U.S. Army Corps of Engineers'
Upper Mississippi River Restoration Program
Long Term Resource Monitoring Element
Research Framework
LTRM-2019R2

Scientific Framework for Resilience Research on the Upper Mississippi River System

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October 2019

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by

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Summary

The goal of this research framework is to outline research that would continue to improve our understanding of ecological resilience of the Upper Mississippi River System (UMRS) and inform management of the system for health and resilience. We provide a broad overview of recently completed and ongoing work that has been funded as a part of the UMRS Ecological Resilience Assessment and related efforts to provide context for how proposed research questions build upon our current knowledge and may inform restoration planning and design. We describe two primary objectives within this research framework - the first objective is to investigate hypothesized drivers and feedbacks related to specified resilience, and the second is to expand our utility of general resilience indicators through further development and evaluation.

The intended audience for this framework is the Upper Mississippi River Restoration Program (UMRR). The UMRR partnership is made up of natural resource agencies from five states (Illinois, Iowa, Minnesota, Missouri and Wisconsin) and five federal agencies (U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, U.S. Fish and Wildlife Service, U.S. Geological Survey, and USDA Natural Resources Conservation Service).

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Introduction

With ever increasing anthropogenic pressures affecting natural resources, there is growing interest in managing ecosystems for resilience (Benson and Garmestani 2011, Brown and Williams 2015). Resilience is defined as "the capacity (of an ecosystem) to absorb disturbances and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Holling 1973, Walker et al. 2004). Implicit in this definition is that ecosystems are self-organizing, meaning that internal interactions and feedbacks maintain an ecosystem's state or regime (Levin 1998, Walker and Salt 2012). However, abrupt and unexpected shifts to alternate regimes maintained by novel interactions and feedbacks can occur if a disturbance moves ecosystem components across critical thresholds (Holling 1973, Gunderson 2000). Therefore, managing an ecosystem for resilience requires description and anticipation of critical thresholds, understanding feedbacks and interactions at different scales, and incorporating expectations of variability and uncertainty to improve a system's ability to respond and adapt to anticipated as well as unforeseen changes and stress (Allen et al. 2011, Walker and Salt 2012).

To support the U.S. Army Corps of Engineers Upper Mississippi River Restoration (UMRR) Program's vision for a "healthier and more resilient ecosystem that sustains the river's multiple uses," the UMRR partnership is currently undertaking an ecological resilience assessment (Upper Mississippi River Restoration Program 2015). Broadly, the purpose of the assessment is to gain a deeper understanding of complex ecosystem dynamics to inform the planning and design of restoration projects. More specifically, the resilience assessment aims to provide insight into how resilience is created, maintained, or broken down within the Upper Mississippi River System (UMRS) and how restoration projects and management actions might influence those processes. In assessing the resilience of the UMRS, we have adapted the Resilience, Adaptation and Transformation Assessment Framework (O'Connell et al. 2015), which includes three major elements: 1) a system description, 2) assessment of resilience, and 3) adaptive governance and management (Figure 1). A resilience working group, made up of individuals across the UMRR partner agencies (Appendix: Table A), provides guidance and feedback on the direction and specifics of the assessment.

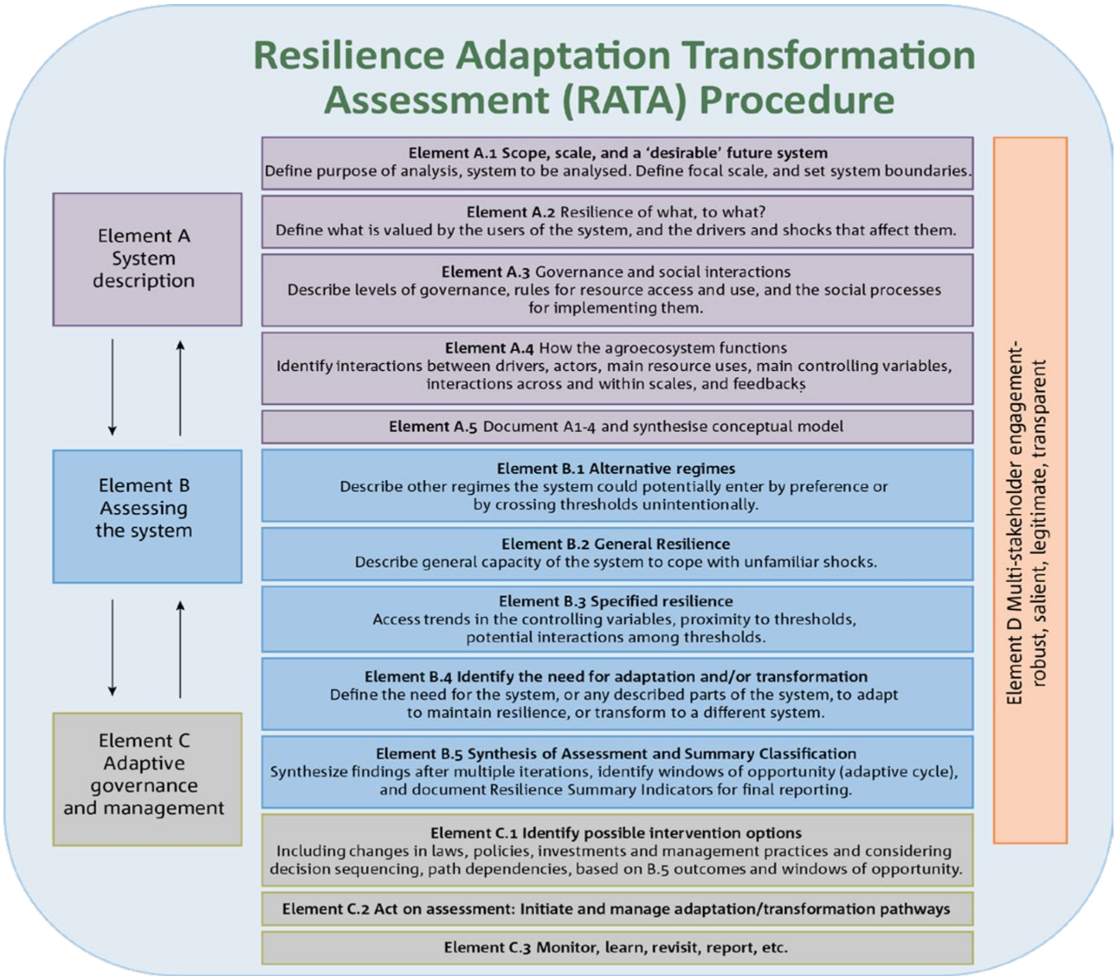


Figure 1. The Resilience, Adaptation, and Transformation Assessment framework (source: O'Connell et al. 2015).

The goal of the UMRS system description was to simplify a complex system to identify its fundamental characteristics. In doing so, we reviewed the relevant historical context that has shaped the current state of the UMRS, recognized valued uses of and services provided by the UMRS, and identified key ecological resources that are needed to support those valued uses and services (Bouska et al. 2018). Further, we identified three sub-systems: lotic channels (i.e., main channel and side channels), lentic areas (i.e., backwater lakes, floodplain lakes, and impounded areas), and floodplains (i.e., aquatic-terrestrial transition zone; Figure 2), and the major controlling variables that are known to influence key ecological resources within each subsystem (Figure 3). Identification of a relatively small number of controlling variables that influence major resources aids in narrowing the focus of subsequent analyses to support the resilience assessment. Because the resilience assessment is intended to inform restoration decisions and a system description is considered the foundation for a resilience assessment, UMRR partner agencies were engaged throughout the development of those conceptual models.

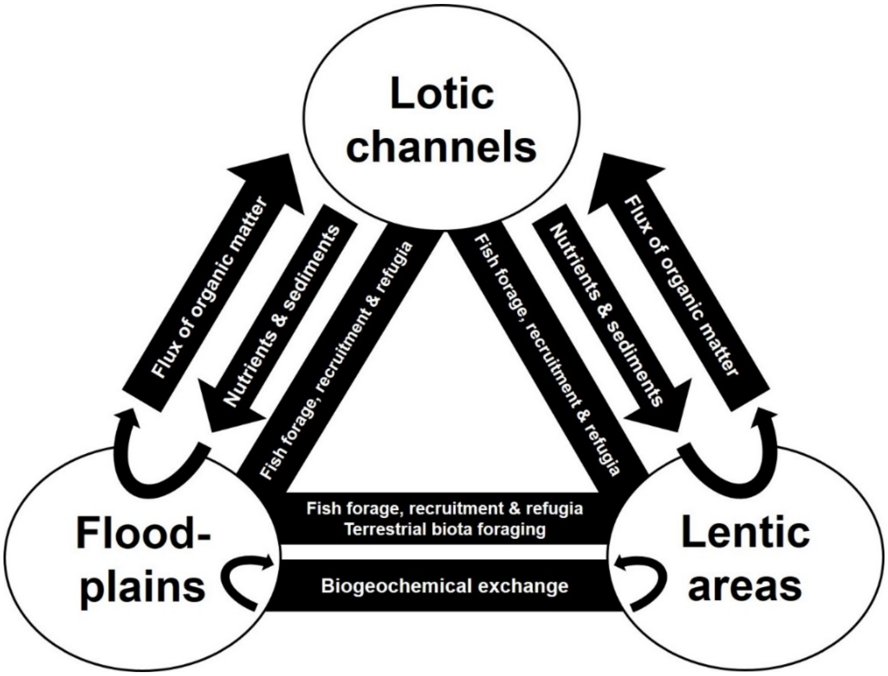
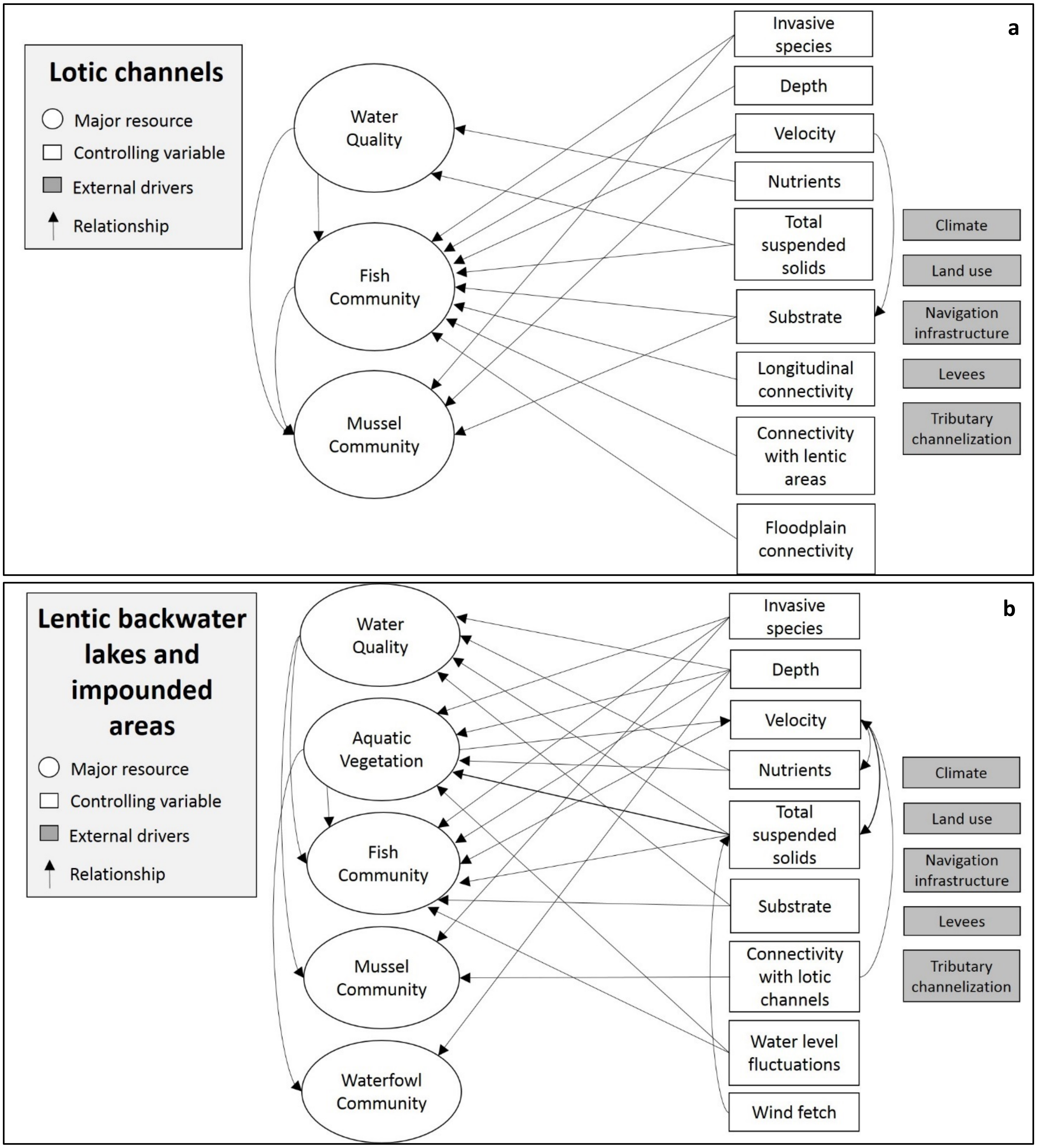


