundation, we examined spatial and temporal differences in average inundation duration among the hydrogeomorphic and future hydrological scenarios. We averaged inundation duration across all cells in the landscape at 10-year time steps and across the full 100-year period for each scenario. In addition to assessing differences in landscape-level floodplain inundation among scenarios, we sought to assess differences in inundation only where elevation enhancement treatments were implemented, as we expected the largest reductions in flooding in these areas. We therefore averaged inundation duration at both the landscape-level and at the scale of sites with elevation enhancement. To evaluate differences in the spatial patterns of inundation, we

also averaged inundation duration at each individual grid cell across the 100 rasters (simulation years 2020–2119) for each hydrogeomorphic scenario. We then calculated the difference in average inundation duration for each cell in the landscape by subtracting the baseline scenario average inundation raster from each of the three average inundation rasters corresponding to scenarios with hydrogeomorphic management (closures, elevation enhancement, and their combination). This allowed us to evaluate differences in patterns of flood duration among scenarios in a spatially explicit manner. We replicated this procedure for the random and trending hydrology scenarios.

We simulated forest succession under a combination of management and hydrology scenarios using a factorial design, for a total of 24 simulations (4 hydrogeomorphic management scenarios $\times$ 3 forest management scenarios $\times$ 2 hydrology scenarios; Table 1). Hereafter, we refer to the simulation with no hydrogeomorphic or forest management treatments as the reference scenario, and the simulation with all possible treatments as the maximal treatment scenario. Three replicates of each scenario were run to account for variability in model projections due to stochastic processes such as seedling establishment and flood mortality. Consistent with other LANDIS-II modeling efforts in the UMR floodplain (De Jager et al. 2019), we found very minor differences among the replicate simulations. We therefore selected one simulation replicate for

Table 1 Scenario design for the LANDIS-II forest simulation model

Model scenario type	Scenario description
Hydrogeomorphic management	Baseline conditions (B)
	Channel closures (C)
	Elevation enhancement (EE)
	Elevation enhancement and channel closures (EEC)
Forest management	No forest management
	Planting, RCG suppression, and forest expansion (Planting)
	Planting, thinning, RCG suppression, and forest expansion (Planting & thinning)
Hydrologic regime	Random
	Trending

The model was run with four scenarios of potential hydrogeomorphic management actions, three scenarios of potential forest management actions, and two future hydrological scenarios. The random hydrology scenario represents a future where average inundation durations observed over the past 48 years remain stable. The trending hydrology scenario represents a future with increasing inundation durations. Reed canarygrass (*Phalaris arundinacea* L.) is abbreviated as RCG

further analysis. Simulations were run for 100 years at 5-year time steps starting in 2020.

To evaluate the effects of alternative management and hydrological regimes on forest production, we analyzed changes in total and species-specific aboveground biomass (hereafter biomass). We also assessed changes in tree species composition by calculating relative biomass (species biomass/total biomass) for each species at each time step. Following a similar approach to Suárez-Muñoz et al. (2023), we evaluated trends in biomass at both the landscape-level and the cell-level, allowing us to evaluate spatial patterns of change. Trends in biomass for each cell were calculated using the Mann–Kendall trend test (Mann 1945). We used Kendall's tau statistic to evaluate to whether biomass was consistently increasing or decreasing over time (values ranging from -1 to 1). Trends were interpreted as statistically significant when tau values exceeded ± 0.4 , which corresponds approximately to $p < 0.01$ for our trend tests. Next, we used the Theil–Sen slope (Sen 1968) to estimate the magnitude of change ($\text{g m}^{-2} \text{decade}^{-1}$). Landscape-level changes in biomass were analyzed by averaging total and species-specific biomass across the study area at each time step.

Finally, we quantified the relative importance of hydrogeomorphic management, forest management, and hydrological regime on total biomass. We assessed the relative importance of these factors, also referred to as agents of change, using a method similar to that of several LANDIS-II studies (e.g., Boullanger et al. 2018; Hotta et al. 2023; Leblond et al. 2022). The effect size of each factor was assessed by calculating omega-squared values (ω^2) following a three-way factorial Analysis of Variance. The ω^2 values represent an estimate of how much variance in biomass can be explained by each factor. We calculated ω^2 values for biomass at both the landscape-level and the cell-level for each time step. For the cell-level analysis, we determined the most important factor across space by assigning each cell to the factor that had the largest effect size on biomass. This approach allowed us to assess spatial and temporal patterns in the relative importance of each factor. All analyses were conducted in R v4.3.3 (R Development Core Team 2024) using the tidyverse (Wickham et al. 2019), terra (Hijmans 2024), sf (Pebesma 2018), and Kendall (Hipel and McLeod 1994) packages.

Results

Changes in inundation duration

Average floodplain inundation durations decreased across the study area in scenarios with hydrogeomorphic management relative to the baseline scenario (Table S2; Fig. 2a; Figure S1a). As expected, the largest reductions in inundation duration occurred in areas with elevation enhancement treatments (Fig. 2b; Figure S1b). Within these treatment sites, average inundation durations were spatially variable but decreased by up to 15 days on average compared to the baseline scenario. For example, under the trending hydrology scenario, average inundation duration decreased from 100 days per growing season in the baseline scenario to 85 days in the scenario with elevation enhancement and closures. When aggregated at the landscape level, the decreases in average inundation duration were less pronounced, with up to a 7-day reduction on average compared to the baseline scenario (i.e., from 97 days inundated per growing season to 90 days under the trending hydrology scenario). The implementation of channel closures alone had a small effect on reducing average inundation durations compared to elevation enhancement treatments (Fig. 2b). Average inundation durations were higher under the trending hydrology scenario relative to the random hydrology scenario, particularly after the first 30 years of the simulations (Fig. 3). However, all management treatments had similar effects in reducing average inundation durations relative to the baseline scenario across both simulated hydrological regimes (Table S2).

