OF LIMPKINS AND APPLE SNAILS:

INVASIVE SPECIES, NOVEL ECOSYSTEMS, AND AN UNCERTAIN FUTURE

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REFERENCE: *Proceedings of the 2019 Georgia Water Resources Conference*, held April 16-17 2019, at the University of Georgia.

Abstract. Novel ecosystems, combinations of species without historical analog, are now abundant across the landscape providing opportunities to study characteristics of communities that are composed of invasive or nuisance species. Reservoirs are common novel ecosystems created where dam construction has altered river flow to support human needs. Here, we examine Lake Seminole as a case study for such interactions. Lake Seminole is a run of the river reservoir in southwestern Georgia completed in 1957 for hydropower and navigation. It lies at the confluence of the Chattahoochee, an urbanized highly regulated river, and the Flint River, which is largely free-flowing and rural. Multiple invasive species exist in the lake, including *Hydrilla verticillata* and *Corbicula fluminea* introduced in the 1960s, as well as *Pomacea maculata*, first noted in the early 2000s. Examination of *Hydrilla* coverage revealed variation with both seasonal and annual hydrologic conditions with coverage ranging from 35-50% of the lake. During the *Hydrilla* growing season, we have observed substantial reductions in nutrient levels as water moves through the lake. Nutrient uptake within beds and by *Hydrilla* tissue has also been documented. Water column mixing within the beds changes during development providing heterogeneous nutrient absorption potential through time. Corbicula populations were sufficiently abundant to affect water quality through filtration, with estimates ranging from 6-181 days to filter the lake volume, depending on temperature (55±29 individuals/m^2). Egg mass surveys revealed *P. maculata* populations to be rapidly expanding, which has resulted in more permanent Limpkin (*Aramus guarauna*) populations on the lake. While each of these species is generally viewed as a nuisance outside of their native range, at a whole-lake or ecosystem scale, they provide important services and functionality considered 'desirable' to the river basin. Considering these services and often limited management resources, should the focus be on extirpation or integration?

INTRODUCTION

Ecosystems are subject to multiple drivers of change including disturbances, climate change, land-use, species introductions, and adjacent ecosystems. While the boundaries of an ecosystem are conceptually based, long term data can shed light on shifts over time.

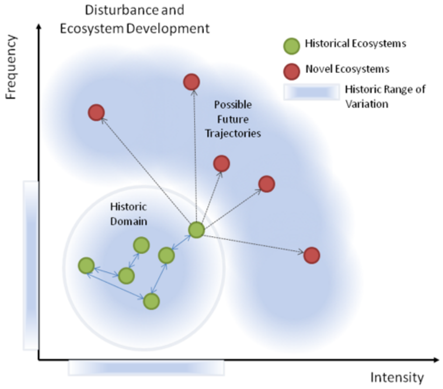

Figure 1: The effects of disturbance on ecosystem development. Modified from Harris et al. 2006

The intensity and frequency of disturbances influence the nature and pace of ecological change. Over time species composition can be permanently altered, processes changed, and new or novel ecosystems develop (Hobbs and Harris 2001, Harris et al. 2006, Scheffer et al. 2009) (Figure 1). Once novel ecosystems form, it is difficult to return to historical conditions. Predicting how an ecosystem will shift once a threshold is reached is difficult, particularly during periods of environmental variability and climatic uncertainty (Harris et al. 2006, Scheffer 2009).

Few ecosystems remain that are not influenced by human activity (e.g., Seasted et al. 2008, Hobbs et al. 2009). Our ability to influence climate, alter the landscape through technology and move species for our needs has resulted in modern landscapes with few analogs to the past (Vitousek et al. 1997). Historically, the creation of novel ecosystems through human action was generally local; however, modern landscapes are influenced at the continental scale with fragmented patches having little ecological connection and species intentionally or inadvertently moved long distances from their native ranges.