Figure 2. The Upper Mississippi River System can be described as three interacting subsystems: lotic channels, lentic areas, and floodplains. Connectivity and exchange between subsystems are critical to the structure and function of large floodplain rivers. Curved arrows represent biogeochemical processing within a subsystem (source: Bouska et al. 2018)


a
Lotic channels
○ Major resource
☐ Controlling variable
▨ External drivers
↑ Relationship
Water Quality
Fish Community
Mussel Community
Invasive species
Depth
Velocity
Nutrients
Total suspended solids
Substrate
Longitudinal connectivity
Connectivity with lentic areas
Floodplain connectivity
Climate
Land use
Navigation infrastructure
Levees
Tributary channelization
b
Lentic backwater lakes and impounded areas
○ Major resource
☐ Controlling variable
▨ External drivers
↑ Relationship
Water Quality
Aquatic Vegetation
Fish Community
Mussel Community
Waterfowl Community
Invasive species
Depth
Velocity
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Water level fluctuations
Wind fetch
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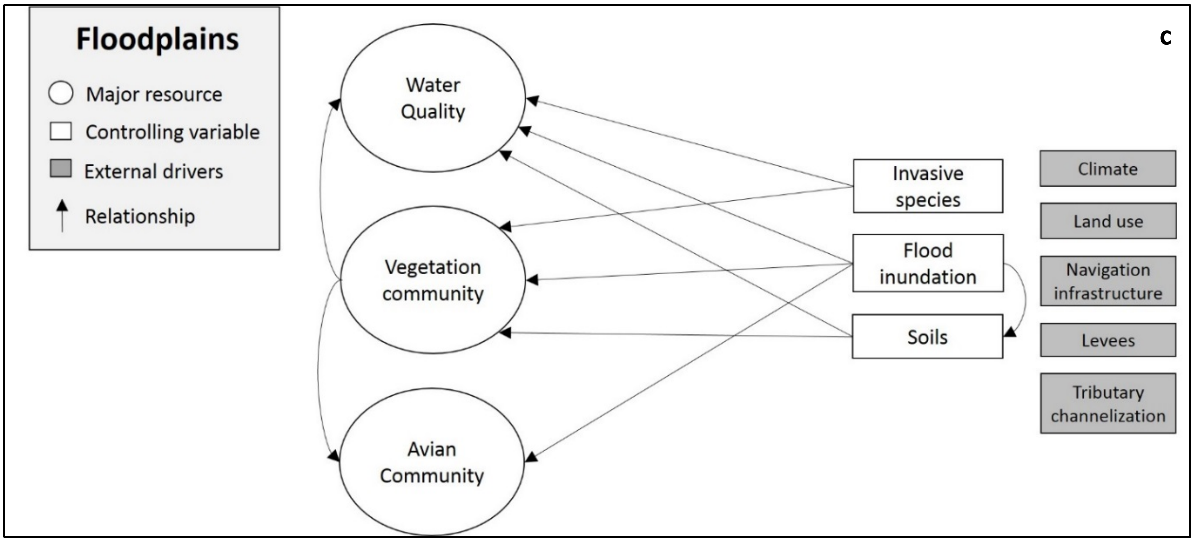

Figure 3. Conceptual models of lotic (a), lentic (b), and floodplain (c) subsystems, highlighting the major resources and the controlling variables known to influence patterns of distribution and abundance of the identified major resources. For further details, see Bouska et al. 2018.

In the second element of the assessment, assessing the resilience of the system, there are two separate evaluations: general resilience and specified resilience (Figure 1). The evaluation of general resilience focused on understanding properties of the system that support its ability to cope with anticipated as well as unforeseen disturbances and changes. Seven generic principles have been recognized to support the coping capacity of ecosystems to disturbances: 1) maintaining diversity and redundancy, 2) managing connectivity, 3) managing slow variables and feedbacks, 4) fostering an understanding of social-ecological systems as complex adaptive systems, 5) encouraging learning and experimentation, 6) broadening participation, and 7) promoting polycentric governance systems (Biggs et al. 2012). We applied the first three principles of general resilience to our understanding of how the UMRS functions, to develop broad-scale, systemic indicators of general resilience (Table 1) (Bouska et al. 2019). These indicators provide information about the general adaptive capacity of the river at a navigation pool and floodplain reach scale from which restoration actions can be identified that, in theory, would bolster resilience to future disturbances. The results of the general resilience assessment suggest that of the four river-floodplain reaches defined by geomorphology, distribution of aquatic vegetation, and distribution of federal levees (Lubinski 1993), the Upper Impounded Reach has the greatest capacity to adapt to changing environmental conditions, while the Lower

Impounded and Illinois River Reaches have a lesser capacity, and the Unimpounded Reach has the least capacity (Bouska et al. 2019). A subset of these of these indicators (shown in Table 1) was integrated into the Habitat Needs Assessment II to support the inclusion of resilience concepts in restoration planning (De Jager et al. 2018, McCain et al. 2018).

Table 1. In application of three general resilience principles, the following indicators were developed for the Upper Mississippi River System (source: (Bouska et al. 2019).

General Resilience Principle	UMRS Resilience Metric
Maintain diversity and redundancy	Aquatic habitat diversity and redundancy
	Floodplain inundation diversity
	Fish functional diversity and redundancy
Manage connectivity	Longitudinal aquatic connectivity
	Lateral connectivity
Manage slow variables and feedbacks	Water surface elevation ranges
	Total suspended solids
	Nutrient concentrations
	Sedimentation rates
	Aquatic invasive species

The second element of the resilience assessment also evaluates specified resilience. Specified resilience focuses on understanding the resilience of a particular part of the system in response to a specific disturbance (Walker and Salt 2012). Work on specified resilience of the UMRS has focused on describing alternative regimes that are likely to occur if the system crossed a critical threshold (Bouska et al. In Review). The resulting manuscript describes three sets of potential alternate regimes in the UMRS that expand upon the conceptual models derived from the system description: 1) a clear and vegetated regime vs. a turbid and sparsely vegetated regime in lentic, off-channel areas 2) a diverse native fish community regime vs. an invasive-dominated fish community regime in aquatic areas and 3) a regime characterized by a diverse and dynamic mosaic of floodplain vegetation types vs. regime characterized by an invasive wet meadow monoculture in floodplain environments. These three alternate regimes were selected because collectively they span the entire UMRS, and they address three of the major changes that have occurred in the UMRS over the last three decades. For each set of alternative regimes, the biological characteristics of each regime, hypothesized drivers of regime transitions, and the potential feedback mechanisms that reinforce each regime are described following the approach outlined by Bestelmeyer et al. (2011). Important objectives of assessing specified resilience include identifying potential thresholds for controlling variables, assessing how far the system may be from those thresholds, understanding trends in those controlling variables, and considering how restoration actions could be used to influence the proximity to thresholds. Further, understanding future projections of controlling variables under different climate and land use scenarios may be beneficial when evaluating resilience under changing temperatures, flows, and fluxes.

The final element of a resilience assessment is to inform adaptive governance and management. Managing for resilience means that the selection and design of restoration actions will depend upon whether the system is in a desirable or undesirable state, how close the system is to a threshold (i.e., specified resilience), its adaptive capacity (i.e., general resilience), and the desired future conditions for the system. For example, if current conditions in a system are acceptable, high general resilience, but is trending towards a threshold, management actions will likely focus on avoiding the threshold. In contrast, if current conditions are unacceptable and the system is far beyond a threshold to a point where management actions are unlikely to transition to a more desirable condition, consideration should be given to how a system might be transformed, that is how might novel societal changes influence an ecosystems' capacity to deal with disturbances (Loorbach et al. 2017). Transformative changes are generally beyond the scope of the UMRR program but inform long-term actions and policies that would require collaborations across programs and agencies. A resilience perspective views interventions (i.e., restoration actions, transformative actions) as experiments that test our assumptions. Products from this last element will synthesize our understanding of specified and general resilience of the UMRS with implications for restoration and management.

Given the breadth and iterative nature of resilience assessments, several important questions remain unanswered. The following research framework relies upon the structure of the ongoing resilience assessment to organize additional research objectives and questions not currently being investigated.

Objectives

The underlying goal of the research questions outlined is to aid the UMRR program and management agencies in developing strategies to support resilient native communities. In the application of resilience concepts, both specified and general, to the Upper Mississippi River System, we aim to identify mechanisms that sustain desired conditions and weaken undesired conditions, understand driving variables that lead to regime transitions, and evaluate sources of adaptive capacity that together inform our ability to manage the system for health and resilience, and contribute to the larger study of ecological resilience.

Objective 1 – Investigation of hypothesized drivers and feedbacks related to specified resilience

Relying on recent conceptualizations of alternative regimes, we present a series of research questions to test hypothesized feedbacks thought to maintain regimes, evaluate suspected drivers of regime shifts, and answer other fundamental questions regarding the application of alternative regimes to the UMRS. Further, we describe potential application of an alternative regime framework to other major ecological resources and physical processes within the river-floodplain.

Objective 2 – Quantitative evaluation of general resilience indicators

The application of general resilience to ecosystem management is relatively new and untested. Building upon the recent development of general resilience indicators, research questions are presented that evaluate system responses to disturbances across a gradient of coping capacity, assess the ecological meaning of indicators, and expand the development of indicators more broadly.

OBJECTIVE 1 – Investigation of hypothesized drivers and feedbacks related to specified resilience

Specified resilience research questions included here focus on understanding the mechanisms that maintain regimes and drive regime shifts. Regimes are characterized by feedbacks that stabilize the structure and function in a system (Walker and Salt 2012). When a different set of dominant processes emerge that create and sustain changes in structure and function, the system is said to have undergone a regime shift. As ecosystems accumulate stress, there is an increased likelihood of a regime shift from desired to undesired conditions, emphasizing the importance of understanding the complex interactions that sustain regimes (Scheffer et al. 2001). For example, description of feedback loops that stabilize regimes and identification of key variables that drive regime shifts can inform the types of management actions required to keep a system in a desired regime, or to shift from an undesired to desired regime (Hobbs et al. 2011). Currently a manuscript has been submitted for peer review that develops conceptual models of three sets of regimes: 1) a clear and vegetated regime vs. a turbid and sparsely vegetated regime in lentic, off-channel areas, 2) a diverse native fish community regime vs. an invasive-dominated fish community regime in lotic channels, and 3) a regime characterized by a diverse and dynamic mosaic of floodplain vegetation types vs. regime characterized by an invasive wet meadow monoculture in floodplain environments (Bouska et al. In Review). Under this objective, we expand upon relevant research questions and approaches for improving our understanding of each of these sets of regimes.