Biomass trends

Total biomass exhibited negative trends across large areas of the landscape, especially under the trending hydrology scenario, in all simulations. However, the magnitude and spatial extent of negative trends in biomass were mediated by management activities (Fig. 4a). Negative trends in total biomass were progressively less extreme and less spatially widespread under more intense hydrogeomorphic and forest management treatments (Fig. 4a; Figures S2–S4). For example, under the random hydrology scenario, the proportion of the study area experiencing significant negative trends in total biomass ranged from 48% in

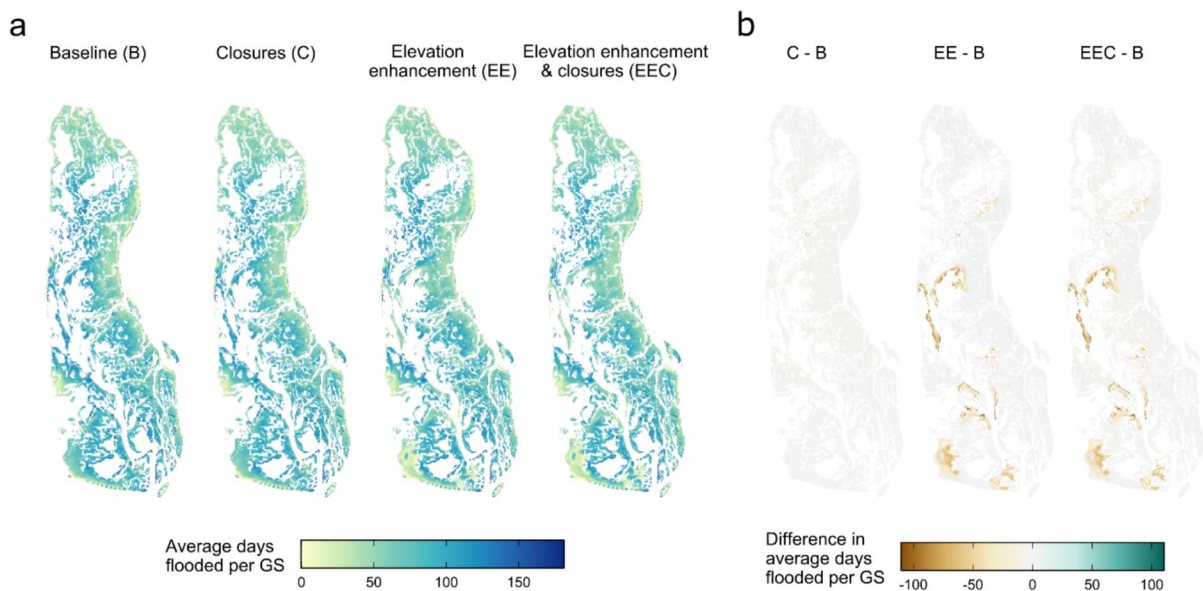


Fig. 2 Spatial patterns of floodplain inundation at Reno Bottoms. **a** Maps of growing season inundation duration averaged over the 100 simulation years for each hydrogeomorphic management scenario. **b** Maps of the difference in average inundation duration relative to the baseline scenario among

the hydrogeomorphic management scenarios. Only maps for the random hydrology scenario are shown here. Maps for the trending hydrology scenario can be found in the supplementary material (Figure S1). GS stands for ‘growing season’

the reference scenario (no hydrogeomorphic or forest management treatments) to 28% in the maximal treatment scenario. Under the trending hydrology scenario, the proportion of the study area experiencing significant negative trends in total biomass ranged from 61% in the reference scenario to 49% in the maximal treatment scenario.

Biomass trends showed different spatial patterns across the study area. Negative trends in total biomass were widespread but tended to concentrate in areas with longer average inundation durations (Fig. 4a; Figures S3–4). Positive trends in total biomass occurred in areas including the northeast portion of the landscape bordering the main channel of the Mississippi River, sites with elevation enhancement, and the non-forest expansion zone. Trends in silver maple biomass closely resembled these spatial patterns of change in total biomass (Figures S5–6). Conversely, swamp white oak biomass increased across large swaths of the landscape (e.g., up to 980 ha) in scenarios with forest management. Positive trends in swamp white oak biomass were especially evident along the northeast edge bordering the main channel and the southwest

portion of the landscape (Figures S7–8). Trends in eastern cottonwood and willow biomass were weak and less spatially coherent relative to the other species (Figures S9–12). Intensified management treatments tended to have a positive effect on biomass accumulation of silver maple and swamp white oak biomass, whereas management effects were inconsistent for eastern cottonwood and willow biomass (Figures S13–14).

At the landscape scale, average total biomass decreased in all simulations, with greater declines under the trending hydrology scenario (Fig. 5). Total biomass decreased less under more intense management scenarios. These declines in total biomass were primarily driven by declines in silver maple biomass over the first 50 years of the simulations (Figure S15). In contrast, swamp white oak is projected to increase in biomass across all scenarios, with larger increases projected under intensified management treatments and the random hydrology scenario (Figure S16). Eastern cottonwood biomass is projected to decrease consistently across scenarios, with the largest losses occurring in roughly the first 60 years of the simulations. Willow biomass is projected to decrease over

