



A Floodplain Continuum for Atlantic Coast Rivers of the Southeastern US: Predictable Changes in Floodplain Biota along a River's Length

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Abstract

Floodplains are among the world's economically-most-valuable, environmentally-most-threatened, and yet conceptually-least-understood ecosystems. Drawing on concepts from existing riverine and wetland models, and empirical data from floodplains of Atlantic Coast rivers in the Southeastern US (and elsewhere when possible), we introduce a conceptual model to explain a continuum of longitudinal variation in floodplain ecosystem functions with a particular focus on biotic change. Our hypothesis maintains that major controls on floodplain ecology are either external (ecotonal interactions with uplands or stream/river channels) or internal (wetland-specific functions), and the relative importance of these controls changes progressively from headwater to mid-river to lower-river floodplains. Inputs of water, sediments, nutrients, flora, and fauna from uplands-to-floodplains decrease, while the impacts of wetland biogeochemistry and obligate wetland plants and animals within-floodplains increase, along the length of a river floodplain. Inputs of water, sediment, nutrients, and fauna from river/stream channels to floodplains are greatest mid-river, and lower either up- or down-stream. While the floodplain continuum we develop is regional in scope, we review how aspects may apply more broadly. Management of coupled floodplain-river ecosystems would be improved by accounting for how factors controlling the floodplain ecosystem progressively change along longitudinal riverine gradients.

Keywords Ecotonal interaction · Flood-pulse continuum · Hydrology · River continuum · Wetland functions

Introduction

In terms of ecosystem services, floodplains (US\$25,681/ha) and their associated river channels (\$12,512/ha) are among the world's most valuable resources (Costanza et al. 2014). While river channel area has not changed appreciably in recent decades, floodplain area has declined precipitously world-wide

(Brinson and Malvarez 2002; Costanza et al. 2014). Regrettably, despite their high value and threatened status, floodplain ecosystems remain poorly understood. In contrast, rivers are among the world's best understood habitats, and several comprehensive models have been developed and tested to assess how and why river channel ecosystems vary across space and time. Because river and adjacent floodplains operate in parallel, with intimate links as fluvial systems, the wealth of knowledge about streams and rivers is a logical basis for any conceptual framework of floodplain ecology.

The River Continuum Concept (Vannote et al. 1980) is a prominent riverine model. Briefly, it takes a longitudinal perspective, maintaining that headwater streams are tightly linked to adjacent riparian zones through allochthonous inputs of leaves and wood to the channel, and via the shading that limits algal growth. As streams morph into larger rivers, broader channels are less shaded by trees, and algal production within the channel increases to become an important autochthonous base for foodwebs. The River Wave Concept (Humphries et al. 2014) is another longitudinal paradigm that states that

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flood pulses, referred to as waves, can vary in shape, amplitude, wave length, and frequency along the length of a river, and wave character affects the relative contributions of allochthonous and autochthonous sources of organic matter to river channels, and influences their biota. Creed et al. (2015) follow by describing how dissolved organic concentrations and dissolved organic matter changes progressively from the headwaters to large rivers downstream.

Junk et al. (1989), Bayley (1995), and Junk (2005) take a lateral perspective and propose a paradigm for large tropical rivers called the Flood Pulse Concept, which maintains that lateral movements of floodwaters, nutrients, and organisms into and out of floodplains are crucially important to the functioning of both river channels and their associated floodplains. Others have applied the Flood Pulse Concept to rivers outside the tropics, and to smaller river-floodplain complexes (e.g. Tockner et al. 2000). Gallardo et al. (2008) relate how lateral connectivity of floodplain with the channels, via flood pulses, controls floodplain biota. Mertes (1997) subdivided the lateral gradients of floodplains based on the degree of transport of water from the river channel during flood events. Junk and Wantzen (2006) suggest that characteristics and impacts of flood pulses can change along a river's length.

Ward (1989) combines longitudinal and lateral perspectives, and adds a vertical (i.e. with the sub-surface hyporheic zone) and temporal perspective into a four-dimensional model of channel control. Brinson (1993) developed a holistic hydrologic conceptual model to describe variation among wetlands, including floodplains, considering the relative inputs of different water sources (precipitation, lateral flow, groundwater discharge). He concluded that headwater floodplains are strongly influenced by lateral overland flows off adjacent uplands, while lower river floodplains become increasingly dominated by lateral flows from the river (i.e. flood pulses). Harvey and Gooseff (2015) and Covino (2017) further expand on the impacts of combined lateral and longitudinal hydrologic exchange along fluvial systems.

Each of these models has merit, and each builds upon the others. Each considers the importance of the riparian floodplain, although the river channel itself remains a focal point and an abiotic perspective prevails. Apart from the Flood Pulse Concept, floodplains and especially their biota have received minimal conceptual development. Those specifically studying floodplains are none-the-less now adapting riverine models to help explain floodplain processes. For example, Noe (2013) adapt the 4-D concept of Ward (1989) to explain interactions among vegetation, biogeochemistry, and hydrogeomorphology in floodplains. Biota are an especially important focus for floodplains, because of the enormous diversity of resident plants and animals, yet most recent modeling describing continuums in fluvial systems takes an abiotic perspective (e.g. Humphries et al. 2014; Creed et al. 2015; Harvey and Gooseff 2015; Covino 2017).

In this paper we propose a continuum for floodplains that borrows conceptual aspects from all of the paradigms outlined above, and we conclude that major controls on floodplain ecology are either 1) external or 2) internal, and the relative importance of each source changes from headwater to mid-river to lower-river floodplain. We develop our idea based on existing data from floodplains of Atlantic Coast rivers of the Southeastern US, a location where abiotic, organismal, and community-level perspectives on floodplain ecology have all been well-developed empirically. After creating this regional perspective, we then explore how well concepts developed from the Southeastern US might apply more broadly, and discuss how unique conditions for rivers in other climates and geomorphic settings might alter biotic continuums along their floodplains.