Native species are experiencing high rates of extinction or displacement resulting in regional species pools trending toward homogenization (e.g. Rahel 2000, Olden and Poff 2003, Marzluff 2005). Novel ecosystems continue to emerge as a result of degraded "natural/wild" or abandonment of "intensive commodities-oriented" landscapes, predicting the path of development is uncertain but vital in understanding the future global ecological change (Hobbs et al. 2006).

Disciplines focused on solving ecological problems (ecology, conservation biology and restoration ecology) have begun to shift focus to managing and conserving a world with novel ecosystems and climate change (Harris et al. 2006, Hobbs et al. 2009, Baker and King 2010, Hilderbrand et al. 2010). However, reluctance to acknowledge the potential value of novel ecosystems and transplanted species makes understanding and mitigating impending changes difficult (Seastedt et al. 2008, Hobbs et al. 2009). The inevitability of global ecological change makes adopting strategies of embracing and adapting rather than reacting necessary.

OBJECTIVE

The objective of this paper is to use Lake Seminole in Southwestern Georgia as a case study for examining regional influences on the development of a novel ecosystem. It lies at the base of a watershed spanning 3 physiographic provinces with one major tributary draining an urbanized highly regulated area and the other being largely free-flowing and rural. Thus, integrating multiple human-caused drivers in ecological change. Reservoirs, by their constructed nature, are novel ecosystems. Collectively, these characteristics make Lake Seminole an excellent study area for considering environmental change and influences on the ecosystems of the future.

SOUTHEASTERN BIOPHYSICAL DOMAIN

The SE-US is noted as a center of diversity for many faunal groups (e.g. amphibians, freshwater mollusks). It has a long history of commodities production including leading the US in timber production and substantially contributing to national agricultural production. Currently, SE-US is undergoing rapid development pressure with Atlanta growing from a population of ~1 million in 1960 to a projected 8-10 million in the near future (Golladay et al 2016). In addition, the Piedmont-Atlantic megalopolis expanding west, and northeast of the Atlanta metro area is one of the fastest growing areas in the US. While water resources are abundant, they are showing signs of stress as growing populations, industries, and agricultural use increase.

Climate models vary; however, most predict warming in the SE-US with highly variable rainfall (i.e. more floods and droughts) (Pederson et al. 2012). The increasing population puts a stress on regional forest, rivers, and aquifers that have further been altered by land-use change. Not only are endemic biological communities at risk but ecological services outside of water supply and commodities production are at risk as well in the face of on-going change (Figure 2). Because most land ownership is private and in relatively small parcels, large-scale change from regulation and technological developments are unlikely to solve these stressors.

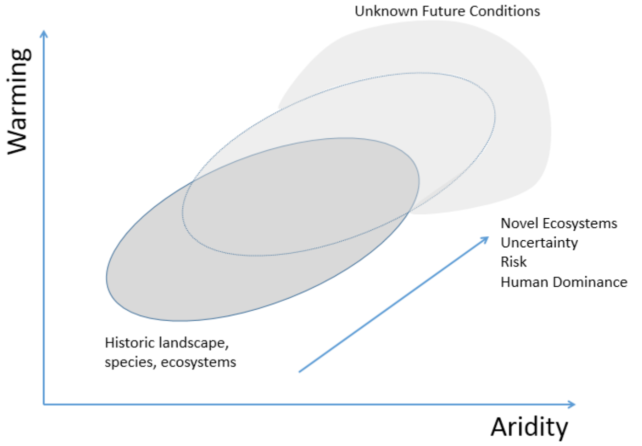

Figure 2: The Southeastern biophysical template showing how aridity and warming affect uncertainty, risk, and human impacts.