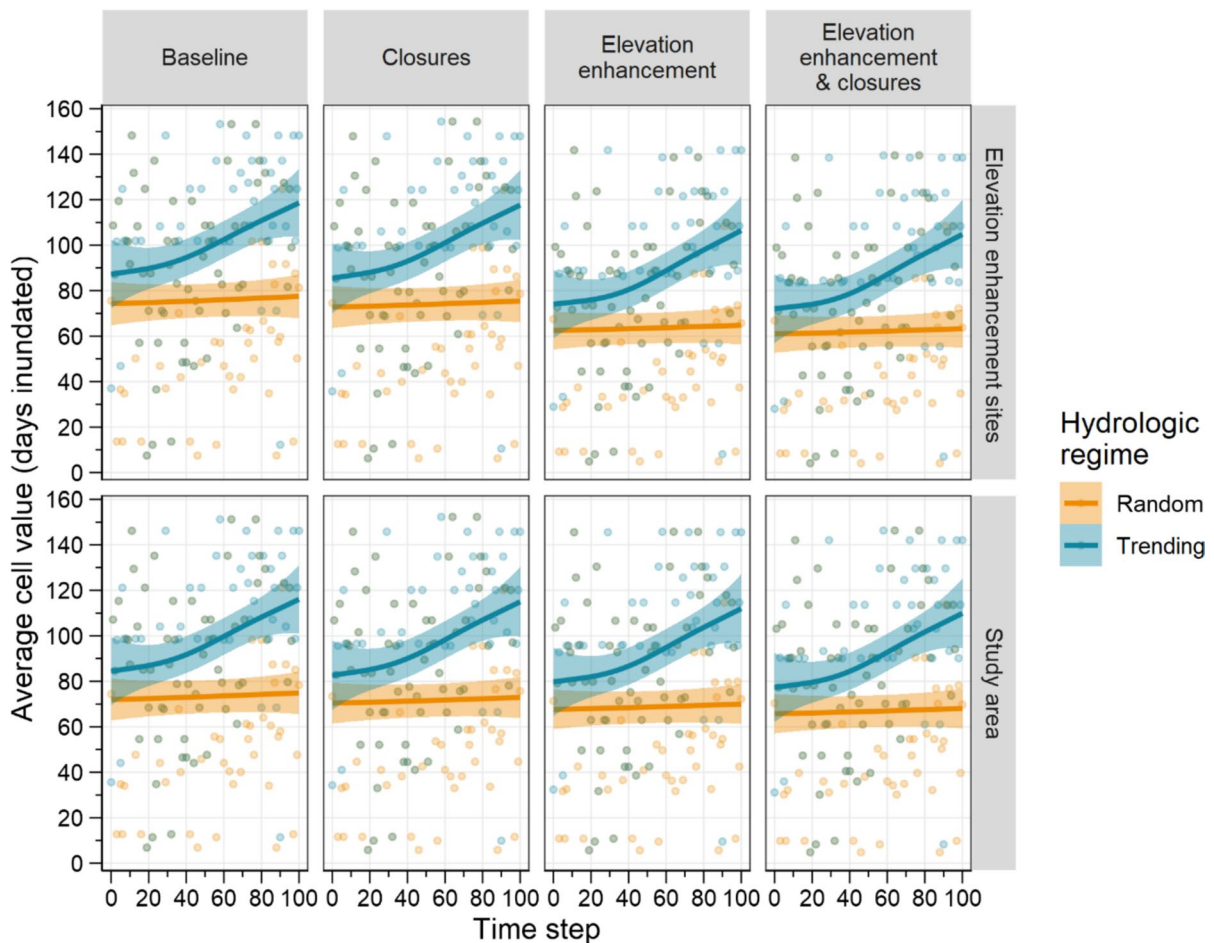


Fig. 3 Changes in the number of days inundated per growing season averaged by area among the hydrogeomorphic management and hydrology scenarios. Lines represent generalized additive models of trends, and shaded areas represent the standard error. The top row shows inundation durations averaged in areas with elevation enhancement treatments. The

bottom row shows inundation durations averaged across the whole study area. The largest reductions in inundation duration occurred in areas with elevation enhancement treatments, whereas reductions in flooding were relatively small across the study area

the first 50 years before stabilizing or increasing compared to current conditions.

Forest composition

Silver maple is by far the most abundant species in the current landscape based on absolute and relative biomass (Figs. 5 and 6). Silver maple is projected to decrease in relative biomass under both random and trending hydrological scenarios (from as high as 82% in year 0 to as low as 49% in year 100) but remain the most abundant species throughout the simulations. In contrast, swamp white oak relative biomass

is projected to increase over the next century under both hydrological scenarios (from as low as 6% in year 0 to as high as 29% in year 100; Fig. 6). Eastern cottonwood relative biomass is projected to decrease slightly under both hydrological scenarios (Fig. 6). Willow relative biomass is projected to remain low and generally stable over time under both hydrological scenarios (Fig. 6). In addition, American elm relative biomass is projected to increase modestly over time under both hydrological scenarios, ranging from as low as <1% in year 0 to as high as 6% in year 100.

Collectively, forest composition showed little response to hydrogeomorphic and forest management