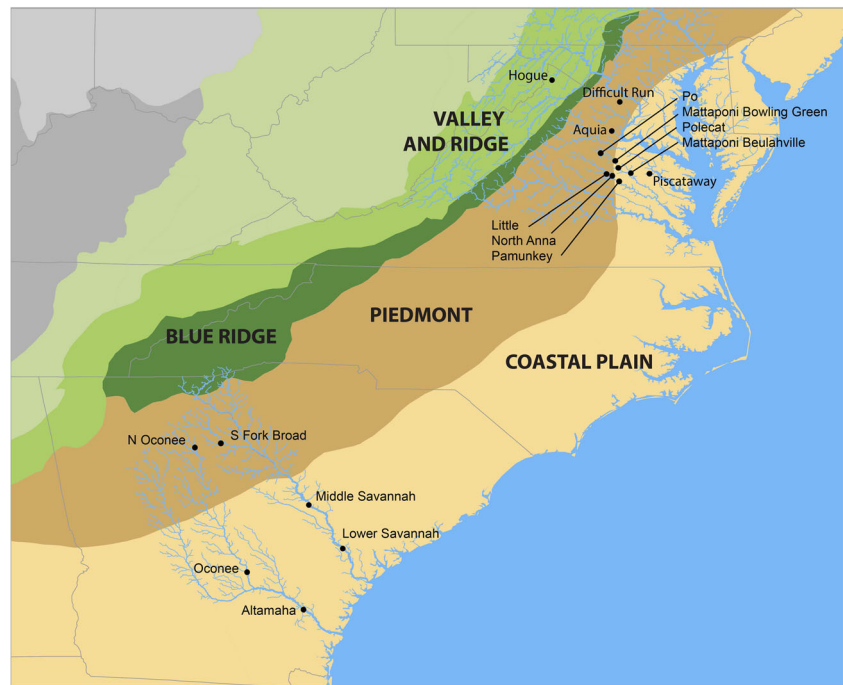
Changes in Abiotic and Biotic Conditions on Floodplains along the Lengths of Atlantic Coast Rivers of the Southeastern US

Here we synthesize our collective work on Southeastern Atlantic Coast floodplains, gathered primarily in the Altamaha and Savannah watersheds of Georgia and South Carolina, and the Mattaponi, Pamunkey, and Difficult Run watersheds of Virginia (Fig. 1), and supplement our findings with data from others working across the Southeast. We begin by describing the abiotic template (geology, hydrology, soils), which largely controls how biota respond, and then turn our focus to how important floodplain biotic assemblages change along river lengths.

Geology and Hydrology

An obvious change in floodplain along a river's length is its width (Markewich et al. 1990). In Georgia's Altamaha River system, for example, active floodplain widths in the upper-reaches (Piedmont) range from 0 to 600 m, in the upper-Coastal Plain (mid-river) they range from 700 to 1200 m, and in the lower-Coastal Plain they range from 1500 to 3000 m, becoming even broader in the terminal delta. This progression in floodplain width with increasing stream order mimics that proposed by Brinson (1993), although widths associated with larger channels are somewhat wider than predicted, perhaps because of the very flat terrain of Georgia's lower-Coastal Plain. This size progression means that floodplains in the Piedmont lie in close proximity to the river channel, the adjacent uplands, or both, and thus these floodplains occur spatially as ecotones between the river and the uplands. In the Coastal Plain, in contrast, much of the floodplain is far removed from either the river channel or uplands, and these floodplains largely occur as wetland habitats, unique from the river channel or the uplands.

Fig. 1 Map of the Southeastern US showing the rivers and streams highlighted by this paper in regards to hydrology, soils, flora, and fauna. Locations of USGS gauges cited in Figs. 2 and 3 are indicated



Flood-pulse variation (frequency, duration, amplitude, timing, and rate of change) influences floodplain connectivity with the channel (Junk et al. 1989; Poff et al. 1997; Humphries et al. 2014) and the ecology of floodplains (Junk et al. 1989; Junk 2005; Opperman et al. 2010), including Southeastern US floodplains (King et al. 2009, 2012). It is likely (Brinson 1993; Ward and Stanford 1995), but poorly documented, that the attributes of flood-pulse connectivity to floodplains should vary predictably along a river's length. For example, regional changes in stream gradient cause changes in floodplain connectivity. Bankfull discharge occurs more frequently in Coastal Plain than in the higher gradient Piedmont or Valley and Ridge physiographic provinces (McCandless 2003; Sweet and Geratz 2003). However, it should be noted that floodplain inundation can also occur at discharges less than bankfull when water is transported via floodplain channel cuts through natural levees (Phillips 2013). Rivers that originate in the Piedmont or mountains experience more frequent overbank inundation when they cross the fall line into the lower-gradient Coastal Plain (Hupp 2000). Furthest downstream the longitudinal river gradient, tidal freshwater floodplain forests experience greater frequencies of inundation both compared to upstream nontidal floodplain (Kroes et al. 2007) and downstream towards the estuary (Rheinhardt 2007).

In general, increasing drainage area is associated with increasing duration but decreasing frequency of floodplain inundation (greater than bankfull) (Hodges 1998; Dodov and Foufoula-Georgiou 2005). In the Virginia Piedmont, hydroperiod (cumulative duration of flooding) of both levee and backswamp increased along a gradient of watershed size in Difficult Run (ranging from 3 to 117 km²; Hupp et al. 2013).

The Cache River, in the Mississippi Alluvial Plain, experiences a lower flood peak and greater flood duration due to the cumulative effects of upstream floodplain inundation on flood hydraulics (Walton et al. 1996). Here we analyzed changes in flow pulse characteristics along several Atlantic Coast rivers that have USGS gages nested longitudinally through their watersheds (Fig. 2). We analyzed river discharge normalized by drainage area ("discharge yield", m³ km⁻² s⁻¹), in comparison to bankfull discharge where available, in order to compare flood pulses and floodplain inundation from headwater to mid-river to lower-river floodplain. In Virginia, the Mattaponi and Pamunkey rivers originate in the Piedmont and have extensive bottomland hardwood floodplains through their Coastal Plain reaches. Both rivers show flood peak attenuation, with decreases in flood magnitude and increases in flood duration, from headwater and Piedmont reaches to the lower watershed and Coastal Plain reaches. In Georgia, the Altamaha and Savannah watersheds also originate in the Piedmont and/or Appalachians, flow across the Atlantic Coastal Plain, and are among the larger river systems in the Southeastern US. While flood pulses in the smaller Virginia watersheds occur over days, pulses in the larger Georgia systems can persist over weeks, with water remaining on the floodplain long after pulses pass. But the same general pattern exists, with pulses in the upper Piedmont being high in magnitude but short in duration, and with magnitudes declining and durations increasing as the pulses flow downstream. The hydrographs for the Savannah River show how a large dam located near the transition of the Piedmont and Coastal Plain greatly reduces flood pulse magnitude downstream (Middle Savannah at Waynesboro, Fig. 2). However, as inputs of water