Clear and vegetated state vs. turbid and sparsely vegetated state in lentic areas

In large river-floodplain ecosystems, connected backwaters and floodplain lakes can fluctuate between clear and vegetated conditions to turbid and sparsely vegetated conditions (Figure 4), in a manner ostensibly similar to transitions described in shallow lakes (Scheffer et al. 1993, Scheffer and Jeppesen 2007). The northern reaches of the UMRS experienced significant declines in the diversity and overall prevalence of submerged aquatic vegetation (SAV) during a severe multi-year drought in the late 1980's, particularly in shallow, open-water impounded areas and to a lesser extent in contiguous backwaters (Rogers 1994, Fischer and Claflin 1995, Wiener et al. 1998). For several years, turbidity remained relatively high (Fischer and Claflin 1995) and blue-green algal blooms were common (Rogers 1994, Heiskary and Walker 1995). The exact mechanisms underlying this shift to turbid, sparsely vegetated conditions remain unknown; one hypothesis is that drought-triggered algal blooms limited the availability of light to submersed macrophytes. The subsequent loss of macrophytes resulted in increased wind re-suspension of sediments, which contributed to poor light conditions and limited the re-establishment of aquatic vegetation in a negative feedback. Sediment resuspension and drought also may have increased nutrient supply in the water column, fueling the growth of epiphyton, filamentous algae, and phytoplankton and further degrading the light environment (Vis et al. 2007).

More recently, increases in the frequency of occurrence of SAV in Navigation Pools 4, 8, and 13 coincided with a long-term decline in common carp abundance (Giblin 2017), long-term decline in tributary inputs of total suspended solids (Kreiling and Houser 2016), and a multi-year period of lower discharge (specific to Navigation Pool 4) (Popp et al. 2014). Further, restoration and management actions including water level drawdowns and island construction likely influenced conditions conducive for aquatic plant growth (Kenow et al. 2016, Drake et al. 2018, Carhart and De Jager 2019). However, the relative contributions of external drivers (e.g., water clarity), internal feedbacks, management activities (e.g., drawdowns, island construction), and successional processes on the ecological state and shifts between states of increased extent of aquatic vegetation remain unclear.

Similar to other systems that have shifted from turbid to clear conditions (Bettoli et al. 1993, Parks et al. 2014), there has been a documented shift in the fish community of the upper reaches of the UMR reflecting an increased abundance and biomass of phytophilic and vegetation-associated species with corresponding increases in water clarity and SAV (Popp et al. 2014, Giblin 2017). A co-occurring decline in common carp (*Cyprinus carpio*) biomass suggests that feedbacks between carp, water clarity, and aquatic vegetation may be occurring. Multiple hypotheses can be proposed: 1) an increase in water clarity increased aquatic vegetation that supported recruitment of phytophilic piscivores, which limited recruitment of common carp and led to further increases in water clarity (Giblin 2017); 2) a decline in bioturbating common carp crossed a biomass threshold that led to increased water clarity and aquatic vegetation, subsequently supporting increased abundance of phytophilic-spawning piscivores that further limit recruitment of bioturbating common carp to increase water clarity. Closer examination of the long-term data considering these hypotheses could inform the initial driving factor behind this fish community shift.

Within the SAV-dominated state of the UMRS, two primary community types exist with respect to water velocity tolerance: a lotic-adapted SAV community, and a lentic-adapted SAV community (Yin, unpublished data; (Carhart and De Jager 2019). The lotic-adapted community is dominated by American wildcelery (*Vallisneria americana*), a species that has a well-developed, perennial root system, relatively low light requirements and thin, flexible, hydrodynamic leaves that can extend high into the water column to receive sunlight. The lentic-adapted community is usually dominated by weakly rooted species with low tolerance for water flow and relatively high light requirements (especially *Ceratophyllum demersum* and *Elodea canadensis*). Under sufficiently low flow conditions, lentic communities can also include dense growths of filamentous algae and duckweeds. The lentic-adapted species tend to form dense mats close to the water surface. Given the physical characteristics of the two community types, it is hypothesized that they are susceptible to different disturbances. Extreme drought conditions during which water depth and velocity are reduced (such as which occurred in Upper Impounded Reach in the late 1980's) may allow lentic-adapted taxa to shade out and displace wildcelery (Rogers 1994, Fischer and Claflin 1995, Spink and Rogers 1996). In contrast, the weakly rooted and unrooted species of the lentic-adapted community are easily dislodged by moving water and are likely more susceptible to flood events. Understanding the resilience of these community types to disturbance extremes and how physical conditions may provide refuge during such a disturbance may inform our understanding of available refugia at broad scales.

Downstream of Navigation Pool 13, SAV is largely limited by light availability, which is directly influenced by water clarity, distribution of depths, and water level fluctuations (Sparks et al. 1998, Yin and Langrehr 2005, Moore et al. 2010), and may further be limited by herbivory and the available seed bank (Sass et al. 2017). Because light availability is influenced by several factors, understanding the relative importance of each of these factors as well as synergistic effects in a spatially-explicit manner will improve our ability to evaluate where restoration strategies for aquatic vegetation are likely to be effective.

The proposed research aims to advance our understanding of uncertainties associated with the resilience of water clarity and aquatic vegetation regimes. More specifically, these research questions focus on assessing 1) the drivers of regime shifts, 2) feedbacks that maintain regimes, and 3) the relative resilience of different community types to specific disturbances.

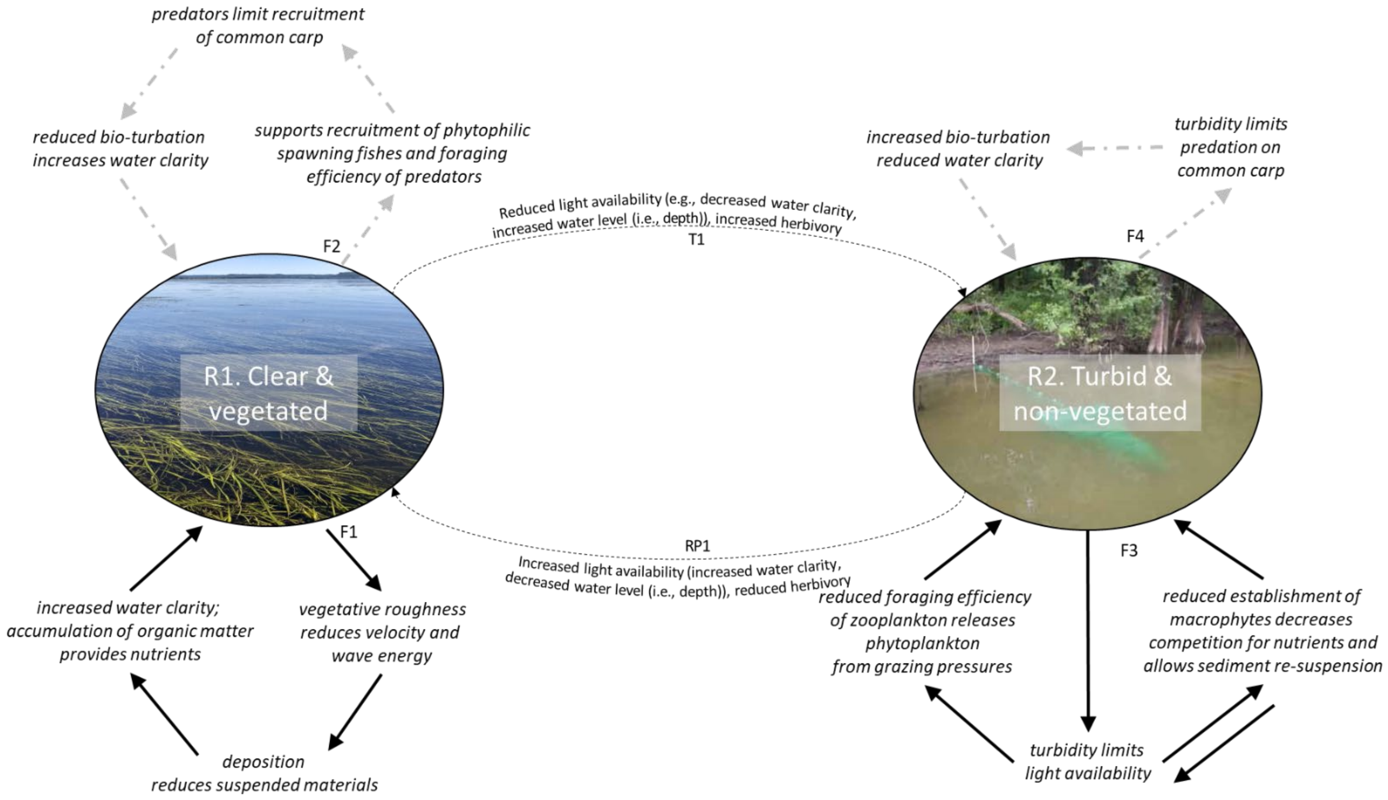

Figure 4. Conceptualization of feedbacks and transitions between alternative regimes of water clarity and aquatic vegetation abundance (Bouska et al. In Review).

Research question 1.1.1: What are the primary drivers of water clarity in lentic areas? How do connectivity and flow influence feedbacks of the clear and vegetated regime.

Approach: Long Term Resource Monitoring (LTRM) has documented increased water clarity in the Upper Impounded Reach of the UMRS over the last two decades (Moore et al. 2010). To investigate the relative importance of external forces (e.g., input total suspended solids, nutrient loads) and internal feedbacks (e.g., aquatic vegetation, common carp biomass) on water clarity in large river-floodplain ecosystems, Deanne Drake (WDNR) and colleagues have an ongoing project assessing LTRM data from Navigation Pool 8 (Drake et al. In prep.). Expansion of these analyses to the other LTRM study reaches could provide additional insights into the relative contributions of external and internal drivers to long-term changes in water clarity (e.g., do identified drivers operate at a broader scale, or do they differ locally, or both?). If consistent drivers are apparent across river reaches, thresholds of concern could be further investigated to determine if thresholds vary by river reach. Temporal analysis of internal and external drivers of water clarity could also indicate if the system is experiencing trends over time.

Extensions to this work could investigate the role of connectivity and scale on drivers and feedbacks (e.g., does connectivity influence the relative contributions of drivers). Selection of sites that represent gradients of connectivity and flow could be used to investigate feedback strength relative to these gradients. Alternatively, areas where connectivity and flow are planned to be modified could be monitored over multiple years (before and after) to evaluate feedbacks more closely. Such analyses could be informative of how restoration projects or projected changes in discharge might influence feedbacks. Further, analyses are needed to examine the drivers of regime shifts and feedbacks at several spatial scales (e.g., localized patches, single backwaters, backwater complexes with varying connectivity gradients, and pool reaches) to improve our understanding of the mechanisms operating within biologically-meaningful scales.

Research question 1.1.2: Are there feedbacks between the fish community and water clarity?

Approach: Simultaneous changes in the fish community, water clarity and aquatic vegetation abundance raises the question: what direct or indirect feedbacks exist between the fish community and water clarity? For example, there has been a significant decline in the biomass of common carp, an important ecosystem engineer with numerous direct and indirect ecological effects resulting from their benthic foraging behaviors that resuspend sediment and physically uproot aquatic vegetation (Figure 5). Hypotheses suggested by the associated long-term changes in common carp, water clarity, and aquatic vegetation are described below.