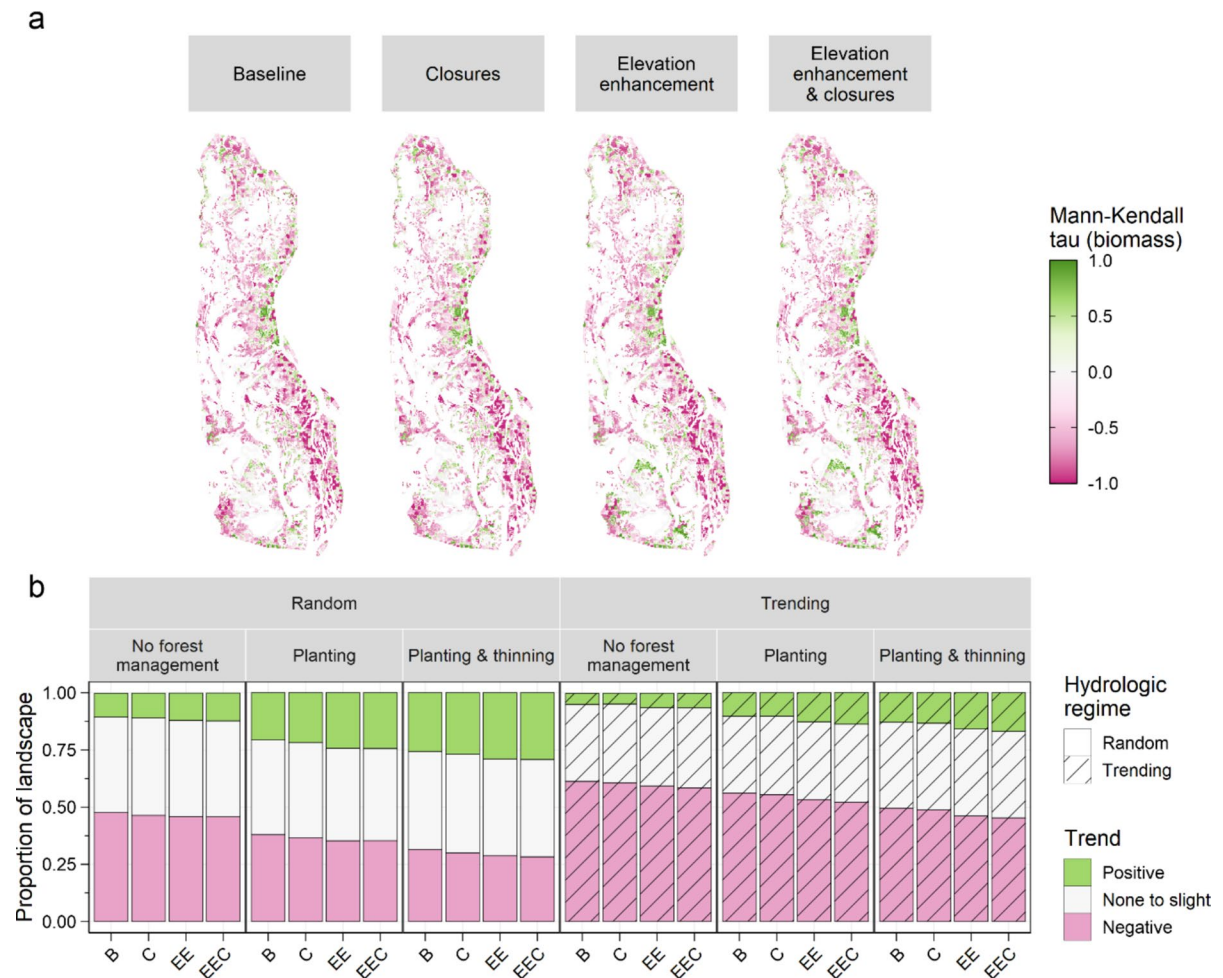


Fig. 4 Trends in total biomass across the study area. **a** Example maps of trends in biomass for each hydrogeomorphic management scenario under the no forest management and random hydrology scenarios. Cell values represent Kendall's tau statistic. Trend maps for all scenarios can be found in the Supplementary Information. **b** The proportion of pixels across the

landscape with significant positive ($\tau > 0.4$), significant negative ($\tau < -0.4$), and no significant ($-0.4 \leq \tau \leq 0.4$) trends in total biomass. Hydrogeomorphic scenario names on the x-axis are abbreviated as *B* Baseline, *C* Closures, *EE* Elevation enhancement, and *EEC* Elevation enhancement and closures

treatments at the landscape scale, as indicated by changes in the relative biomass of individual tree species. Intensified management treatments reduced the magnitude and extent of biomass loss, largely by mitigating silver maple losses and promoting gains in swamp white oak and river birch. The largest shifts in forest composition were decreasing silver maple relative biomass and increasing swamp white oak relative biomass, and these changes were consistently projected across all alternative management scenarios. Although management treatments generally did not have a large effect on the relative biomass of most

species, river birch was one exception; relative biomass of this species is projected to increase modestly by the end of the simulations under scenarios with forest management (from as low as <1% in year 0 to as high as 5% in year 100).

Relative importance of management and hydrological regime

The relative importance of management and hydrological regime on total biomass varied spatially and temporally in our simulations. Forest management

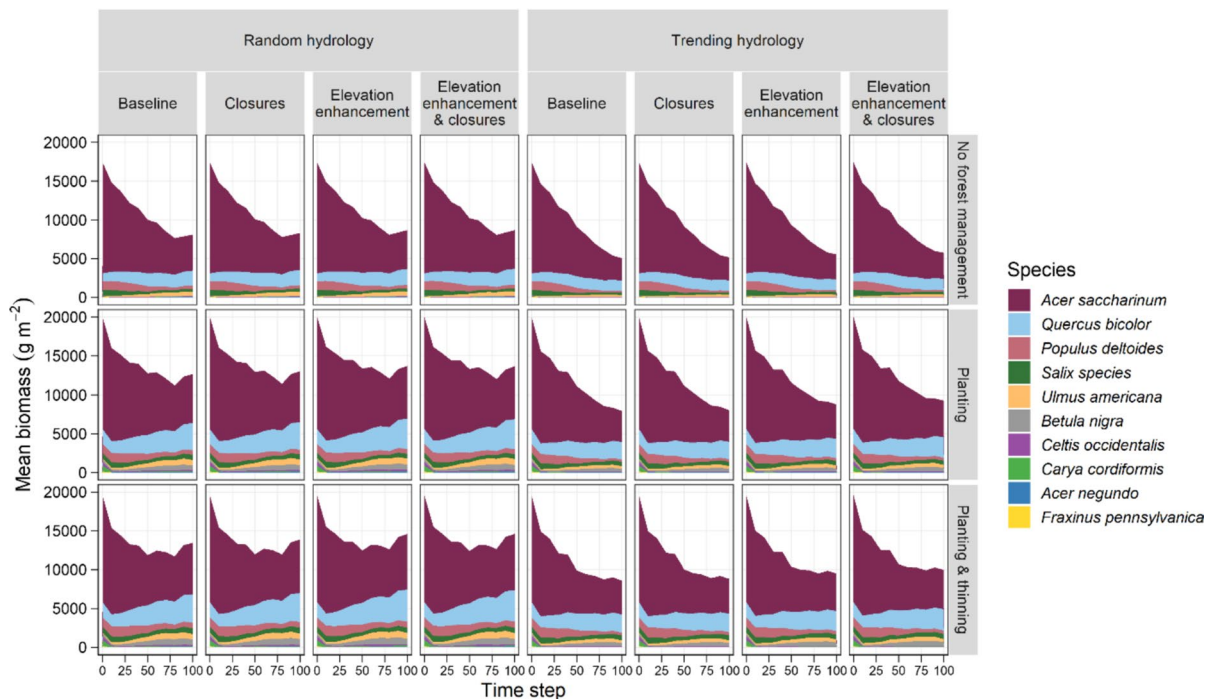


Fig. 5 Trends in average biomass at the landscape scale for each species simulated in the 24 management-hydrology scenarios. Columns show different hydrogeomorphic and hydrology scenarios. Rows show different forest management scenarios