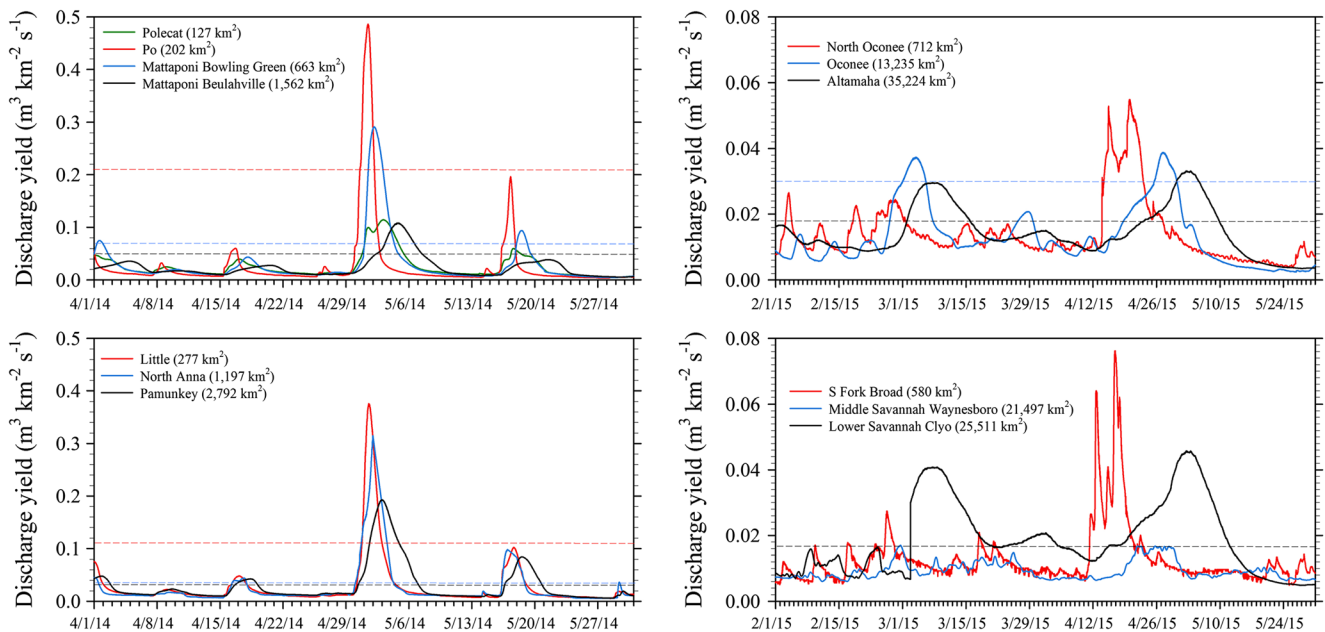


Fig. 2 Hydrographs of discharge yield (discharge normalized by drainage area) for four Southeastern US watersheds from the Piedmont to the Coastal Plain, with red and green lines being the headwater (Piedmont and Coastal Plain, respectively), blue lines mid-river, and grey lines being the lower-river gauge locations in each watershed. Bankfull discharge yield at each gauge, where available, is shown with dashed lines (Hess and Stamey 1993; Austin and Wiegand 2009). Polecat = USGS

01674182, Po = USGS 01673800, Mattaponi Bowling Green = USGS 01674000, Mattaponi Beulahville = USGS 01674500, Little = USGS 01671100, North Anna = USGS 01671020, Pamunkey = USGS 01673000, North Oconee = USGS 02217770, Oconee = USGS 02224500, Altamaha = USGS 02226000, S Fork Broad = USGS 02191743, Middle Savannah Waynesboro = USGS 021973269, Lower Savannah Clyo = USGS 02198500

from tributaries and precipitation downstream of the dam accumulate, flood pulses redevelop (Lower Savannah at Clyo, Fig. 2).

Regional topography can have an important influence of the specifics of any hydrologic continuum, with differences occurring in high versus low gradient systems or where slope gradients do not gradually decrease downstream. For example, Fig. 3 shows hydrographs of Atlantic Coast headwater streams of similar drainage area but set across a topographic gradient, from the steeper Valley and Ridge mountains to the

lower gradient Piedmont to the Coastal Plain, where similar amounts of precipitation can lead to divergent floodplain inundation characteristics depending on local geology (all have mostly forested land cover). The amplitudes and durations of flood pulses in similar sized streams across this topographic gradient have many similarities to longitudinal changes of different sized streams within single watersheds (as shown in Fig. 2).

Brinson (1993) maintains that relative inputs of overland flows vs. overbank flows into floodplains change along the

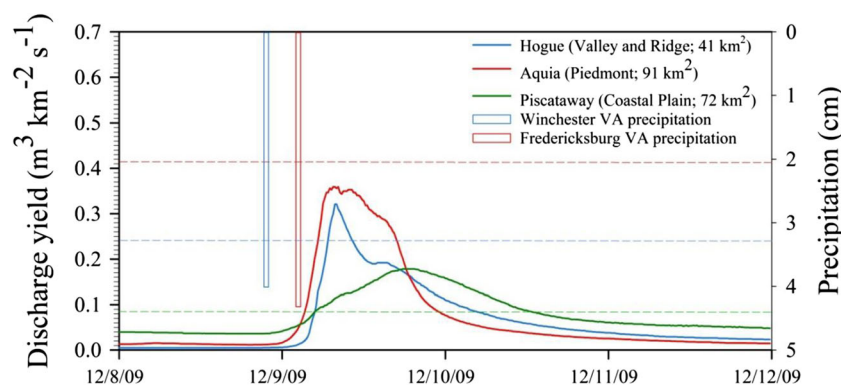


Fig. 3 Hydrographs of discharge yield (discharge normalized by drainage area) compared to bankfull discharge yield (dashed lines) after precipitation events (<http://w2.weather.gov/climate/xmacis.php?wfo=lxw>) of three Virginia, Southeastern US, watersheds from the Valley and Ridge (watershed slope = 11.3%; USGS 01613900 Hogue Creek