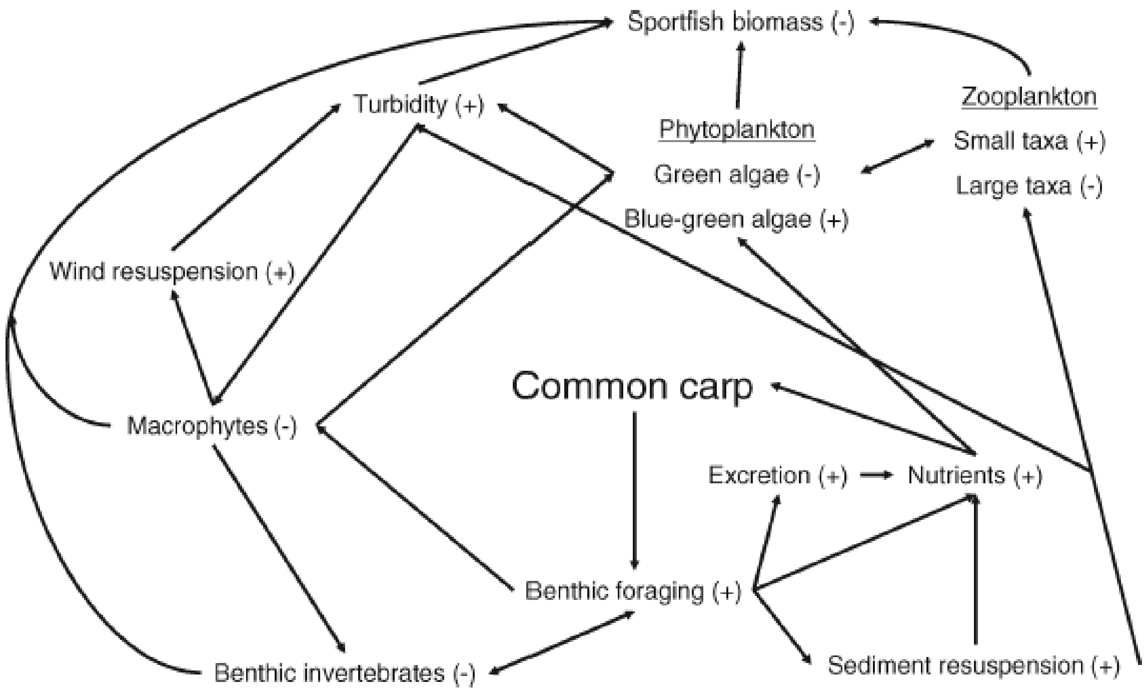

Figure 5. Direct and indirect effects of abundant common carp populations (from (Weber and Brown 2009).

One hypothesis is that a decline in common carp biomass, driven by a variety of potential factors such as disease (Gibson-Reinemer et al. 2017) and low recruitment (Lubinski et al. 1986), has contributed to increased water clarity and aquatic vegetation. The abundance of aquatic vegetation has, in turn, led to increased recruitment of species that rely upon vegetation as spawning substrate (Giblin 2017), and increased water clarity likely improves conditions for visual predators. As the populations of these species increase, so does predation upon carp eggs and young-of-year, which limits common carp recruitment. In this example, an initial decline in common carp abundance is thought to lead to several ecological changes that maintain low common carp abundance. Alternatively, Giblin (2017) suggests that increased water clarity improved conditions for aquatic vegetation, which led to increased predator populations that drove declines in common carp.

Existing LTRM data could be used to assess the evidence in support of these alternative hypotheses. For example, a structured equation modeling framework could be used to formally test hypotheses using annual estimates of common carp biomass, predator biomass, aquatic vegetation abundance, total suspended solids or turbidity derived from the LTRM fisheries, vegetation, and water quality datasets for Navigation Pools 4, 8, and 13. Alternatively, a comparative approach that assessed backwater-scale estimates of carp abundance, predator abundance, Secchi depth, and aquatic vegetation using the LTRM fisheries database to test hypotheses at finer spatial and temporal scales (and increase sample sizes). In such an analysis, individual backwaters or backwater complexes would be considered "sites." Understanding the interactions of fish community composition, water clarity, and aquatic vegetation will be useful in predicting and assessing the effects of various restoration actions conducted on the UMRS. For example, if common carp are an important driver of SAV distribution and abundance, active management of the population may be a necessary management tool to secure benefits for SAV when populations are above a particular threshold (Bajer et al. 2009, Sparks et al. 2017).

Research question 1.1.3: What is the relative influence of water clarity and water level fluctuations on the distribution of aquatic vegetation?

Approach: It is well understood that light availability and water level fluctuations are important to the distribution of SAV. Ongoing work by John Kalas and Alicia Carhart (Wisconsin Department of Natural Resources) and colleagues is assessing photic zone depth and water level fluctuations across the UMRS to estimate the area of suitable habitat for SAV in each navigation pool. By improving our understanding of the factors limiting SAV colonization and persistence, the results will aid in identifying locations most and least likely to benefit from restoration efforts to maintain and restore aquatic vegetation beds and improve our understanding of how changing river conditions may affect SAV distribution. Additional work assessing trends in water column light availability and water level fluctuations would indicate the extent to which those trends need to be considered when prioritizing future management actions.

Research question 1.1.4: How do various aquatic vegetation community types/phases differ in their resilience to common disturbances (e.g., floods, droughts, drawdowns)?

Approach: Community types can be differentially susceptible to disturbances. Understanding of the community type vulnerability may be investigated through analysis of spatial persistence following disturbances that have occurred within the UMRS over the past two decades. Methods like those used by Carhart and De Jager (2019) that rely upon species-specific information collected by the LTRM vegetation component and interpolation could be used to assess similarity of community composition among standardized sample sites. Shifts in community composition surrounding occurrence of known disturbances could be examined at several scales to better understand community shifts in response to droughts, floods, drawdowns, or other disturbances. Further, encompassing a spatial gradient will allow for assessing whether responses differ longitudinally or along connectivity gradients.

Research question 1.1.5: What are the feedbacks that maintain turbid conditions? How do factors such as herbivory, bioturbation, wind fetch, waves, and more frequent high discharge events contribute to a turbid regime?

Approach: One approach to investigate feedbacks that reinforce turbid conditions is to develop a multi-year field study that focuses on different areas (e.g., backwater, impounded area, side channel) based on their regime status to assess responses associated with hypothesized feedbacks (i.e., turbidity, zooplankton community, common carp). More specifically, in the case of the clear vs. turbid regimes we can consider four regime statuses: 1) clear, vegetated and stable (i.e., has been considered clear and vegetated for substantial period of time), 2) clear, vegetated and transient (i.e., was recently turbid, but now clear and vegetated, 3) turbid and transient (i.e., was recently clear and vegetated, but now turbid), and 4) turbid and stable (i.e., has been turbid for substantial period of time). Those areas considered transient are presumed to have weaker reinforcing feedbacks. Alternatively, locations could be identified based on gradients of herbivore population abundance, common carp abundance, wind fetch, waves, or where actions have been implemented to alter connectivity or flow to evaluate the strengthening or weakening of feedbacks with these factors. Examination of feedbacks at several spatial scales (e.g., localized patches, single backwaters, backwater complexes with varying connectivity gradients, and pool reaches) would benefit our understanding of the effects of scale on feedbacks.

Research question 1.1.6: What are the major causes of aquatic plant disturbance that induce regime shifts to the turbid-state?

Approach: We hypothesize there are many possible drivers to regime shifts, but we lack an understanding on the relative contributions of each that push the system from a clear-water state to a turbid-state. In shallow lakes, the literature concurs that shifts happen from a coupling of increased nutrient loading and a severe disturbance to the plants. Based on field observations and discussions with persons observing the river over the past few decades, an emerging conceptual framework proposes other mechanisms (e.g. turbidity, drought) may cause regime shifts in the UMRS (Bouska et al. in review).

First, we propose to use the LTRM data in a structural equation model that assesses the conditions that have caused significant plant loss in areas that have shifted turbid in the last few decades; these conditions could include turbidity, nutrients, chlorophyll *a*, carp biomass, water-level, and available aquatic area. Second, we would use LTRM species assemblage data to understand the functional traits of plant species (e.g. deep rooting system, lotic vs. lentic preference) and plant communities (e.g. diversity and redundancy) that influence sensitivity and resilience to disturbance. Third, meta-analysis review could address common disturbances that have affected loss of aquatic plants worldwide and translate to the UMRS. Lastly, mesocosm experiments at UMESC artificial ponds could be designed to mimic vegetation communities of the UMRS and alter factors that were identified as key drivers (e.g., turbidity levels, carp biomass, wave action potential, etc.) to quantify vegetation response.

Research question 1.1.7: How do turbid systems return to the desirable clear-water state?

Approach: As we further understand the feedbacks that maintain a system within a state by addressing the research questions herein (Research questions 1.1.1, 1.1.2, 1.1.5), we can work with managers to evaluate upcoming restoration projects that have a primary goal of re-establishing aquatic vegetation. For example, restoration projects and management actions have been and will continue to be designed to promote submersed aquatic vegetation in backwaters and impounded areas. Such project and actions can be used as opportunities to evaluate how various management techniques can be used to shift a turbid-state to a clear-state.

Diverse native fish community state vs. invasive-dominated fish community state in lotic and lentic areas

Over the past 150 years, the Upper Mississippi River and Illinois River have undergone extensive physical modifications. We hypothesize that, similar to the back-seat driver concept (MacDougall and Turkington 2005, Bauer 2012), the accumulation of stressors (e.g., habitat degradation, pollution, exploitation) allowed non-native fishes to dominate, which subsequently drove further changes in ecosystem structure and function. Regardless of native or invasive status, disruptions to the numbers of fish (e.g., overharvest, stocking in fishless lakes, and biological invasions) can drive further structural and functional changes within the physical environment and biotic communities based on how the dominant species interact with the environment (Baxter et al. 2004, Daskalov et al. 2007, Osterblom et al. 2007, Collins and Wahl 2017, Detmer et al. 2017). We discuss two potential alternate regimes, one characterized by the dominance of a diverse, native fish community and one by the dominance by invasive fish species, specifically common carp, silver carp (*Hypophthalmichthys molitrix*), and bighead carp (*Hypophthalmichthys nobilis*; Figure 6).

We hypothesize that a diverse, native fish community is characterized by a relatively high evenness, functional diversity, and functional redundancy that is well-adapted to dynamic resource availability, which promotes compensatory effects, competitive exclusion and allows the system to absorb and adapt to disturbances in ways that promotes persistence of the native fish community (Odum 1969, Peterson et al. 1998). Under this hypothesis, if an invasive species was introduced, it may establish and persist but not in sufficient abundance to substantially influence the structure and function of the system.

The UMRS invasive dominant fish community is currently characterized by high biomass of large-bodied invasive cyprinid fish species, including common carp, introduced in the late 1800's, and more recently established silver carp and bighead carp. Common carp are well-known ecosystem engineers. Their benthic foraging activities can cause structural change (i.e., loss of aquatic macrophytes, sediment re-suspension), which in turn affect abiotic conditions (i.e., turbidity and nutrient dynamics) that cause subsequent changes in biotic communities (i.e., phytoplankton, zooplankton, fish) through which common carp populations are sustained (Matsuzaki et al. 2009, Weber and Brown 2009, Kaemingk et al. 2017).

As silver and bighead carps have increased in abundance throughout the system, there have been subsequent effects on food resources that have likely altered energy flows and potentially contributed to a shift in the fish community. For example, since the establishment of silver and bighead carp there has been a significant reduction in the density and biomass of zooplankton taxa (DeBoer et al. 2018), reduced chlorophyll concentrations, reduced condition and abundance of native planktivorous fish (Irons et al. 2007, Pendleton et al. 2017, Fritts et al. 2018), and shifts in the overall fish community of the Illinois River (Solomon et al. 2016). Reduced zooplankton densities likely negatively affect native fish species whose juvenile life stages rely upon zooplankton resources, and as a result, may compound the negative effects caused by stressors such as sedimentation of backwater habitats on native fish recruitment (Chick in Review). Controlled mesocosm experiments have shown that through high egestion rates, silver and bighead carp are able to transform planktonic resources to benthic resources to the apparent benefit of benthic macroinvertebrates (Yallaly et al. 2015, Collins and Wahl 2017). Diversion of energy from pelagic to benthic pathways likely supplements and potentially contributes to changes to the composition of benthic invertebrate communities, the forage base of common carp and a variety of native invertivores.