was the most important factor influencing total biomass across large swaths of the landscape, especially at the beginning of the simulated period. For example, forest management had the largest effect on total biomass for 56% of the study area in year 50, decreasing to 39% of the study area in year 100 (Fig. 7). The area where hydrological regime had the largest effect on total biomass increased from 27 to 48% of the study area between years 50 and 100 (Fig. 7). The area where hydrogeomorphic management had the largest effect on total biomass was concentrated where elevation enhancement treatments were implemented and was relatively stable over time, decreasing from 17% in year 50 to 13% in year 100 (Fig. 7).

At the landscape scale, forest management explained nearly all the variability in total biomass at the beginning of the simulations (Figure S17). The relative importance of forest management decreased over time and was gradually overtaken by hydrological regime by the end of the simulations. Hydrogeomorphic management was the least important factor influencing landscape-scale total biomass, with effect sizes that were near zero and stable over time.

Discussion

Our simulations indicate that forest biomass in the Reno Bottoms area of the Upper Mississippi River will decline over the next century regardless of management-hydrology scenario. However, management treatments were effective in limiting the magnitude and extent of projected declines in biomass. By contrast, management treatments did not substantially alter forest compositional trajectories, which reflect the legacies of past land use change, altered hydrology, insect pests, and disease in our study area. Among the factors influencing variation in forest biomass trajectories, forest management was the most important in the first half of the simulations whereas the hydrological regime became increasingly more important by the end of the century. Hydrogeomorphic management was an important factor in areas where elevation enhancement was implemented, but it had little influence on forest biomass trajectories at the landscape scale. Our results deepen our understanding of potential future forest conditions under plausible alternative

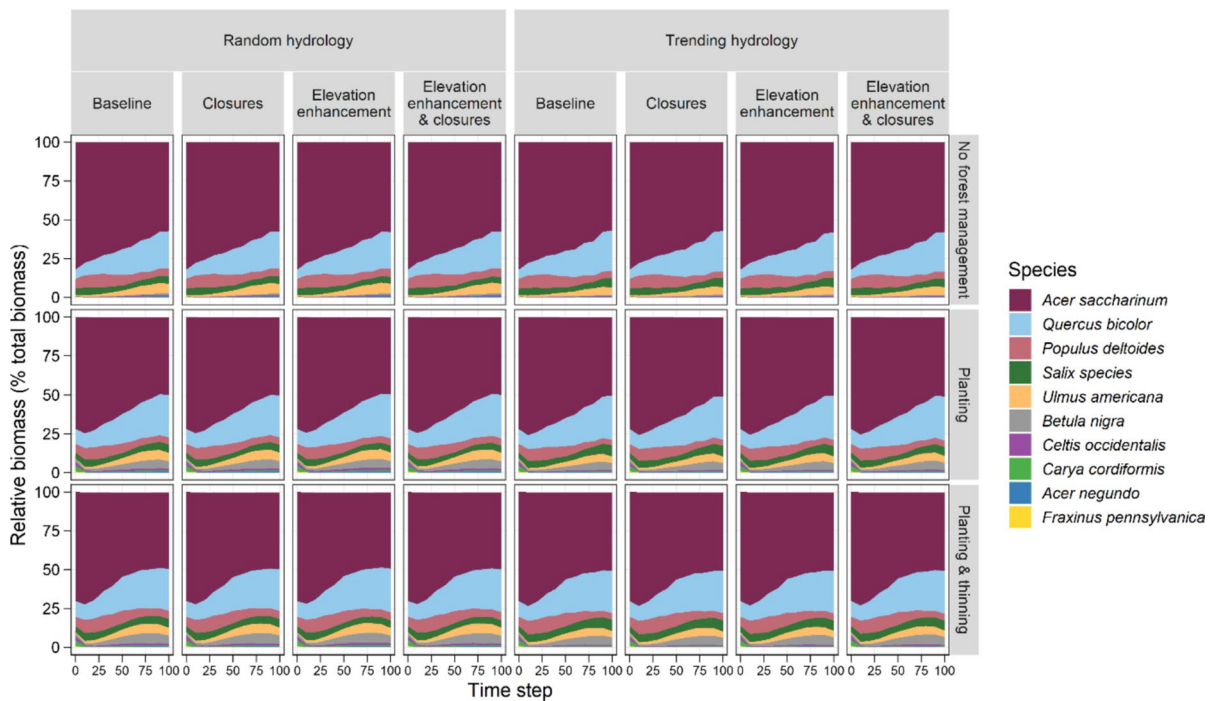


Fig. 6 Trends in average relative biomass (percent species biomass of total) for each species simulated in the 24 management-hydrology scenarios. Columns show different hydrogeo-

morphic and hydrology scenarios. Rows show different forest management scenarios

scenarios of management and hydrologic change in the UMR.