near Hayfield, VA; bankfull discharge: Keaton et al. 2005) to Piedmont (3.0%; USGS 01660400 Aquia Creek near Garrisonville, VA; bankfull discharge: Lotspeich 2009) to the Coastal Plain (2.9%; USGS 01669000 Piscataway Creek near Tappahannock, VA; bankfull discharge: Moyer and Bennett 2007)

length of a river. He acknowledges that groundwater discharges onto floodplains, but maintains that in terms of overall water budgets, these inputs increasingly become volumetrically dwarfed by river flood pulses in downstream areas. While this is true, groundwater maintained habitats on floodplains remain crucial resources for floodplain wetland vegetation and aquatic animals, and the importance of these habitats increases from upper to lower watershed habitats. In the Altamaha watershed, permanent-water lentic waterbodies on floodplains, mostly deeper oxbow lakes tied to surficial aquifers, are common features of the floodplain. These permanent-water floodplain lakes are rare in Piedmont areas, however, except where created by beavers or humans. In the upper Coastal Plain, permanent oxbows begin to appear more frequently (~0.15 oxbow lakes/river km), and become common (~0.54 oxbow lakes/river km) and sometimes large (>5 ha) in the lower Coastal Plain. As oxbow lakes are hotspots of aquatic biologic activity (for invertebrates, fishes, herpetofauna, birds), this continuum of groundwater-influenced habitat represents another important hydrological and ecological gradient in the floodplain along a river's length. Additionally this water storage on lower-river floodplains antecedent to floods can limit the area of floodplain inundated by river water (the perirheic zone), decreasing the flux of riverine sediment and nutrients onto the floodplain (Mertes 1997).

Soils and Biogeochemistry

Floodplain soils along the Difficult Run watershed, and mid-river portions of the Altamaha watershed, both in the Piedmont, reflect a tight erosional connection from uplands and the river channel, to the floodplain. Soils are homogenous, comprised almost exclusively of clay and silt (consistently >85% by mass), but with increasing spatial variability of physico-chemical characteristics as watershed size increases (Noe et al. 2013). Craft (University of Indiana, unpublished data, Altamaha watershed) and Noe (unpublished data, Chesapeake Bay watersheds) have both found that phosphorus levels in mid-river floodplain are higher than in downstream lower-river floodplain, likely reflecting inputs of upland sediments to mid-river floodplains. Jackson et al. (2005) maintain that sediments in Southeastern Piedmont streams largely consist of legacy erosion from historic agriculture, and thus floodplain soils in the upper watersheds of the Southeastern US likely reflect this historical landscape connection (Hupp et al. 2013). The characteristic orange-tinge of floodwaters in upper-watershed rivers of the Piedmont reflects continued upland soil erosion in the region.

In contrast to mid-river, floodplain soils in lower-river floodplain sections of the Altamaha watershed are heterogeneous, with soils ranging from being mineral sands (bulk density $\gg 1 \text{ g/cm}^3$) to being organic (bulk density $< 0.5 \text{ g/cm}^3$). Levels of clay/silt in soils are similarly variable, ranging from

<2 to >85%. This variation in soils likely reflects variation in scour, deposition, and decomposition throughout lower-river floodplain, representing a mixture of autochthonous and allochthonous sources and of deposition and erosion, rather than blanket deposition of river-born sediment occurring in upper-river floodplains. Piedmont-derived sediments are minimal on floodplains of some larger Coastal Plain rivers with Piedmont headwaters (Phillips 1992), while storage of legacy Piedmont sediment can be important to floodplain soil formation in the upper reaches of other large Coastal Plain rivers (Hupp et al. 2015).

Several authors have hypothesized on the impact that floodplain biogeochemistry has on river channel chemistry, but there has been little focus or data generated on how internal floodplain biogeochemical processes vary longitudinally along river networks. Brinson (1993) postulated that (upland) riparian transport to the floodplain remains roughly constant per unit of stream length, while overbank transport to the floodplain increases with increasing stream order because of increasing discharge downstream. The modeling effort of Gergel et al. (2005) identified that cumulative N retention on the floodplain would be greatest with frequent, low-amplitude floods compared to infrequent, larger floods, suggesting that floodplain N-retention along a river continuum would be greatest in mid-river reaches. Poole (2002) hypothesized that floodplain influence on reactive solute concentrations in the channel is greatest in the mid-river reaches of stream networks, due to less lateral connectivity in headwater and lower-river reaches. Hydric status of soils changes from upper- to lower-river floodplains. In the Altamaha watershed, hydric soils are wide-spread on lower-river floodplain, but are very limited upstream in headwater or mid-river floodplain (occurring only in the lowest lying areas). In contrast, few soils in the floodplain of the relatively small, Difficult Run watershed on the Piedmont exhibited hydric characteristics (Noe et al. 2013). Changes in the extent of hydric soils along the continuum undoubtedly affect soil microbes and biogeochemical processes in floodplains, with aerobic processes becoming more important upstream, and anaerobic processes becoming more important downstream (e.g. Difficult Run, Noe et al. 2013). More research is needed to document changes in nutrient, carbon, or other elemental cycling and fluxes within floodplains along longitudinal river gradients.

Plant Communities

As the abiotic template changes longitudinally, a continuum of biotic change also develops. Hupp (1986) examined the vegetation of 1st-5th order streams in the Massanutten Mountain area, Virginia, finding a greater frequency of floodplain development and changes in floodplain vegetation along higher order streams. Floodplain forests along all study streams were a mix of facultative, facultative upland, and facultative

wetland species (as defined by the National Wetland Plant List, Lichvar et al. 2016). Wetland obligates were absent from these floodplains regardless of order, and many 1st-order streams lacked floodplains at all.

Lee (2008) examined floodplain forest composition in the Altamaha and Savannah river watersheds, finding strong differences between floodplain forests of headwater and mid-river tributaries (3rd–5th order) and the lower rivers (7th order), as well as some longitudinal differences within each province. Like Massanutten Mountain, upper-river floodplains in the study area were comprised of facultative, facultative upland, and facultative wetland hardwoods. Facultative or facultative wetland species dominated all Piedmont sites, and facultative upland species were co-dominant at an upper Savannah tributary site (importance value [IV] = 25; maximum IV = 100). Wetland obligates were rare at the upper-river sites. Rybicki et al. (2015) found similar patterns in the Difficult Run (4th–5th order) watershed, with increasing abundance of facultative wetland canopy trees (but not shrubs or herbaceous species) in the lower portions of the watershed.