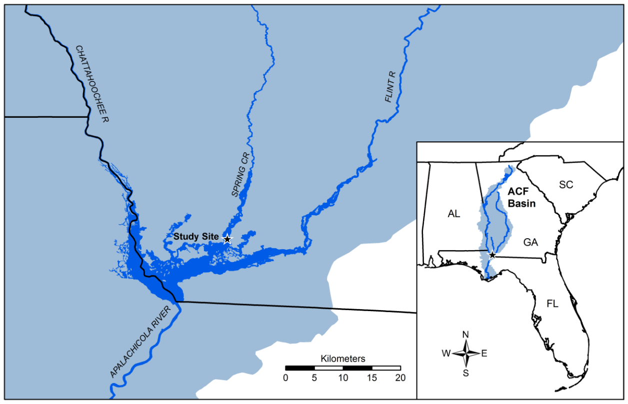

Figure 3. Lake Seminole in southwestern Georgia is formed from the confluence of the Flint and Chattahoochee Rivers.

LAKE SEMINOLE: A CASE STUDY

Lake Seminole, located at the confluence of the Flint and Chattahoochee, was completed in 1957. It is a run-of-the-river reservoir and is authorized for electricity production and navigation (Figure 3). It is an important site for fishing tournaments and duck hunting, generating tourism revenue that is substantial and regionally important. Nutrient runoff from human land-use raises long term concerns about the health of Lake Seminole. On the Flint arm, the primary nutrient is nitrate consistent with agricultural runoff while the Chattahoochee arm has elevated phosphorous consistent with municipal waste water discharge. Interestingly, nutrients leaving the lake are lower in concentration than those entering suggesting that Lake Seminole is sequestering nutrients and improving water quality prior to release into the Apalachicola River.

Paleolimnological Studies

Waters et al. (2015) collected sediment cores from the Flint and Chattahoochee arms showing depositional differences for each arm linked to material inputs, primary producer communities and flow. Phosphorous, while not a concern for water column samples, was deposited in the Flint arm at double the concentrations of the Chattahoochee arm and higher than many hypereutrophic systems in the SE US and the globe. In addition, photosynthetic pigment analysis showed a substantial benthic cyanobacteria population of *Lyngbya* in the Flint arm capable of sequestering nutrients from the sediments and maintaining low water column phosphorous concentrations. The Chattahoochee arm deposited sediments largely characterized as a mixture of local *Hydrilla* organic matter and silts and metals from the upstream industrial areas. These findings support the importance of in-lake processes capable of influencing ecological services and complicating management decision based on water column samples and modeling efforts.

Invasive Species

Hydrilla. In the late 1960s, *Hydrilla verticillata,* an invasive aquatic macrophyte, was introduced into the lake. Currently extensive beds dominate shallower areas causing a serious impediment to recreational boating, particularly in late summer and autumn. Home owners and recreational boaters advocate aggressive *Hydrilla* control measures; however, the beds provide habitat for largemouth bass, other fish species, and seasonal water fowl. To evaluate variation in coverage, Shivers et al. (2018a) conducted annual whole lake vegetation surveys during the peak growing season from 2012-2015 that included years with drought and seasonal flood pulses. Physical measures including photosynthetically active radiation (PAR), discharge (Q) and turbidity were either directly measured or obtained from USGS river gages to examine the relationship between flow conditions and *Hydrilla* coverage.

During the first year, 2012, discharge was lower than the 50-year median daily Q and *Hydrilla* coverage was the greatest (35.5 km^2). In subsequent years increased discharge and greater turbidity resulted in reduced coverage (22.9 km^2 and 18.3 km^2, respectively) due to reduced light availability early in the growing season. In addition, Shivers et al. (2018b) found that NO3-N concentrations were lowest within *Hydrilla* beds and in the outflow during the growing season, particularly within the Flint River and Spring Creek arms of the lake. This highlighted the potential for these beds to act as nutrient sinks within the lake.