Effects of management on floodplain inundation patterns

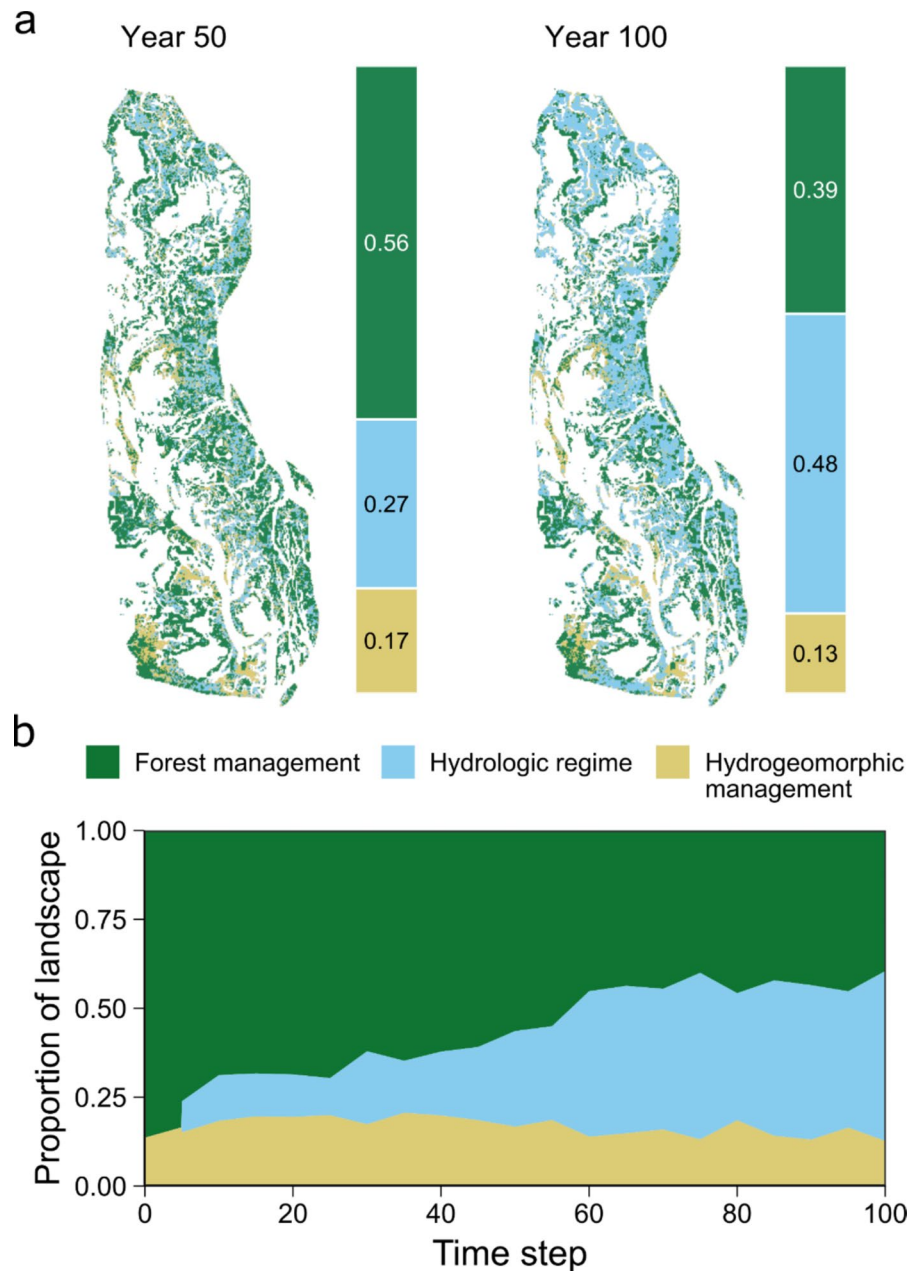
Average inundation durations decreased across the study area in hydrogeomorphic management scenarios that included elevation enhancement. This result was expected given that these treatments were intended to reduce flood durations and support higher elevation floodplain forest. Although reductions in average inundation duration were relatively small at the landscape scale, some areas with elevation enhancement (e.g., constructed islands) had reductions in inundation duration of up to several weeks or months per annual growing season. These local-scale reductions in inundation duration could be relevant to floodplain forest succession given the well-documented association between flooding duration and the distribution and productivity of floodplain vegetation (e.g., Clark and Benforado 1981; Johnson et al. 2016; Marks et al. 2014; Naiman et al. 2010), including on

the Upper Mississippi River (De Jager et al. 2012, 2016; Ingvalson et al. 2020). In our model, we simulated the effects of inundation duration on forest succession using inundation maps that influenced the locations of species-age-cohort mortality (De Jager et al. 2019). Thus, it is plausible that reductions in floodplain inundation at elevation enhancement sites could drive local-scale differences in tree communities that would “scale up” via dispersal to alter landscape-level forest succession trajectories. Although hydrogeomorphic management treatments did influence biomass trajectories in our simulations, they ultimately did not alter large-scale patterns of forest composition, the potential reasons for which are discussed below.

Changes in forest biomass and composition

We observed a negative trend in biomass over the next century across all management-hydrology scenarios. This decline could be driven by senescence of the existing mature tree canopy as the UMR floodplain is heavily dominated by mature silver maple

Fig. 7 Spatial and temporal patterns in the importance of each factor influencing total biomass. **a** Maps of the main agent of change (factor that had the largest effect size) on biomass at each cell for year 50 and 100. Bar charts show the proportion of the landscape associated with each agent of change at that time step. **b** Trends in the importance of each agent of change as a proportion of the landscape over time. Effect size values were calculated using three-way factorial Analysis of Variance analyses at each cell in the landscape at each time step



forests (Knutson and Klaas 1998). The natural ageing and senescence of existing silver maple cohorts and replacement by younger cohorts with far less biomass could explain the general decline in forest biomass. However, extensive forest inventory data and previous modeling studies have pointed to a widespread lack of forest regeneration, resulting in a loss of forest cover (De Jager et al. 2019, 2024). Our results also show stronger decreases in forest biomass under the

trending hydrology scenario, indicating that more areas of the landscape are likely to be too wet to support woody plant recruitment. Although we did not explicitly evaluate changes in forest cover, the strong negative trends in biomass we observed indicate that a conversion from forest to non-forest cover types is likely to take place in some parts of the study area. Future biomass loss would add to the already ongoing trend of decreasing forest cover in the UMR from

pre-settlement levels (De Jager et al. 2013a; Nelson et al. 1994; Yin et al. 1997).