By contrast, floodplain forests along the lower Savannah and Altamaha rivers are a mix of facultative and facultative wetland hardwoods interspersed with wetter areas dominated by wetland obligates, reflecting the physical heterogeneity of soils and landforms reworked by fluvial activity. Some facultative upland species occur, but only as minor components (IV 1–6; Lee 2008). The extent of wetland obligates depends on local geology (e.g. extent of groundwater discharge), but wetland obligates were a strong component (IV = 20–30) in the upper Coastal Plain, and comprised nearly half of the forest (IV = 45) on floodplains in the lower Coastal Plain.

Rheinhardt et al. (2013) examined variation in forest composition on 1st–7th + order streams across the Southeastern USA, but restricted their study to Coastal Plain physiographic provinces. As in systems with Piedmont headwaters, facultative and facultative upland species here exhibited decreasing importance from mid-river (4th–6th order) to large lower-river (7th + order) floodplains; however, in most cases they exhibited lower importance in the headwaters (1st–3rd order) as well (Rheinhardt et al. 2013). Wetland obligates and wetland facultatives were typically an important component at all positions in the stream network, with their strongest presence in both headwater (1st–3rd order) and lower-river (7th + order) floodplains. Despite the lack of a meaningful flood pulse, Coastal Plain headwaters often exhibit saturated soils for much of the year due to groundwater discharge. Both headwater and lower river floodplains of the Coastal Plain exhibit wetland characteristics, although species compositions differ (Rheinhardt et al. 2013). Hydrology, vegetation, and nutrient cycling interact in floodplains (Noe 2013) and the longitudinal changes in floodplain plant species composition should directly influence nutrient availability, decomposition rates, and other ecosystem processes.

Animal Communities

Invertebrates

Reese and Batzer (2007) assessed progressive changes in macroinvertebrate assemblages from Piedmont headwater to lower-river Coastal Plain floodplains, employing many of the same Altamaha watershed floodplain used for hydrology, soils, and plant work, described above. Distinct macroinvertebrate assemblages were associated with floodplains of 1) Piedmont headwater streams (2nd and 3rd order), 2) mid-river channels of the Piedmont (4th to 6th order), and 3) the large lower-river channels (7th order) of the Coastal Plain. Headwater floodplains were dominated by flood-tolerant terrestrial soil invertebrates (annelids, mites, collembolans) and a few aquatic taxa adapted to short flood durations (e.g. mosquito larvae, microcrustaceans). Mid-river floodplains were dominated by lotic invertebrates (assorted mayfly nymphs, riffle beetles) that migrated into the floodplain from the river channel. Lower-river floodplains were dominated by lentic invertebrates (dytiscid beetles, isopod crustaceans) that were full-time floodplain residents, either spending low water periods as desiccation-resistant stages in soils and leaf litter, or in shallow permanent-water lakes on the floodplain (e.g. oxbows). Mid-river floodplains supported 18 families of lotic invertebrates, of which several were highly abundant, and only 7 families of permanent-water lentic invertebrates, none of which were abundant, while lower-river floodplains supported 12 families of permanent-water lentic invertebrates, most of which were abundant, and only 3 families of lotic invertebrates, none of which were abundant (desiccation-resistant aquatic and flood-tolerant terrestrial families were ubiquitous) (Batzer et al. 2016).

Galatowitsch and Batzer (2011) assessed how and why mayfly nymphs originating from the channels exploited mid-river Piedmont floodplains. These nymphs (*Leptophlebia* and *Siphonurus*) were not simply swept into floodplains during floods but actively swam and crawled from the channels into floodplain interiors. What motivated this dramatic behavior was unclear; food quality and quantity, temperature conditions, and nymphal growth rates were not superior on the floodplain than the channel, and nymphs were vulnerable to fish predation while migrating, and to salamander larval predation in floodplain interiors. None-the-less, a strong linkage was established between floodplains and mid-sized river channels for these invertebrates.

Bright et al. (2010) assessed ecotonal linkages for invertebrates in broad lower-river floodplains, hypothesizing that floodplain close to the river channel edge might support numerous lotic taxa, floodplain close to uplands might support numerous terrestrial taxa, and the floodplain interior would support mostly obligate wetland taxa. However, assemblages were fairly homogenous across the widths of those floodplains, with every portion of the habitat being dominated by

obligate wetland taxa (either desiccation-resistant forms or those that spend dry periods in oxbow lakes). Lotic taxa were rare everywhere, even immediately adjacent to river channels. Terrestrial invertebrates were more common, but did not concentrate near upland edges, suggesting that they were flood-tolerant wetland forms, rather than migratory upland forms. This study concluded that invertebrate assemblages on lower-river floodplains were dominated by an obligate wetland fauna (whether aquatic or terrestrial).

Floodplain invertebrate assemblages can develop from: 1) soils, leaf litter, and plants, where desiccation-resistant aquatics persist and flood-tolerant terrestrials live; 2) permanent water bodies on the floodplains, from which lentic aquatic invertebrates incapable of tolerating drying persist and then disperse; 3) the river channels, from which lotic aquatic forms migrate; and 4) the adjacent uplands, from which terrestrial forms migrate. All of these forms can intermingle, but the relative contribution from each group varies depending on where in the watershed the floodplain is located. In headwater floodplain, Groups 1 and 4 dominate, as flooding is so brief and unpredictable that few aquatics establish. In mid-river Piedmont floodplains, Groups 1, 3 and 4 are important, but Group 2 (permanent-water lentic taxa) is not, because lentic, permanent water bodies are lacking here. In lower-river floodplain, Groups 1 and 2 are important, but not Group 3 (ecotonal lotic forms) or Group 4 (ecotonal upland species). For the aquatic fauna of lower-river floodplains, the prevalence of Group 2 organisms likely reflects the wide-spread occurrence of oxbow lakes that serve as refugia between floods; the paucity of lotic invertebrates, however, is unexpected (Batzner et al. 2016).