Currently, we are sampling along the Flint arm of the lake both within the main channel as well as at measured intervals toward the shore to examine the heterogeneity of the *Hydrilla* beds as a nutrient sink. Preliminary results suggest that during the *Hydrilla* growing season, substantial reductions in nutrient levels occur as water moves through the lake. Nutrient uptake within beds and by *Hydrilla* tissue has also been documented. Water column mixing within the beds changes during development providing heterogeneous nutrient absorption potential through time.

Corbicula. *Corbicula fluminea* is an invasive bivalve noted in Georgia first in the late 1960s and is abundant in Lake Seminole. Patrick et al. (2017) sampled the distribution, density and potential ecological effects in relation to abiotic factors of *Corbicula* from 2012-2014, as well as examining nutrient content of the *Corbicula* tissue. An estimated 55 ± 29 (mean ± SD) per m^2 were found resulting in a lake wide estimate of ~4.3 billion. *Corbicula* can siphon large volumes of water and with the estimated population, the entire lake volume could be filtered in 6-181 days depending on temperature. Tissue analysis revealed a significant accumulation of zinc, copper and phosphorous. These results show the important link *Corbicula* provide between the pelagic and benthic environments through filtering activity.

Apple Snails. *Pomacea spp.,* or apple snails, are native to South and Central America and are largely drought tolerant, moderately amphibious, and generally fecund. They have been transported by human activity and become a widespread invader globally. While adult apple snails are difficult to locate and identify, egg masses deposited on emergent vegetation are unique to each species and easy to observe. Egg masses were first observed in Lake Seminole in 2003 and Marzolf et al. (2018) conducted annual shoreline surveys of the entire lake from 2013-2016 and monthly surveys of target areas from April 2016-September of 2017. Both *P. maculata* and *P. paludosa* (native) were present in the lake across a variety of emergent surfaces.

Over the years, *P. maculata* showed rapid expansion and dispersal particularly in the carbonate rich waters of the Flint River and Spring Creek arms. Monthly variation showed a positive correlation with temperature; however, new egg masses were observed at temperatures as low as 11.3 C, previously thought unlikely. Difficulty in sampling adult *P. maculata* makes estimating population size difficult; however, the abundance of egg masses coupled with scarcity of adults suggests that Lake Seminole has abundant predators to limit the abundance of the non-native snail, particularly among the small hatchlings and juveniles. Recently, limpkins (*Aramus guarauana*), a predator of mature apple snails, have been observed on the lake. Lake Seminole lies at the top of their native range suggesting that an increased food resource has allowed them to expand their native range. With climate projections showing the SE-US to have warming temperatures, the potential for *P. maculata* to reproduce year-round could increase its dispersal throughout aquatic habitats.

Food Webs. During 2017, we collected samples of primary producers and consumers using a stratified design to look at the stoichiometry of food webs along the riverine/lacustrine gradient in the arms of the lake. Samples were analyzed for isotope ratios (d15N/14N, d13C/12C) and showed that biota from the same species trophic group were not similar along the gradient. The upper Flint and Spring Creek arms showed primary consumers to have relatively depleted 15N consistent with inorganic fertilizers and agricultural run-off, while down-lake 15N signatures were less depleted suggesting local animal or human origins of nitrogen. This further highlights that the lake is subject to varying and heterogeneous nutrient inputs related to adjacent patterns of human land-use during the growing season when *Hydrilla*/SAV is abundant.

HOW DO WE MANAGE THIS NOVEL ECOSYSTEM?

Lake Seminole represents a novel ecosystem created by humans on a large river with no historical analog. As biota have colonized, the species assemblage of the lake has become largely comprised of invasive species (e.g. *Hydrilla, Corbicula, P.maculata*) that are undesirable or nuisance species when viewed in isolation. These species all have been documented to have adverse ecological effects outside their native range; however, when viewed at an ecosystem scale, Lake Seminole is extremely productive and provides multiple ecosystem services. Among these services are improved water quality through sequestration of nutrients and other contaminants, wildlife habitat, important subsistence/recreational fishing. Considering these services and often limited management resources, should the focus be on extirpation or integration?

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