Forest composition is not projected to change greatly over time in our simulations, despite changes in relative biomass for some species. This finding is consistent with a growing number of modeling studies that indicate a general inertia of forest growth over the next century (Duveneck et al. 2017; Nevins et al. 2021; Thompson et al. 2011; Wang et al. 2017). In our study system and the UMR more broadly, forest compositional shifts appear to be strongly influenced by species life history attributes and the current distribution of species and tree ages across the landscape (De Jager et al. 2019). For example, land use change, altered hydrology, and recruitment problems have been linked to the increased dominance of mature silver maple communities in the UMR (De Jager et al. 2012; Knutson and Klaas 1998; Nelson and Sparks 1998; Yin et al. 2009). The steep declines in biomass in our simulations partly reflect the age-related mortality of these silver maple forests that emerged in the late nineteenth and twentieth centuries from the abandonment of agricultural fields and altered hydrology associated with river impoundment. Nonetheless, silver maple is projected to remain the dominant species in our study area over the next century. Altogether, our projections indicate that inundation-related mortality will likely limit the recruitment of mid- to late-successional species with low flood tolerance, thereby preventing a reorganization of species composition. We also recognize the possibility that we would have observed larger shifts in species composition had we simulated forest succession beyond the next century, as shown in other studies using LANDIS-II (e.g., Nevins et al. 2021).

Unlike most other species in our model, swamp white oak is projected to fare better over the next century. The relatively strong increase in swamp white oak relative biomass observed in our simulations is consistent with regional modeling work from the UMR, which projected increases in biomass for this species (De Jager et al. 2019). These results can be attributed to the moderate flood and shade tolerance of swamp white oak, as well as its longer lifespan compared to other floodplain species. Field studies and outdoor laboratory experiments also support the strong performance of swamp white oak under variable hydrological conditions. For instance, Windmüller-Campione et al. (2022) conducted an experimental

underplanting study in the UMR floodplain and found that swamp white oak had high survival rates across a gradient of elevation and inundation durations compared to three other species. Further, Kabrick et al. (2012) examined the response of hardwood seedlings to flooding in an outdoor laboratory and found that swamp white oak maintained high survival and growth after partial inundation. The increased abundance of swamp white oak in higher and less frequently flooded sites across our study area is consistent with a general pattern of floodplain forest succession in the Mississippi River (Hodges 1997).

Effects of hydrology and management on forest biomass and composition

Hydrologic regime became the most important factor affecting total biomass across the study area by the end of the simulation period. The increasing importance of hydrologic regime over time partly reflects the fact that average inundation durations were initially similar between the two hydrology scenarios and increasingly diverged over time (Fig. 3). Moreover, it was expected that variation in the hydrologic regime would have a substantial influence on forest biomass given that strong linkages between flooding duration and vegetation establishment, growth, and mortality rates have been documented in both observations and model simulations in the UMR (De Jager et al. 2016, 2019; Yin et al. 2009).

The trending hydrology scenario enhanced the magnitude and spatial extent of biomass declines, indicating that wetter conditions may accelerate forest decline in the study area. On the other hand, future changes in hydrology remain a large source of uncertainty in this research. Recent evidence indicates a general trend towards wetter conditions in the UMR (Van Appledorn 2022). This upward trend is projected forward in our trending hydrology scenario and may result in unrealistically large increases in inundation duration. However, we currently lack robust basin-scale projections of critical variables such as discharge and water surface elevation across the UMR. Recent periods of anomalously low river discharge, including the fall of 2022 (Muñoz et al. 2023), also serve as a reminder of the high variability in river conditions that may be expected in the future. The errors associated with estimating local-scale water surface elevations and inundation based

on discharge conditions add further uncertainty to our understanding of the future hydrological conditions that these forest communities will experience.

Forest management was the main factor explaining variability in forest biomass and composition across the study area up until the final decades of our simulations. There are several likely reasons why forest management was the main agent of change throughout most of the simulated period. First, the full suite of forest management treatments (planting, thinning, and vegetation control) covered almost the entire study area and represent a hypothetical maximum level of management effort scenario. The large spatial scale of these treatments resulted in substantial variation in the initial forest communities that served as the starting point for the simulations. Second, we assumed that natural regeneration of floodplain forest could be possible in areas that are currently wet meadow or marsh habitat. This non-forest expansion zone comprises 391 ha where forest regeneration was only possible in scenarios with forest management. Finally, we assumed that reed canarygrass could be eradicated in areas with mechanical and chemical treatment, and therefore would no longer limit woody plant establishment across the duration of our simulations. In practice, these assumptions are simplistic compared to the actual dynamics of reed canarygrass suppression. For example, field studies in the UMR indicate that the suppression of reed canarygrass is possible but successful forest regeneration may still be limited by other factors such as herbivory (Miller-Adamany et al. 2019; Thomsen et al. 2012).

Although forest management was the main agent of change throughout much of our simulations, it did not prevent decreases in total biomass or substantially alter forest composition. The effectiveness of forest management was limited in part by the simulated high mortality of planted seedlings due to repeated flood events. This mortality is evident from an abrupt dip in the biomass of planted species between year 0 and year 10 of our simulations (Figure S16), particularly for species with low flood tolerance such as bitternut hickory. The limited survival of planted seedlings is a major challenge in floodplain forest management and restoration due to the risk of mortality from prolonged inundation and/or shoot overtopping (Hosner 1958; Stanturf et al. 2001), among other complicating factors such as invasive species competition or herbivory (e.g., De Jager et al. 2013b). In our model,

two-year-old cohorts in the planting scenarios were highly susceptible to flood-related mortality. Simulating the planting of older trees could have lowered this risk and led to larger differences in future forest succession, yet this strategy may not be feasible in practice due to added costs and logistical challenges.