Studies of floodplain invertebrates in other Southeastern US watersheds suggest landscape position affects assemblage compositions. Smock (1994) examined a small headwater floodplain, and Starr et al. (2014) examined a mid-river floodplain, but in both cases habitats occurred on Coastal Plain rather than the Piedmont (as was the case for the above studies). This shift in topographical setting appeared to shift resident invertebrate assemblage compositions, at least compared to floodplains of similar-sized channels in the Piedmont. The influx of mayflies associated with mid-sized river floodplains of the Piedmont was also observed by Smock (1994) for a small headwater-stream floodplain on the Coastal Plain. The largely obligate-wetland invertebrate fauna of large-river Coastal Plain floodplains was also observed by Starr et al. (2014) for a smaller, mid-sized river Coastal Plain floodplain. Regardless of channel size, floodplains on the Coastal Plain may flood for longer durations than Piedmont floodplains, affecting the overall invertebrate composition.

Fishes

Mirroring the longitudinal studies of floodplain invertebrates, Garnett and Batzner (2014) compared floodplain fish

assemblages between mid-river Piedmont and lower-river Coastal Plain areas of Georgia (Altamaha and Savannah River watersheds); some headwater Piedmont floodplains were examined but were found to be fishless. In mid-river floodplains, the majority of fishes were lotic species that migrated from the channels onto the main floodplain during flood pulses (e.g. red-breasted sunfish, *Lepomis auritus*, and assorted cyprinids); few lentic fishes occurred. In lower-river floodplains, in contrast, the majority of fishes were lentic species that migrated from floodplain lakes onto the main floodplain during flood pulses (e.g. grass pickerel, *Esox americanus*; bowfin, *Amia calva*; pirate perch, *Aphredoderus sayanus*), and few lotic species occurred. As for invertebrates, fish assemblages in mid-river floodplains were controlled by external interactions with channels, and fish assemblages in lower-river floodplains were controlled by internal interactions with floodplain lakes. When lateral patterns in fish assemblages were examined across broad lower-river floodplains, similar obligate-wetland species dominated the entire expanse (Bright et al. 2010).

Amphibians

Variation of overall amphibian assemblages along floodplain gradients has not been described. However, habitat ranges of eastern newts in the Southeastern US follows the same patterns described for overall invertebrate and fish assemblages. In Georgia, two sub-species of eastern newt are recognized; the red-spotted newt *Notophthalmus viridescens viridescens* occurs on the Piedmont, and the central newt *N. viridescens louisianensis* occurs on the Coastal Plain. Both occur on regional floodplains. Gabor and Nice (2004), however, found that red-spotted and central newts are the same genetically, and thus do not reflect valid sub-species. Despite the genetic similarity, red-spotted and central newt life cycles vary. Red-spotted newts have a well-developed eft stage, a terrestrial morph existing in transition between aquatic larvae and aquatic adults. Central newts tend to be wholly aquatic, with the eft stage often being absent and adults being neotenus (i.e. retaining larval gills). This species may have life-cycle plasticity where headwater and mid-river individuals are ecotonal, with uplands, while lower-river individuals are obligate wetland organisms.

Ecosystem Changes from Headwater to Lower-River Floodplains along Atlantic Coast Rivers

Patterns in hydrology, soils, biogeochemistry, and plant and animal communities all indicate that floodplains along Atlantic Coast rivers of the Southeastern US function differently from headwater to mid-river to lower-river reaches, with predictable changes occurring in the relative strengths of

external ecological processes (ecotonal interactions with adjacent channels and uplands) versus internal ecological processes (unique wetland interactions) (Fig. 4).

Headwater Floodplains

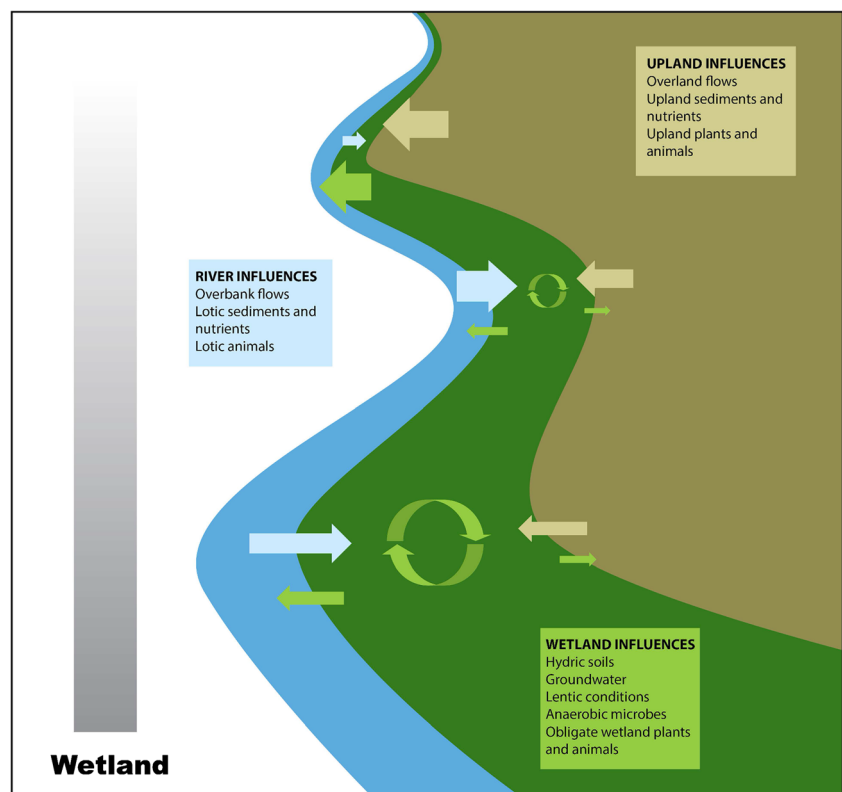
Floodplains in the headwaters are narrow, and as such are logically influenced strongly by adjacent habitat (Fig. 4). Upland influences will be especially intense on headwater floodplains because these floodplains are low points in the landscape, and hillslope processes will deliver copious water, sediment, and nutrient to these habitats (Brinson 1993). Terrestrial plant growth here will be lush due to moist, nutrient-rich conditions, and because soils do not become sufficiently wet to inhibit their growth. However, because headwater floodplains are small and low lying, it is unlikely that these floodplains will have much reciprocal impact on upslope upland. As dictated by the River Continuum Concept (Vannote et al. 1980), the impacts of riparian floodplain on headwater channels will be large, with trees shading the small channels and contributing leaf litter for food webs. On the other hand, the influence of headwater stream channels on their floodplains will be weak because channels are often deeply incised and over-bank flooding is rare and unpredictable (sometimes only occurring at decadal intervals). If flood pulses do enter headwater floodplains, their durations will be brief (measured in hours). While ecotonal interactions will be

strong in headwater systems, they will flow downhill from upland to floodplain to channel, and generally not the reverse. Wetland processes will be minimally important in headwater floodplains because habitats do not become sufficiently wet for anoxic conditions to develop; in fact, due to a lack of hydric soils, these floodplains would not be considered wetlands under some legal definitions (Environmental Laboratory 1987). However, groundwater can discharge onto headwater floodplains, and some wetland organisms (e.g. fast-developing mosquito larvae) may occur.