The basis for this set of regimes is that the establishment and dominance of several large-bodied invasive cyprinid fish species within the Upper Mississippi River Basin have altered energy flows and resource availability in ways that reinforce invasive dominance, whereas a diverse, native fish community has greater biotic resistance to invasion (Figure 6). The following research questions focus on evaluating 1) hypothesized feedbacks that sustain a diverse, native fish community, 2) feedbacks that promote an invasive dominant state, and 3) the LTRM fish dataset for evidence consistent with concepts of regime shifts.

Commercial fishing does occur throughout the river with differing effort and target species (Klein et al. 2018). State commercial fishing datasets are available, but are not standardized for effort. Therefore, commercial fishing activities will not be formally accounted for in analyses but will be acknowledged with respect to the research questions.

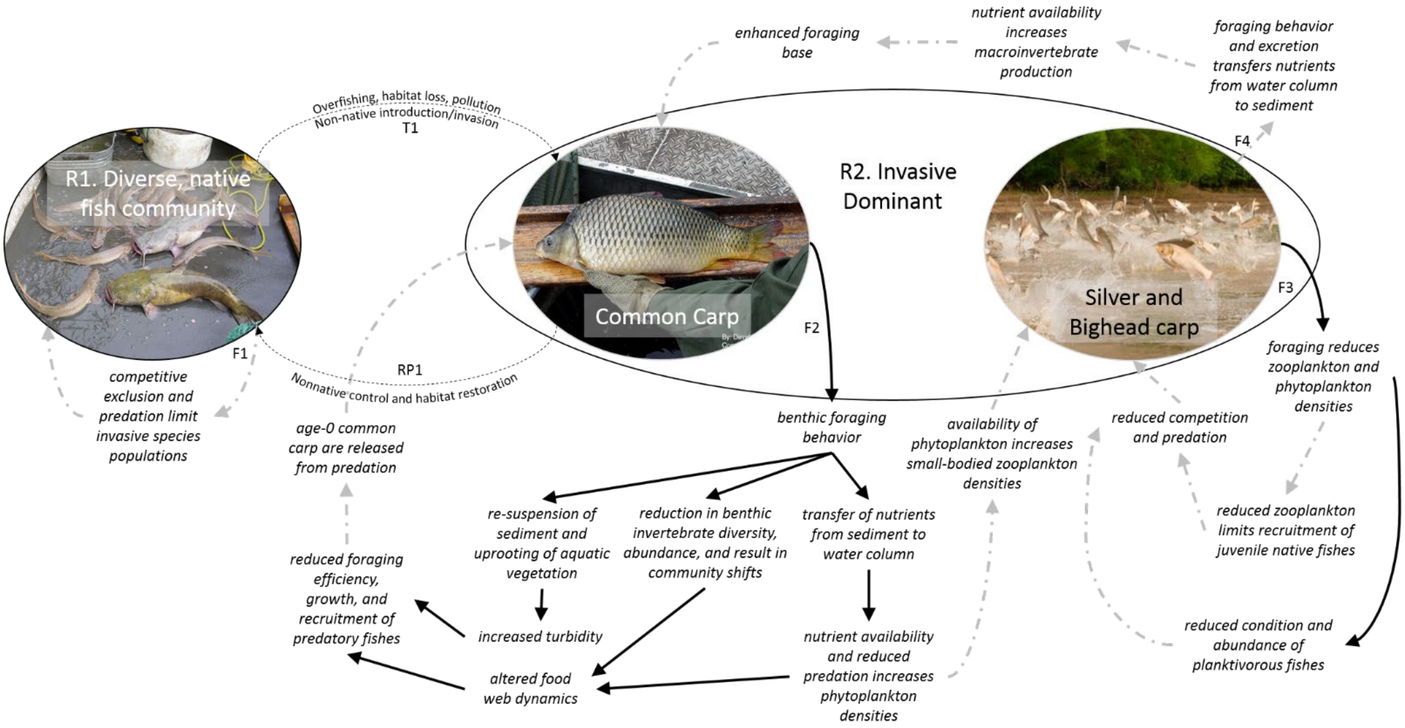

Figure 6. A conceptual model of two alternative regimes, one characterized by a diverse native fish community and another characterized by dominance by invasive carp species.

Research question 1.2.1: Is there evidence of a regime shift based on changes in biomass of functional groups?

Approach: The ideas contained within the set of regimes characterizing fish communities remain hypotheses with most work to date documenting shifts in species composition and condition in response to invasive of silver and bighead carp (Irons et al. 2007, Solomon et al. 2016, DeBoer et al. 2018). Increasing variability in system-level properties (i.e., total biomass, functional group biomass) and directional change in such properties are thought to indicate an impending regime shift (Sundstrom et al. 2018). To test hypotheses consistent with our conceptualized regime shift associated with changing biomass of common carp, silver carp, and bighead carp, the LTRM fisheries standardized random sampling monitoring dataset would be used to evaluate whether variability in biomass of functional groups within and across scales (as determined by body size, see Bouska (2018)) has changed over time and whether directional change is apparent in functional biomass, which would suggests there have been changes to the underlying resource availability. This analysis would be completed and compared across all six LTRM study reaches to investigate the differing degrees of reduced biomass of common carp and increased biomass of silver and bighead carp on functional biomass variability. If the data suggest regime shifts have occurred, size spectra approaches can be used to better understand how changes in biomass of invasive carp have influenced shifting food web capacity and efficiency, similar to approaches used on other large rivers (Murry and Farrell 2014, Broadway et al. 2015, Kopf et al. 2019).

Research question 1.2.2: Is the dominance of silver and bighead carp associated with increased biomass of benthic macroinvertebrates in a floodplain-river ecosystem? If so, does the re-routing of energy sources to the benthos support an invasive dominant regime?

Approach: Research conducted in mesocosms has found that silver and bighead carp consume large quantities of planktonic resources from the water column, and through egestion, supplement the benthic nutrient supply, consequently providing resources for benthic organisms (Yallaly et al. 2015, Collins and Wahl 2017). Specifically, Collins and Wahl (2017) found substantially higher standing crop of Chironomidae midge larvae and adults but lower numbers of adult Chaoboridae midges in the presence of foraging bighead carp. One approach to this question could rely upon multi-year macroinvertebrate sampling within at least two navigation pools of the UMRS. At a minimum, selection would include both a navigation pool with high silver and bighead carp biomass (e.g., La Grange) and a navigation pool absent of these two species (e.g., Navigation Pool 13). Ideally, all six field stations would engage in the macroinvertebrate collections to allow for comparison across the entire system with varying densities of silver and bighead carp and other gradients. If contrasts in macroinvertebrate biomass are consistent with specific hypotheses of invasive dominance, understanding the relative influence of increased abundance of this foraging resource to the broader fish community may be assessed in diet studies or may be apparent in functional biomass trends (research question 1.2.1).

Research question 1.2.3: Does the dominance of silver and bighead carp affect the recruitment of native fishes through competition of zooplankton, to effectively maintain invasive dominance?

Approach: It is well established that abundant silver and bighead carp populations have reduced the density and biomass of zooplankton taxa (Sass et al. 2014, DeBoer et al. 2018), and reduced condition of native planktivores (Irons et al. 2007), likely indirectly through limiting zooplankton resources for which these species compete (Sampson et al. 2009). Zooplankton are a common food resource for juvenile fishes whom may be negatively affected by reduced zooplankton densities (Chick et al. In review). Several approaches could be used to address this question. In the ongoing Vital Rates study, the effects the silver and bighead carp biomass could be considered as a constraining variable in models of year-class strength of the species examined (in addition to variables describing hydrology, temperature, and habitat quality/quantity). Detailed diet studies or gut content metabarcoding (Casey et al. 2019) of larval fishes could also be pursued to assess relative composition, quality, and abundance of diets relative to silver and bighead carp biomass.

Research question 1.2.4: Do retrospective body-mass patterns in the fish community predict the invasiveness of silver and bighead carp?

Approach: Allen et al. (1999) found that invasive species across taxa groups were nonrandomly distributed at the edges of body-mass aggregations. Under discontinuity theory, the edges of body-mass aggregations signify transitions between spatial scales that resources are available to biological organisms. Species near the edges of body-mass aggregations are thought to be the first to experience changes resulting from changing ecological structure of a system and either exploit or fall victim to shifting ecological resources depending upon the types of resources the species are reliant upon. To assess whether invasions of silver and bighead carp are similarly nonrandomly distributed at the edges of body-mass aggregations, this work would build upon previous work looking at body-mass patterns of the UMRS fish communities using LTRM fisheries data (Bouska 2018). More specifically, the analysis here would investigate the distribution of silver and bighead carp body-mass relative to the entire fish community present within each LTRM pool. Of interest is whether body-mass scale transitions are consistent with the distribution of silver and bighead carp body-mass at the time of invasion, and whether the distributions of body-mass of silver and bighead carp have changed relative to body-mass aggregations as these species have become established (i.e., if changes in body mass aggregations are consistent with a regime shift). If silver and bighead carp body sizes are nonrandomly distributed at the edges of body mass aggregations at the time of invasion, this association could be used as an indicator of invasibility. Body mass aggregations in non-invaded pools would then be examined to determine if body size aggregations are like invaded reaches (suggesting susceptibility). Methods similar to Roberts et al. (2019) would be employed.

Research question 1.2.5: How does habitat connectivity and heterogeneity influence the resilience of a diverse, native fish community to fluctuating environmental conditions through resource availability, recruitment dynamics, and accessibility of refugia? What do projected changes in habitat composition suggest for the resilience of a diverse, native fish community?

Approach: Diverse resources, dynamic recruitment, and availability of refugia promote resilience in biological communities of riverine systems and are thought to be strongly linked to habitat heterogeneity and connectivity (Van Looy et al. 2018). Validation of these ideas would improve our understanding of the controlling variables and mechanisms that underlie and maintain a diverse native fish community regime. To assess how habitat heterogeneity and connectivity relate to mechanisms of resource availability, recruitment, and refugia, a series of hypotheses would first be made regarding the expected responses of a fish community to specific disturbances. For example, we would hypothesize that a river reach with high diversity and connectivity of habitats would have a greater capacity to absorb disturbance through compensatory effects (e.g., negative effects of a disturbance to a particular guild would be offset by positive effects to other guilds) as compared to a reach with low habitat diversity and connectivity (Ghedini et al. 2015). The ongoing vital rates project will allow for systemic testing of life history-specific recruitment hypotheses as related to physical complexity and flow at the navigation pool scale (Humphries et al. 2019) and should provide information regarding mortality dynamics.

Habitat diversity and connectivity can be quantified in various manners. A static quantification of habitat diversity could rely upon metrics developed from the revised aquatic areas dataset (De

Jager et al. 2018, Bouska et al. 2019). A dynamic quantification of habitat diversity could be derived from a statistical analysis based on the frequency and distribution of specific depth criteria resulting from the overlaying of water surface elevation onto topobathy at fine temporal scales (see 2.2.1). Similarly, habitat connectivity could be evaluated from a dispersal concept whereby potential upstream and downstream movement is quantified by 'open river' conditions at lock and dams, or by ongoing genetic analysis component of the Vital Rates project. Alternatively, habitat connectivity could be quantified through a landscape ecology perspective whereby connectivity of habitat patches is quantified at specified spatial scales. To assess potential mechanisms through which habitat diversity and connectivity influence the resilience of the native fish community, a functional perspective would be applied to quantify cross-scale functional diversity and redundancy (see 2.1.1) and functional biomass (see 1.2.1) of the LTRM fish data through time. In specific, trophic and spawning groups would be assessed as well as other life history characteristics or habitat requirements.