The limited effectiveness of thinning treatments was another reason why forest management did not lead to larger differences in forest succession. Thinning treatments were intended to release existing trees from competition and create canopy gaps that promote the regeneration and growth of understory trees. Although there is evidence that thinning can enhance long-term aboveground carbon storage and diversity in floodplain and riparian forests (Horner et al. 2010; Pollock and Beechie 2014), thinning produced relatively small additional benefits in terms of maintaining forest biomass or promoting species compositional diversity in our simulations. Thinning may be more beneficial in other forest community types along the UMR, such as southern UMR forests with pin oak (*Quercus palustris* Münchh.), which has shown a strong positive response to thinning (McQuilkin 1990). Additionally, increasing the intensity of thinning treatments in the model—currently limited to removing silver maple age 50 and 70 from selected sites—may provide valuable insights into drivers of productivity and diversity. Ultimately, the potential benefits of intensified thinning for biomass storage may not be realized if young cohorts are repeatedly killed by flooding, as shown in our simulations.

Hydrogeomorphic management was an important agent of change in areas with elevation enhancement, but these localized effects did not scale up to substantially alter landscape-level biomass. Management agencies in the UMRS commonly use water-level management and geomorphic modification as tools for ecosystem restoration (Guyon et al. 2012). Elevating the floodplain surface can have a critical effect on forest succession by reducing inundation durations, which help structure floodplain communities (Junk et al. 1989; Hupp and Osterkamp 1996). In our projections, hydrogeomorphic management remained the most important factor influencing biomass trajectories in many areas where elevation enhancement caused a large reduction in inundation duration (e.g., constructed islands; Fig. 2b; Fig. 7). Thus, our results indicate that elevation enhancement can be an effective management tool to buffer the negative effects of

wetter conditions on forests at local scales. However, the local effects of hydrogeomorphic management observed here were obfuscated when evaluating differences in forest biomass projections at the broader landscape scale (Figure S17). Although the goal of such local-scale management actions is primarily to change trajectories in the locations where they were applied, management agencies might be interested in understanding how local actions could scale up to influence the broader landscape. Further spatially explicit modeling work could improve our understanding of the effects of restoring relatively small, scattered areas of habitat on larger-scale forest conditions in the UMR.

Conclusions and management implications

As floodplain forests continue to change in response to anthropogenic stressors and altered hydrological conditions, their future successional trajectories remain uncertain. Our simulations indicate that forest biomass will decrease in the Reno Bottoms area of the UMR floodplain over the next century, especially under a wetter future hydrological scenario. However, this decrease was primarily driven by the age and flood-related mortality of one species—silver maple—which dominates the current landscape and is approaching maximum longevity in many areas. Our work therefore indicates that forest successional trajectories are heavily influenced by the current distribution of species-age cohorts across the landscape, which in turn reflects legacies of past land use change, altered hydrology, insect pests, and disease. This finding is likely general to floodplain forests in the UMR, and perhaps in other floodplain systems that have become increasingly dominated by even-age cohorts of a single species (e.g., Johnson et al. 2012). In our modeling framework, uncertainties in tree age estimates and species maximum longevity affect simulated biomass trajectories, including the magnitude and timing of declines in silver maple biomass. Further efforts to improve our understanding of age structure and stand dynamics in UMR floodplain forests could help to increase confidence in model projections.

Forest management, and to a lesser extent hydrogeomorphic management, altered landscape-scale projections of forest change by mitigating

declines in forest biomass, especially under intensified treatment scenarios. In addition, management treatments promoted increased compositional diversity through the enhanced establishment and growth of several late-successional species including swamp white oak. However, the potential benefits of management could vary substantially across a spatially heterogeneous landscape with different patterns of inundation duration. For example, increasingly wet conditions could overwhelm current management strategies in low-lying areas with longer inundation durations, or across broader areas of the landscape. In light of this uncertainty, our spatially explicit modeling framework can help managers prioritize where treatments may or may not be effective in shaping successional trajectories. Such strategies are already being considered and implemented in the UMR, for example, using management frameworks to prioritize where resisting, accepting, or directing ecological change would be the most appropriate (i.e., the Resist-Accept-Direct framework; Bouska et al. 2022; De Jager et al. 2024; Ward et al. 2023). In our study, areas where forest or hydrogeomorphic management remained the most important agents of change represent sites where management may be most consequential for resisting or directing change in floodplain forests over the next century.

Our projections indicate the potential for substantial declines in forest biomass at Reno Bottoms, even under a ‘best-case scenario’ featuring stable hydrology and maximum restoration effort. Although this loss of biomass can be explained in part by natural succession and the senescence of mature silver maple cohorts, it could also signify habitat degradation and loss of floodplain forests related to prolonged flooding, invasive species, and a lack of regeneration. Floodplain forest loss would have far-reaching implications for the natural functions and services of this river-floodplain area, including reduced carbon storage, loss of critical wildlife habitat and shifts in habitat quality (Guyon et al. 2016), and changes in large wood supply (Van Apple-dorn et al. 2024). Although all simulations from a complex process-based model like LANDIS-II come with inherent uncertainty, our results can provide insight into the range of plausible forest successional trajectories under the combined effects of management and altered hydrology. Improving our basic understanding of forest community development in relation to flooding dynamics, including refining estimates of species

and age-specific flood tolerance, will help reduce the uncertainty associated with projecting forest succession in riparian and floodplain settings.

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Author contributions NDJ, MVA, and AM designed the study and helped develop model input datasets. AM led the process for identifying and selecting locations for management. MVA conducted floodplain inundation modeling. NDJ and MT conducted forest simulation modeling. MT compiled results, conducted analyses, and wrote the first draft of the manuscript. All authors reviewed and edited the manuscript text.

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Data availability The data supporting this study are available at <https://doi.org/10.5066/P13TYTXX> (Trumper et al. 2025).

Declarations

Competing interests The authors declare no competing interests.

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