Mid-River Floodplains

Floodplains associated with mid-sized rivers of the Piedmont (Fig. 4) are wider than headwater floodplains, but still lie in close proximity to uplands. Thus water, sediment, and nutrient flux from upland to floodplain via overland flows should still be important here. However, because these mid-sized floodplains are larger features on the landscape, it is likely that they begin to affect upslope habitat (e.g. animals may migrate seasonally between floodplains and uplands; Naiman et al. 2005). In mid-river habitats, the influence of the channel on the floodplain becomes an important factor. Flood pulses into mid-river floodplains occur regularly (most years and sometimes multiple times per year) and at times can be hydrologically dramatic events. Rapidly rising, high amplitude flood pulses in the river channel and rarity of antecedent standing water on the

Fig. 4 A floodplain continuum for Atlantic Coast rivers of the Southeastern US to describe progressive changes in abiotic and biotic conditions along a river floodplain from the mountains to the sea (i.e. from high-gradient headwaters (top) to mid-river (middle) to low-gradient lower-river floodplains (bottom)). Horizontal straight arrows indicate directional ecotonal interactions between adjacent habitats (river-floodplain, floodplain-upland), with wide arrows denoting strong interactions and narrow arrows weak interactions. Circular arrows are internal wetland processes within the floodplain, with size reflecting relative importance



floodplain generate large fluxes of material throughout the floodplain. Water, sediment, and nutrient budgets become dictated more by high-energy river floods than by overland flows off uplands. Lotic riverine animals may migrate with flood waters into and out of these floodplains. While reciprocal impacts of shading and direct leaf litter deposition from the riparian floodplains on mid-river channels may decline, relative to headwaters (*sensu* the River Continuum Concept), the impacts of water-borne organic matter (dissolved and particulate) and nutrient flows from these floodplains to the channels may increase (*sensu* the Flood Pulse Concept). Here unique wetland processes first become important, with surficial water persisting for sufficient durations in some of the lowest lying areas for hydric soils to develop. These low spots may support obligate wetland plants and animals. However, unique wetland processes will still be of limited scope because the majority of mid-river floodplain surfaces still flood only briefly and typically remain aerobic, permitting terrestrial biota to establish and inhibiting proliferation of wetland forms.

Lower-River Floodplains

The broad floodplains of large Coastal Plain rivers are mostly controlled by internal processes (Fig. 4), and habitats function in many ways independently of the river channels or adjacent uplands. The influence of overland flows off of uplands will likely be restricted to upland-floodplain edges. Anoxic conditions in floodplain soils will inhibit incursion of upland plants. However, because these lower-river floodplains provide an abundance of resources during dry periods, reciprocal impacts of floodplains on uplands may increase (Naiman et al. 2005), at least in comparison to upstream. Flood pulses from the channels into lower-river floodplains are lower energy events with lower amplitudes spread over long durations. In terms of water budgets, these pulses will be dominant events, but they will not transfer as much sediment or nutrient into the floodplain as pulses do further upstream. Thus, contrary to what Brinson (1993) predicts, we believe the influence of river pulses may not continually increase downstream for all ecological factors, but peak mid-watershed for many. As pulses in lower-river sites are predictable seasonal events, not ecological disturbances, most resident organisms on lower-river floodplains are well-adapted for floods. But unexpectedly, given predictions of the Flood Pulse Concept, few lotic animals appear to migrate from river channels into lower-floodplains of Atlantic Coast rivers, perhaps because a vibrant and unique community of wetland predators exists and discourages such incursions. Like the headwaters, riparian floodplain again has a large impact on river channels, but in this case through mechanisms of the Flood Pulse Concept (*i.e.* dissolved and suspended organic matter), and not via shading or leaf litter flux (River Continuum Concept). While ecotonal interactions may decline in importance to lower-river

floodplains, internal wetland processes become increasingly dominant. Soil formation on these floodplains is mostly controlled by internal dynamics of scour and deposition. Localized aquifers become a strong ecological influence on lower-river floodplains because of discharges to the plethora of small floodplain lakes and other lentic-water bodies (Lewandowski et al. 2009), keeping many flooded year-round and making them focal points for aquatic wetland animals. Plant communities are dominated by obligate- and facultative-wetland species adapted for the anaerobic hydric soils that prevail from long-duration floods and groundwater. Most aquatic invertebrates and fishes are fulltime floodplain residents migrating either between permanent-water floodplain lakes and seasonally-flooded habitat, or between dry soils and flood waters. Terrestrial invertebrates are common but are largely wetland specialists able to tolerate flooding, rather than invaders from the uplands.

Can the Floodplain Continuum for Atlantic Coast Rivers Be Applied to Floodplain Ecosystems more Broadly?

Rivers on the Atlantic Coast of the Southeastern US have a climate and geology unique from most parts of the world, and thus many aspects of the floodplain continuum we describe are also undoubtedly unique (*e.g.* Kroes and Brinson 2004). However, we believe that two broad themes will apply to floodplains elsewhere: 1) the ecologies of floodplains along a river's length likely change in predictable ways from the headwaters to terminal deltas (although the details may be region specific); and 2) these longitudinal changes in ecology will be largely controlled by the relative importances of internal vs. external ecological forces on specific floodplains. Here we review relevant information on floodplain ecology from across the globe, acknowledging that the kind of systematic and multi-disciplinary perspective used along the lengths of our Atlantic Coast study rivers is largely unavailable elsewhere. As ecologists, we focus on biotic patterns. We encourage physical scientists to empirically test our basic tenets about floodplain continuums more broadly from an abiotic perspective; recent overviews by Harvey and Gooseff (2015) and Covino (2017) both provide useful perspectives on how lateral and longitudinal hydrologic-connectivity affects fluvial networks, including floodplains.