Based upon the results of the primary research question, advancements to this research question would focus on integrating recent projected changes in aquatic habitat distributions (De Jager et al. 2018) and disturbance dynamics to learn how long-term hydrogeomorphic changes might influence the fish community.

Diverse and dynamic mosaic of floodplain vegetation types vs. an invasive-dominated wet meadow monoculture in floodplain environments

In their natural form, large river-floodplain ecosystems are shifting mosaics of various aquatic and terrestrial vegetation communities, with patterns and dynamics resulting from spatial and temporal variability in hydrological conditions, other disturbances, and internal feedbacks (Stanford et al. 2005). Today, the ecological structure and function of many of these systems have been modified by anthropogenic activities, including commercial navigation, development, and introduced species. The direct and indirect consequences of human modification of floodplains include changes to the type of vegetation communities present in any given location, as well as the rates and trajectories of shifts among community types. In certain cases what may have been considered a shifting, yet stable, distribution of community types has become unstable and dominated by a few, often non-native, communities. Some of these communities can further impact local environmental conditions in ways that reinforce their own persistence, creating alternative regimes that may persist for centuries.

In the Upper Mississippi River System, forests have historically comprised the majority of floodplain land cover (Nelson et al. 1994, Yin and Nelson 1995, Nelson and Sparks 1998). These forests include a diverse array of species and community types, including early successional cottonwood (*Populus* spp.) and willow (*Salix* spp.) communities, as well as a range of communities at various stages of succession and with a wide range of floodplain forest species (Guyon et al. 2012). Interspersed with these floodplain forests are additional herbaceous grassland and wetland communities. Forest, herbaceous, and wetland community types are distributed throughout the floodplain in a dynamic and diverse mosaic believed to be driven by the effects of shading, inundation, and other disturbances that create forest canopy gaps and reset successional sequences (Figure 7). However, a growing concern among natural resource managers is that certain aspects of this floodplain vegetation regime have been disrupted, creating opportunities for local to landscape-scale shifts to alternative regimes characterized by a dominant invasive herbaceous species (e.g., Johnson grass, Japanese hops, and reed canarygrass). Once established, an invasive herbaceous species may modify local environmental conditions (e.g., light and nutrient availability) in ways that can lead to a monoculture and further promote their persistence as an alternative regime.

The research proposed here addresses key uncertainties related to the resilience of floodplain vegetation regimes with a focus on floodplain forests and transitions to invasive wet meadow monocultures while recognizing that there are other vegetation types and transitions that may occur in the UMRS. These include 1) the processes, interactions, and feedbacks that support dynamic and diverse floodplain vegetation communities and 2) potential processes, interactions, and feedbacks that contribute to the establishment and persistence of invasive herbaceous species. The goal of this research is to aid management agencies in developing plans to build resilient native vegetation communities and the processes that sustain them in the face of a wide-range of potential disturbances.

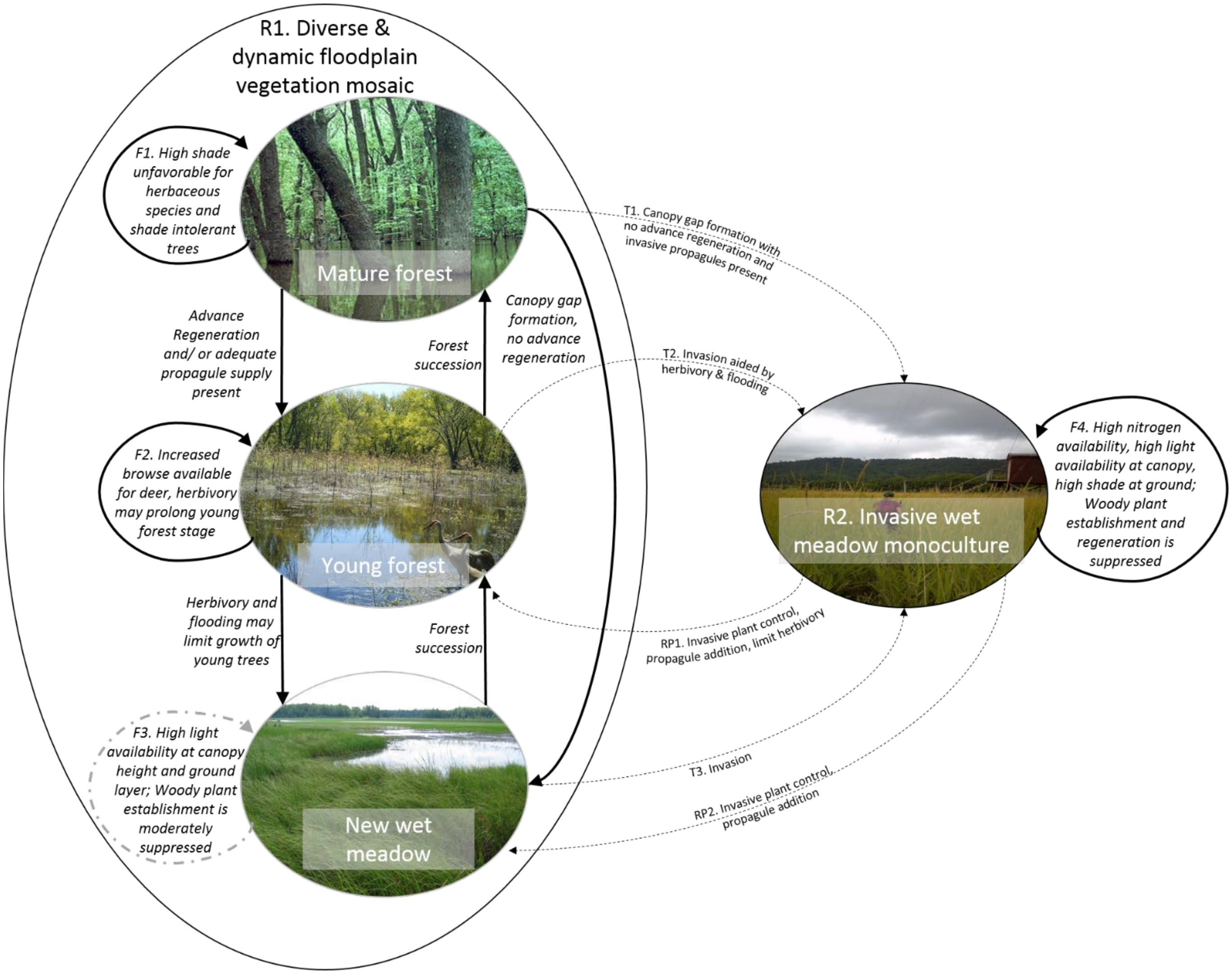

Figure 7. A conceptual model highlighting transitions and feedbacks contributing to alternate states of vegetation communities of the floodplain (Bouska et al. In Review).

Research question 1.3.1: How does the age, structure, and composition of forests vary throughout the UMRS?

Approach: Diversity is a fundamental property for characterizing resilience. In the UMRS, the diversity of forest species and age classes, including species functional classes, and community types can be characterized to provide a general measure of forest resilience (Bouska et al. 2019). LTRM land cover datasets map the distribution of vegetation communities systematically throughout the UMRS, including floodplain forests, lowland forests, wetland meadows, and other community types. These datasets are useful for broad-scale summaries of the distribution of community types for higher level planning purposes but lack more detailed information about forest age, structure, and composition. A new forest resource inventory ("Phase II Forest Inventory") of U.S. Corps of Engineers fee title lands has produced a rich, systemic dataset describing site-specific information on the diversity, health, structure, and invasive species presence in forests. This dataset is currently being analyzed to describe the age, structure, and composition patterns across the UMRS, including the development of a novel, data-driven classification of UMRS floodplain forest communities based on both composition and structural properties of surveyed trees. The resulting classification will be used to understand the abundance and distribution of forest types across the UMRS. Additionally, comparisons between the classification and LTRM land cover datasets can be used to understand patterns of fine-scale diversity within broader land cover classification schemes.

The UMRS traverses broad climatic and hydrologic gradients and species distribution boundaries, complicating efforts to anticipate potential forest responses to future climatic, hydrologic, or management scenarios. Species functional niches can be used as a common currency across gradients and boundaries, serving as a complementary approach to characterizing forest resilience, and can be useful for developing models of forest response to perturbations. Current functional classifications of UMRS floodplain forest plants are coarse. For example, woody species were classified based on empirical measures of flood-related mortality (most, moderate, and least flood toleration) and shade tolerance (high, moderately high, moderately low, low) for use in the LANDIS II model (De Jager et al. 2018). However, tree and shrub species interact with flooding in ways that can be age-dependent, complex, and reflective of trade-offs with other important factors such as light availability (Hall and Harcombe 1998, Lin et al. 2004, Glenz et al. 2006). Defining the functional niches of UMRS forest species in ways that better reflect these realities could be approached using multivariate methods and publicly available datasets on quantitative and qualitative functional traits such as the TRY (https://www.try-db.org/TryWeb/Home.php), FLOWBASE (https://www.isa.ulisboa.pt/proj/flowbase/), USDA PLANTS (https://plants.sc.egov.usda.gov/java/) databases. Descriptions of the geographic distribution of functional classes and their relationships with environmental attributes can be completed to complement species-based analyses, allowing for a more comprehensive description of UMRS floodplain forest diversity.

Research question 1.3.2: How do autogenic processes (e.g., stand dynamics) and allogenic processes (e.g., flooding, wind disturbance, and insects) influence the successional dynamics of forests across the UMRS?

Approach: Linkages between existing forest communities and potential drivers of their persistence on the landscape can be assessed using simulation modeling, empirical, and experimental approaches. First, simulation models (e.g., LANDIS-II; http://www.landis-ii.org/) incorporate autogenic and allogenic processes in describing forest development through time. Such models can facilitate hypothesis testing in ways empirical analyses cannot, especially given the longevity of forests and the broad spatial and temporal scales of interest but are sensitive to the quality of empirical data used in model development. A LANDIS-II model has been developed for the UMRS, revealing important relationships between forest changes and disturbances (De Jager et al. 2018). Future model iterations could be used to explore forest response to management decisions and impacts of herbaceous species (e.g., reed canarygrass), and could benefit from improved empirical datasets that underlie the model (e.g., species-age relationships, establishment rates across ecoregions).

Existing empirical data on forest composition and structure from the Phase II inventory (see section 1.3.1) can be analyzed in conjunction with environmental datasets such as output from the UMRS inundation model (De Jager et al. 2018, Van Appledorn et al. In revision) to establish what environmental attributes are strongly associated with forest characteristics across the landscape, whether there may be any interactions among attributes, and how such associations may vary over different spatial scales. In a similar approach, associations between functional classes (see 1.3.1) and environmental drivers can be characterized across the landscape. Direct comparisons between compositional and structural patterns of long-lived species and hydrologic characterizations provide a first-order understanding of eco-hydrologic associations. These associations may be further explored using more detailed analyses that characterize where and how hydrology has shifted over longer periods of time that coincide with tree or stand age. Dendro-ecological studies are another empirical approach that can reveal detailed information about stand dynamics and successional pathways. Dendro-ecological research could provide important information about stand ages, drivers of transitions between seedling to sapling to established tree, and relationships between age, growth, and environmental factors (e.g., hydrology, sediment dynamics). To better understand the drivers affecting forest regeneration, analyses of regeneration data from existing datasets (e.g., permanent plots) and surveys of past plantings could yield insights into how environmental factors contribute to regeneration success or failure. New regeneration surveys developed strategically to account for gradients of overstory species composition, hydrology, light availability, propagule pressure, and soil conditions may also be used.

Forests typically do not lend themselves well to short-term experimental manipulations due to the longevity of species. However, experimental manipulations of seedling establishment (e.g., plantings) across important environmental gradients could be used to understand what conditions facilitate successful forest regeneration. Silvicultural treatments or environmental manipulations may also be applied within an experimental framework to understand how management actions and habitat conditions may facilitate successful forest regeneration or forest successional transitions over longer time spans.