Other than our work from US South Atlantic Coast, remarkably little empirical study has addressed overall changes in hydrology, soils and biogeochemistry, and biota on floodplain habitats located along a river's length, with even synthetic publications on floodplains focusing mostly on specific river sections rather than any longitudinal continuum (*e.g.* Hauer et al. 2016 for montane floodplains; Wantzen et al. 2016 for lowland tropical floodplains). However, some

studies elsewhere tend to support a broader application of the ecological continuum we develop (Fig. 4). For invertebrates, the increased importance of lotic invertebrates from the river on upstream floodplain, and the increased importance of obligate wetland invertebrates on downstream floodplain is evident along both European (Italy, France, Spain) and Australian floodplain corridors from the mountains to the sea (reviewed in Batzer et al. 2016). For fishes, most studies of river and floodplain interactions have focused on either mid-river or lower-river locations, rather than along the length of a river. As we found in the Southeastern US, lower-river floodplains in tropical (Mekong, Bangladesh, Amazon) and temperate (Volga, Danube) regions were found to be dominated by lentic fishes (Fernandes 1997; Craig et al. 2004; van de Wolfshaar et al. 2011). Here, fisheries production is boosted by inundation when floodplain fishes move among floodplain wetlands to exploit the increased foraging opportunities and nursery habitat for developing offspring. Also, as in the Southeastern US, mid-river reaches of arid Australia, either with predictable annual flood pulses or unpredictable flood regimes, had strong river-floodplain linkages for lotic fish (Balcombe et al. 2007; Stoffels et al. 2016). In Australia, upper-river floodplains experience irregular, short-term flooding that may prevent successful fish spawning, as compared to lower-river habitats that have longer connectivity between the channel and the floodplain, and have longer wetland hydroperiods that can support lentic fish production (King et al. 2003). These patterns are consistent with our findings in the Southeastern US (see Garnett and Batzer 2014).

Geology and climate contribute to global patterns in floodplain flooding frequency, substrate composition, and species distributions (Kroes and Brinson 2004). For example, due to large paleoclimatic differences there are a greater number of endemic species in the geologically older tropical Amazon floodplains compared to younger temperate Central European floodplains (Adis and Junk 2002). High-gradient rivers recently formed by glaciers typically have highly dynamic braided river channels that can readily create or obliterate floodplain pools during large flooding events (Tockner et al. 2000; Hauer et al. 2016). This frequent habitat turn-over can influence the local invertebrate community structure (Arscott et al. 2005; Gray and Harding 2009; Hauer et al. 2016). Despite potential broad regional-scale differences, there can still be remarkably consistent floodplain patterns. Gallardo et al. (2014) compared aquatic invertebrate patterns in floodplains along six rivers with different hydrology (perennial and predictable flooding, intermittent rivers with seasonal floods, and unpredictable flooding) in four climatic regions. While there were taxonomic differences, the trait responses were consistent with more lotic invertebrates in habitats that experience high river-floodplain hydrological connectivity and lentic invertebrates found in more isolated floodplain habitats.

However, some ecological studies outside the Southeastern US deviate from the ecological patterns outlined in Fig. 4. Guan et al. (2017) working in the San Jiang Plain of north-eastern China found that lower-river floodplain was dominated by obligate wetland snails and mid-river floodplain was dominated by an influx of riverine snails, consistent with the pattern along our Atlantic Coast rivers. However, here the headwaters were not highlands, but instead a large plain, with water being sourced by peatlands. Guan et al. (2017) found that headwater floodplains supported numerous obligate wetland snails. This pattern for headwater floodplain snails in China mirrors the patterns found by Rheinhardt et al. (2013) for headwater floodplain forest of the low-gradient Southeastern Coastal Plain; in both settings, the headwaters were often large wetlands, not highlands. Figure 4 may adequately apply to higher gradient watersheds (i.e. from the mountains to the sea), but the continuum may have to be conceptually adapted for low gradient watersheds (interior and coastal plains), where the headwaters are not highlands but instead wetlands (e.g. groundwater discharge areas, peatlands, large depressions or shallow lakes). In these cases, patterns in the mid-river and lower-river locations may still largely conform to the continuum for high gradient systems, but patterns for the headwaters must reflect a wetland origin and the overall impacts of wetland interactions will increase across all watershed positions. Other changes in river slope due to local geologic controls of topography may alter the continuum of floodplain width, hydrologic connectivity to the channel, internal floodplain geomorphic complexity, and soil wetness, all potentially affecting gradients in biota.

Junk et al. (2015) describe how the variety of sub-habitats, termed macrohabitats, on Amazonian floodplains, change among habitats with different geologies (i.e. black-water vs. white-water systems); these kinds of macrohabitat differences are important controls on biota there. Along our Atlantic Coast rivers, changes in macrohabitats also contributed to the continuum we describe, with lower-river floodplains possessing macrohabitats, such as oxbow lakes, backswamps, and organic and hydric soil deposits, that are largely lacking from floodplains upstream. However, it is obvious that the continuum we describe along relatively small Atlantic Coast rivers, probably has minimal application to extremely large and complex tropical floodplains like along the Amazon, beyond perhaps the likelihood that internal ecological processes and variation in those enormous floodplains are of paramount importance.

The details of human impacts on floodplains will likely also be dictated by unique local conditions and specific management strategies (Brinson and Malvarez 2002), and thus impacts of anthropogenic activity on floodplain biota will be difficult to generalize. However, the continuum we describe may suggest some broad patterns about how human disturbance or management may affect floodplain biota at different

watershed positions (e.g. Hupp et al. 2009; Lee et al. 2016). Because external controls from the river channels and adjacent uplands are so important to headwater and mid-river floodplains, biota in these floodplains may be particularly susceptible to changes in external impacts such as alterations of river flows (dams, levees) or impacts on adjacent upland landscapes (upland soil disturbance, creation of impervious surfaces). In contrast, because internal controls within the floodplain itself are so important to lower-river floodplains, these floodplains may be particularly susceptible to direct alterations of the floodplain such as agricultural or silvicultural development on the floodplain or efforts to drain or fill the floodplain. Efficacious management of biota in fluvial systems should account for the unique and changing factors controlling coupled floodplain-channel habitats along a river's length.

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