Research question 1.3.3: How might altered hydrological regimes, climate change, insect pest outbreaks, and management actions alter forest resilience?

Approach: Process-based modeling approaches such as those described in 1.3.2 above can be used to assess the sensitivity of floodplain forests to altered hydrologic regimes, insect and pathogen outbreaks, management interactions, and their interactions. The results of model simulations can be useful for anticipating the magnitude and rates of changes to forests in response to perturbations, and for identifying areas that are the least or most resilient forest communities. Experimental approaches such as implementing silvicultural treatments in forest stands or manipulations of propagules or seedlings could also be used to understand drivers of forest transitions (see 1.3.2 above).

Research question 1.3.4: Where have transitions between floodplain forests and herbaceous wet meadow communities already occurred, and how has the rate and magnitude of transitions differed across the UMRS?

Approach: A primary concern is the potential for conversion of forest to non-forested systems dominated by invasive reed canarygrass. Forest regeneration is inherently a function of forest disturbance (Runkle 1982, Oliver and Larson 1996), which often increases the availability of resources, such as sunlight and nutrients, for tree seedlings and saplings. The loss of canopy trees, or gap formation, is a discrete disturbance event that should create the necessary conditions for the establishment of a new cohort of seedlings or the release of already established saplings (Kern et al. 2017). There is ongoing work by Andy Meier and Andrew Strassman to identify forest canopy gaps using LIDAR data and aerial imagery, and to quantify their abundance and distribution across the UMRS floodplain. A subset of mapped gaps spanning gradients of inundation and gap size will be surveyed in the field to collect site-level vegetation and environmental information (e.g., soil). These data will be used to understand whether forest regeneration is occurring within the gap or whether there is a transition to an invasive or native herbaceous wet meadow community and measure the rates and magnitudes of transitions throughout the UMRS.

Research question 1.3.5: What are the floristic, structural, and hydrogeomorphic conditions associated with transitions between forests and wet meadows and how do they contribute to shifts from forest to herbaceous vegetation communities across the UMRS?

Approach: The data collected using remotely sensed imagery and empirical field data (described in 1.3.4 above) can be used to understand the role of floristic, structural, and hydrogeomorphic conditions on regeneration success and woody-herbaceous vegetation transitions. It is possible to incorporate the results of such statistical analyses into a process-based modeling framework like as LANDIS-II to further explore how woody to herbaceous vegetation shifts may occur across broader spatial and temporal scales.

Research question 1.3.6: What factors contribute to the persistence of high quality native wet meadows?

Approach: High quality native wet meadows are presumed to harbor a substantial amount of unique floristic and invertebrate diversity. While in our conceptual model we consider these communities relatively transient, there are some native wet meadows that have persisted. The Minnesota DNR has a GIS data layer (https://gisdata.mn.gov/dataset/biota-dnr-native-plant-comm) depicting remnant native wet meadow communities. Evaluation of the location of remnant native wet meadows with hypothesized controlling variables would be a first step towards understanding potential reinforcing mechanisms that allow for persistence.

Other potential regime shifts

Concepts of specified resilience may be applicable to other resources not discussed above. Discussions between managers, biologists, and researchers will be essential in characterizing regimes and identifying critical uncertainties. In theory, an alternative regime perspective could be applied to any major ecological resources identified during the system description phase (Bouska et al. 2018). Synthesizing known information, developing theoretical relationships and hypothesis testing can build the foundation of understanding the system and its components as a complex dynamic system.

Research question 1.4.1: Are there distinct mussel communities evident in the UMRS? If so, does substrate stability predict mussel richness/density/biomass/recruitment at coarse scales? Does mussel density reinforce substrate stability within a bed?

Approach: To examine potential regimes characterized based on mussel assemblage using an inductive approach, multivariate analyses, such as a principle components analysis and cluster analysis, could be applied to matrices of species' density, presence, or recruitment estimates from mussel samples. Such an analysis using pool-wide mussel surveys (Navigation Pools 3, 5, 6, 8, 13, and 18) could inform whether separate mussel community types (i.e., species rich community vs. species poor; source vs. sink) exist that may represent alternate regimes or communities of varying resilience. If distinct assemblage clusters are apparent, the development of a continuous substrate stability coverage would allow for the testing of the role of substrate stability on community assembly (Figure 8; (Andersen et al. 2009). If there is no statistical support for distinct assemblage clusters, a quantile regression approach could be used to separate "high" richness/density/recruitment sites from "low" sites to investigate the role of substrate stability.

Mussels may exhibit biophysical feedbacks whereby mussel density increases sediment stability through bed armoring and increasing sediment cohesion through biodeposition (Atkinson et al. 2018). To investigate this feedback, there may be opportunities to utilize a relatively long-term mussel community dataset collected within West Newton Chute in Navigation Pool 5. West Newton Chute has a persistent, self-organized mussel bed with both core and periphery assemblages and has been consistently sampled annually between 2008 and 2017. This side channel has been selected as a priority site by the Minnesota Department of Natural Resources for additional long-term mussel monitoring. Fine-scale quantification of substrate stability throughout the side channel would be collected to test for differences in substrate stability associated with mussel density and recruitment. Understanding how spatial patterns in a persistent mussel bed contribute to reinforcing feedbacks may be informative to future mussel-focused restoration actions (Liu et al. 2014, de Paoli et al. 2017).

Research question 1.4.2: Are there hydrogeomorphic shifts that can be characterized?

The resilience of a river's physical template is critical for understanding river ecosystem resilience because hydrogeomorphic regimes and ecological processes and patterns are interrelated. The importance of hydrogeomorphology to the structure and function of river-floodplain ecosystems is highlighted in important conceptual models of lotic ecology including the Intermediate Disturbance Hypothesis (Connell 1978), River Continuum Concept (Vannote et al. 1980), Flood Pulse Concept (Junk et al. 1989), Network Dynamics Hypothesis(Benda et al. 2004), Shifting Habitat Mosaic (Stanford et al. 2005), and the Riverine Ecosystem Synthesis (Thorp et al. 2006).

In the UMRS, there has been substantial work to describe and characterize both long- and short-term changes in hydrogeomorphic patterns, processes and rates of change as a basis for anticipating aquatic ecosystem responses. Examples of systematic studies include the aquatic habitat classification system (Wilcox 1993), the Cumulative Effects Study (WEST Consultants 2000) and Habitat Needs Assessments (Theiling et al. 2000, De Jager et al. 2018); regional or local studies have also been undertaken in support of HREP projects or to meet programmatic goals such as the mapping of planiform changes in landforms to reveal spatio-temporal variability in sediment dynamics (Rogala and Hanson 2018).

Efforts are currently underway to develop a new geomorphic framework of the UMRS to characterize current and future conditions specific to the river system, including a conceptual model of hydrogeomorphic processes and patterns. The conceptual model, once completed, should be a valuable tool to help identify why, how, and where geomorphic change is happening in the UMRS. The conceptual model also will serve as a framework for empirical tests of hydrogeomorphic processes, patterns, and shifting dynamics, ultimately contributing to a richer understanding of hydrogeomorphic and ecological relationships.

In general, hydrogeomorphic processes and patterns are underpinned by relationships among geomorphology (e.g., slope), hydrology (e.g., discharge), and sediment (Schumm 1979). These in turn can dynamically interact with vegetation and nutrients to impact the form and functioning of river systems through time (Gurnell et al. 2016). Research into how these factors relate to each other to influence the physical template of the UMRS, including the detection and characterization of important shifts in form and function, could be addressed using the following broad approaches: 1) geospatial / remote sensing analyses, 2) empirical studies, and 3) quantitative modeling. For example, spatial patterns of bank erosion rates could be assessed using repeated LIDAR surveys using UAVs (geospatial/remote sensing) and net sediment deposition and erosion could be measured empirically using erosion pins, artificial turf mats, or clay pads distributed strategically across the floodplain (empirical). Measures of sediment dynamics derived from remotely sensed data or empirical measurements can be used to parameterize models of sediment dynamics across broader landscape scales or to test specific hypotheses about drivers and constraints on sediment dynamics (modeling). Similar approaches may also be used to understand the development of delta and island formations and eco-hydrologic feedbacks with vegetation (e.g., reed canary grass, willows and cottonwood), flow/stage, inundation, and sediment dynamics. Another example includes ongoing work that combines a geospatial model of floodplain inundation frequency and *in situ* measurements of biogeochemical cycling rates in Pool 8 with the goal of generating estimates of nutrient retention at broad geospatial scales.

Research question 1.4.3: What are the drivers and feedbacks associated with emergent vegetation regimes?

Approach: Several potential drivers likely influence the distribution and composition of emergent macrophytes, such as aggressive non-natives (*Phalaris, Typha, or Cirsium*), water level dynamics, and changes in substrate (e.g., SAV detritus has accumulated over the past few decades and created more flocculant sediment that has allowed *Zizania aquatica* to flourish). To determine drivers of emergent vegetation regime shifts, first we must develop a characterization of alternate emergent vegetation regimes. An inductive approach could be used whereby LTRM data is used to determine different emergent community types, or land cover data is used to determine where persistent areas of emergent vegetation exist vs. transient areas. Literature review and anecdotal information from UMRS managers would inform a hypothesis-driven approach to determining potential drivers of regime shifts. Analyses to evaluate hypothesized drivers of regime shifts would then require quantification of potential drivers and may require additional field collections.

Research question 1.4.4: How "resilient" are water quality conditions (nutrients and turbidity) and ecosystem metabolism to hydrological events? Does this vary across the lentic-lotic gradient of the URMS?

Approach: Recent evidence suggests shifting flow patterns in the UMRS (Raymond et al. 2008, Schilling et al. 2010). Climate models predict a higher frequency of extreme precipitation events, which could result in more frequent and longer duration high water events (Pryor et al. 2013). This could have widespread implications for water quality and biogeochemical processing, but our understanding of how water quality conditions respond and recover from large flow events in large rivers such as the UMRS is limited. Future research could combine data sources available from GREON and USGS continuous monitoring buoys deployed in Pools 8, 26 and the Open River as well as at several stations along the IL River to evaluate how temperature, oxygen, nitrogen, chlorophyll and ecosystem metabolism in the main channel and backwaters respond to and recover from high flow events. Using these multi-dimensional and high temporal resolution datasets allows for a unique perspective on the drivers and frequency of unstable vs stable water quality regimes.

Objective 1 Summary

Research questions under this first objective focus on improving our understanding of the mechanisms that maintain regimes and drive regime shifts. Testing the hypotheses set out in our conceptual descriptions of regime shifts will lead to an iterative process of improving our understanding of how the system functions to clarify how restoration and management actions might influence specified resilience.

OBJECTIVE 2 – Quantitative evaluation of general resilience indicators

General resilience reflects the ability to cope with uncertainty, or the capacity to absorb both expected and unexpected shocks and disturbances. Several indicators of general resilience have been developed by applying principles of general resilience to the UMRS (De Jager et al. 2018, Bouska et al. 2019). There remain important questions regarding the extent to which these indicators truly reflect adaptive capacity: addressing these questions could inform management targets for these indicators. Under this objective, we describe potential empirical tests of general resilience indicators. The LTRM data provide multiple quantitative avenues for assessing the extent to which general resilience indicators reflect the ability of major resources to persist over time. Evaluation of biological communities along a gradient of general resilience will likely improve our understanding of how to best refine and apply these indicators in making restoration and management decisions.

Evaluation of existing general resilience indicators

If general resilience indicators truly reflect an ecosystems' coping capacity, responses of major ecological resources are assumed to be more persistent where indicators suggest great coping capacity (i.e., greater ability to absorb disturbance) in contrast to reaches with lower coping capacity. Analyses proposed here align with the assumptions behind the development of each general resilience indicator, summarized in Bouska et al. (2019).

Research question 2.1.1: Has functional diversity and redundancy of fish communities changed over time or in response to disturbances? Do resilience metrics predict abrupt community shifts?

Approach: The cross-scale resilience model suggests that ecological resilience is a function of the diversity of functions within a scale, and redundancy of functions across scales of the system (Peterson et al. 1998, Allen et al. 2005). A recent publication documents our approach to delineate biologically relevant 'scales' of the fish community derived from the distribution of body-sizes of individual fish (Bouska 2018). Using these scales, the cross-scale resilience model was applied to fish communities across nine reaches of the Upper Mississippi River to quantify the diversity and redundancy of trophic and spawning guilds. To address the proposed question, metrics of functional diversity and redundancy would be adapted to incorporate body mass or abundance to, in theory, allow a more complete representation of the diversity and redundancy of functional guilds (Sundstrom et al. 2018). Such mass-based metrics have been found to be effective predictors of recovery in coral reef systems (Nash et al. 2016). Both the previously developed cross-scale resilience model and proposed metrics would be quantified for each year of LTRM sampling and evaluated across time to identify temporal trends or shifts. Relying upon long-term data to isolate response of fish communities following a disturbance (e.g., invasive species establishment, flood, drought) will provide a useful evaluation of the functional diversity and redundancy metrics.

Research question 2.1.2. Does the diversity of aquatic area types reflect the diversity of habitat conditions present across the UMR lotic-lentic gradient? How much redundancy in certain conditions exist across within and across reaches?

Approach: The diversity and redundancy of available habitat is a critical element of maintaining diverse biological communities. How the diversity of the physical template of the UMRS translates to habitat conditions is not fully understood, however (but see (Baker et al. 1991). Here we propose to evaluate how habitat conditions (water quality, vegetation) map onto the recently enhanced aquatic areas dataset. In the HNA II, several detailed physical metrics of habitat features were developed, but these have not been evaluated in terms of their implications for water quality conditions or vegetation cover. We will assess how well conditions such as temperature, dissolved oxygen, nutrients and productivity are described by both categorical definitions of aquatic area types (main channel, side channel, secondary side channel, shallow vs deep backwater) as well as metrics that describe a continuum of physical conditions (depth, volume, connectivity, sinuosity, etc.). We will assess how robust these relationships are using seasonal (SRS) water quality data from the six LTRM study reaches. This analysis will allow us to evaluate how generalizable these relationships between the physical template and water quality conditions are in reaches of the river where water quality data are limited and inform our understanding of how changes in the physical template (e.g., HREPs) may alter bio-chemical conditions.

Research question 2.1.3: What are the eco-hydrologic processes and feedbacks that drive the form and function of the UMRS floodplain-river ecosystem?

Approach: In our assessment of general resilience, we relied on a diversity index applied to output from a recently developed inundation model to characterize inundation diversity. However, we recognize that inundation patterns likely have more complex associations with ecological communities and processes than can be inferred from a simple diversity index. Our broader goal with this question is improve our understanding of the role of eco-hydrologic processes and feedbacks. Such knowledge could then inform the development of a more relevant indicator of inundation diversity and connectivity.

The UMRS inundation model characterizes hydrologic dynamics of terrestrial and semi-terrestrial areas throughout the UMRS (Van Appledorn et al., in revision). Outputs from the model, including flooding attributes like inundation event duration or maximum water depths on the floodplain surface, are spatially and temporally explicit and can be tailored to specific research interests. The model has been integrated with a process-based forest simulation model to anticipate forest responses to multiple interacting drivers including hydrology, invasive insects, and forest management decisions (De Jager et al., in revision). Ongoing work includes integrating model results with existing land cover, comprehensive forest inventory, and dendrochronological datasets to understand how floods and flood regimes drive patterns of species composition and forest structure. In addition, results from the inundation model offer the opportunity to scale-up biogeochemical studies with limited spatial extents to characterize the dynamics of nutrient cycling over broader scales. Finally, there is ongoing research to identify floodplain areas that could experience shifts in flooding dynamics with changes to river hydrology, and to characterize the magnitude and nature of flood regime shifts under a range of alternative hydrologic scenarios.

The model is also relevant for testing hypotheses about aquatic-terrestrial linkages. A currently funded UMRR Science in Support of Management and Restoration project to investigate vital rates of select fish species aims to include metrics of inundation in its assessment of factors that influence recruitment and growth of fishes with different life history strategies. For example, it is hypothesized that years with increased duration and extent of inundated areas support strong year classes of fishes with periodic life histories.

Development of additional indicators of general resilience

Research question 2.2.1: How do changes in water surface elevations influence depth distributions? Can depth distribution indices across be useful in making inferences regarding availability of habitat conditions?

Approach: Water surface elevations could be used in conjunction with existing topobathy data to create water depth datasets from which quantification of depth distributions or extent of specific depth criteria could be developed. To do so, flow exceedance probabilities would be quantified to estimate stage at standardized low-flow, average-flow, and high-flow conditions, then overlaid on topobathy to quantify water depth. Indices characterizing depth distributions could be derived from hypsometric curves applied at the selected scale (i.e., Navigation Pool) and compared to determine available depth conditions at each exceedance probability. Alternatively, depth criteria could be quantified and mapped to evaluate how the extent of the depth criteria changes across space and time.

Research question 2.2.2: What does the diversity and redundancy of aquatic vegetation communities suggest about general resilience?

Approach: It is possible that there are functionally different forms of aquatic vegetation that can be identified from functional traits (e.g., rooting structures, branching structure), which serve different functions. For example, wildcelery provides an important energy source for waterfowl and is well-adapted to lotic conditions, yet few other species in the system exhibit similar traits. Plants likely have differential ability to contribute to other ecological functions such as oxygen production, cover for fish, food resources, disrupt wave energy, uptake toxins, and provide detritus for microbes. Identifying important functional forms of aquatic vegetation may rely upon known assessments of aquatic vegetation, field assessments, and the development of hypotheses from which diversity and redundancy of different functional groups can be quantified.

Research question 2.2.3. What is the role of hydraulic connectivity on seasonal backwater conditions and what metrics best capture these effects?

Approach: An ongoing management objective within the UMRS is to promote and maintain habitat in slower flowing off-channel areas that play critical roles in providing food sources and refuge to diverse assemblages of riverine organisms (e.g., overwintering fish species). Characteristics such as flow, depth, and connectivity to the main channel that influence water residence time in these areas have been shown to have strong influences on biogeochemical conditions (e.g., nutrient concentrations, denitrification) and aquatic communities (e.g., vegetation communities/duckweed, food webs). A common restoration approach in the UMRS has been to manipulate connectivity to the main channel (alter residence time) to optimize thermal habitat and oxygen availability during the winter. Although our understanding of the how connectivity impacts water quality conditions has grown because of evaluation of these types of projects (Giblin, Hendrickson), we lack a larger scale perspective on how hydraulic connectivity influences water quality across seasons and types of aquatic areas. Furthermore, our ability to quantify hydraulic connectivity across the diversity of off-channel areas in the UMRS is limited. Therefore, we propose to use the LTRM water quality dataset in the five of six reaches that contain a sufficient number of backwater lakes (Pools 4, 8, 13, 26 and La Grange) and connectivity metrics from HNA II to a) compare metrics of connectivity to evaluate which best capture flow conditions in connected backwaters, b) assess how well these connectivity metrics capture patterns in water quality conditions across seasons.

Research question 2.2.4. What is the role of aquatic-terrestrial connectivity in supporting food webs and ecosystem productivity in the URMS river-floodplain ecosystem?

Approach: Cross-ecosystem subsidies are important stabilizing factors for food webs and ecosystem processes (Polis and Winemiller 1996, Nakano and Murakami 2001). Although these connections are considered relatively less important as stream order increases (Vannote et al. 1980, Thorp et al. 2006), the dynamic nature of large floodplain rivers has been well-documented to support productivity and diversity in both aquatic and floodplain systems (Junk et al. 1989). Thus, understanding and maintaining the capacity for reciprocal aquatic-terrestrial connections is important in a large river such as the UMRS. Some research in the UMRS has examined the role of terrestrial subsidies in supporting aquatic food web productivity (Larson et al, Fritts et al, in prep) and ongoing work is examining input, transport and role of large wood inputs on river functioning (Gahm et al. In prep), but the scope and spatial scale remain limited. In addition, very little work has evaluated subsidies in the reverse-direction onto the floodplain and surrounding terrestrial habitats (Gratton and Vander Zanden 2009, Vander Zanden and Gratton 2011, Bartrons et al. 2013). Thus, there is a large scope for future work in to examine the role of river and floodplain hydrogeomorphology and infrastructure in mediating these transfers.

Research question 2.2.5: What is the general resilience of the UMRS as a socio-ecological system? How does it vary by reach?

Approach: Our general resilience application has focused on ecological attributes, but there is increasing evidence that both ecological and social system attributes are important for managing determinants of general resilience. Principles that focus on social-ecological system properties and governance attributes that promote general resilience of these systems include: 1) maintaining diversity and redundancy, 2) managing connectivity, 3) managing controlling variables and feedbacks, 4) fostering an understanding of social-ecological systems as complex, adaptive systems, 5) encouraging learning and experimentation, 6) broadening participation, and 7) promoting polycentric governance systems (Biggs et al. 2012). As mentioned earlier in this document, the first three have been applied to the ecological aspects of the UMRS. Qualitative approaches (e.g., expert opinion surveys) for estimating social-ecological resilience have been taken for other river systems (Cosens and Fremier 2014, Nemec et al. 2014) and are applicable to the UMRS. More rigorous assessments would require broad stakeholder engagement across economic sectors, communities, and resource managers that rely upon the river for ecosystem services and goods. Broadening our understanding of the socio-ecological resilience of the UMRS would provide an improved understanding of the factors that contribute to resilience, identify potential opportunities for collaboration, and be informative of the social capacity of adapting to change or making transformative change.

Objective 2 Summary

Improving our understanding of how general resilience relates to the persistence and recovery of ecological resources and functions will allow for more informed use of the indicators in restoration and management decisions.

Acknowledgements

Recognition of scientists who provided early comment and discussion to advance this research framework include Nathan R. De Jager (U.S. Geological Survey), Deanne C. Drake (Wisconsin Department of Natural Resources), Jeffrey N. Houser (U.S. Geological Survey), KathiJo Jankowski (U.S. Geological Survey), Danelle Larson (U.S. Geological Survey), Teresa Newton (U.S. Geological Survey), and Molly Van Appledorn (U.S. Geological Survey). We also thank the UMRR Resilience Working Group and the UMRR A-Team for review and discussion.

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Appendix

Table A: Individuals who have participated in the Resilience Working Group and their agency associations. Asterisks denote individuals who have retired or changed positions and are no longer serving on the Resilience Working Group.

Name	Agency
Andy Casper*	Illinois Natural History Survey
Ben Lubinski*	Illinois Natural History Survey
Levi Solomon	Illinois Natural History Survey
Dave Bierman	Iowa Department of Natural Resources
Dave Herzog	Missouri Department of Conservation
Shawn Giblin	Wisconsin Department of Natural Resources
Kenn Barr*	U.S. Army Corps of Engineers
Mark Cornish	U.S. Army Corps of Engineers
Jon Hendrickson	U.S. Army Corps of Engineers
Marvin Hubbell*	U.S. Army Corps of Engineers
Nate Richards	U.S. Army Corps of Engineers
Bob Clevenstine*	U.S. Fish and Wildlife Service
Matt Mangan	U.S. Fish and Wildlife Service
Sara Schmuecker	U.S. Fish and Wildlife Service
Stephen Winter	U.S. Fish and Wildlife Service
Kirsten Wallace	Upper Mississippi River Basin Association
Kristen Bouska	U.S. Geological Survey
Nate De Jager	U.S. Geological Survey
Jeff Houser	U.S. Geological Survey