Species Distributions on Successional and Flooding Gradients in Connecticut River Floodplain Forests

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Abstract - Floodplain forests provide valuable ecosystem services, yet human activity has degraded many of these riverine systems. Previous investigations of floodplain forest composition have frequently focused on flooding without incorporating successional dynamics; however, their restoration requires understanding both. We investigated floodplain forest composition along both flooding and succession gradients. River meandering builds new floodplain land with a variable microtopography and diverse levels of flood exposure. We compared vegetation to floodplain land ages on chronological sequences. Our results suggest that diverse species assemblages in floodplains result at least in part from geomorphic change. Ensuring that flood pulses continue to erode riverbanks and deposit sediments on sandbars and in floodplains is essential to the restoration and conservation of diverse forest assemblages in these ecosystems.

Introduction

Floodplain forests are a frequent priority for ecological restoration because their ecosystem services are exceptionally valuable; such services include nutrient removal, flood regulation, water supply, and fisheries (Carpenter et al. 2011, Tockner et al. 2008). The high productivity of floodplains may also suit reforestation programs whose aim is mitigating rising atmospheric carbon dioxide concentrations (Dybala et al. 2019, Marks et al. 2020). Unfortunately, floodplain ecosystems have been massively declining in extent and integrity on a national and even global scale (Aishan et al. 2015, Kingsford 2000, Klimo and Hager 2001, Knutson and Klaas 1998, Rood et al. 2005, Stromberg 1993). Threats to floodplain forests include alteration of flow and sediment regimes by dams, levees, channelization, land clearing for agriculture, and urban development (Brinson and Malvárez 2002, Malmqvist and Rundle 2002, Tockner et al. 2008, van Diggelen et al. 2006, Wang and Wang 2016). In response, efforts to restore remnant floodplain ecosystems have been initiated over a wide variety of settings and geographies (Ebert et al. 2009, Hughes et al. 2012, Mondal and Patel 2018, Moss and Monstadt 2008, Opperman et al. 2010, Rood et al. 2005, Stanturf et al. 2000).

Restoration practitioners rely on descriptions of less-altered reference sites when designing restoration prescriptions or when assessing restoration progress (Ruiz-Jaen and Aide 2005, White and Walker 1997). While the study of

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succession at reference sites can offer particularly useful insights because ecosystems are dynamic (Christensen 2014, Pickett et al. 2001, Prach and Walker 2011, Walker and Del Moral 2003, Walker et al. 2007), the succession of floodplain trees has not yet been described in detail for rivers in the New England region of the United States. The goal for this study was to describe the successional sequence in floodplain forests on New England's longest river, the Connecticut River (Fig. 1). The general composition of Connecticut River floodplain forests was first described over a century ago (Nichols 1916), and this research has been updated since then (Bechtel and Sperduto 1998; Holland and Burk 1984; Kearsley 1999a, b). However, information has been lacking on how compositional variation relates to succession. Recent floodplain-forest research on the Connecticut River has focused on quantifying flooding thresholds associated with species distributional limits on variable riparian microtopography (Marks et al. 2014, Metzler and Damman 1985, Nislow et al. 2002). By combining these flooding thresholds with new data on succession, we offer a fuller description of the natural history of Connecticut River floodplain forests, potentially helping guide a growing number of floodplain restoration projects in the region.

Floodplain forest succession begins with plants colonizing on bare sediment surfaces created by geomorphic change (Shankman 1993). Growth of new or existing river bars on riverbanks, in the active river channel, or in abandoned channels provides most of this new land (Gurnell 1997). During extreme flood events, scour can also remove existing vegetation in riparian locations where flows have been especially rapid, such as chutes or abandoned channels (Collins and Schalk 1937). Seedlings on recently colonized bars are especially vulnerable to scour (Edmaier et al. 2011). Consequently, not all incipient floodplain vegetation develops into the subsequent stages of succession.

Geomorphic processes on low-gradient meandering rivers, such as the Connecticut River, tend to follow some general patterns. Within a floodplain, the river's course meanders over time, continually redistributing sediment downstream (Bridge 2003, Leopold et al. 1964). During episodic high flows, sediment is eroded from the outside of river bends, or cutbanks, and deposited downstream on the inside of bends, or point bars. Continual erosion of cutbanks allows opposite point bars to aggrade laterally into the area that was formerly river channel, thereby creating new land for plants to colonize (van de Lageweg et al. 2014). Much of this sediment movement occurs episodically, thereby building a rugged microtopography of small ridges and swales referred to as meander scrolls (Strick et al. 2018). This microtopographic variability tends to persist even as more sediments accumulate over time (Strick et al. 2018). Organic matter can accumulate on the soil surface on higher ground or in backswamps farther from the river channel where there is less sediment deposition (Nanson and Beach 1977, Van Cleve and Viereck 1981). Organic-matter accumulation on the soil surface tends to acidify the soil pH (Nanson and Beach 1977, Van Cleve and Viereck 1981). Alternatively, leaf litter, seeds, and even small seedlings may be buried by inorganic sediments where sediment accretion rates are high, such as on sandbars (Kui and Stella 2016, O'Donnell

et al. 2014, Walker et al. 1986). Species need to quickly develop adventitious roots to survive where sediment accretion rates are high (Hook 1984, Steffens and Rasmussen 2016, Walls et al. 2005), but sediments also provide inputs of alluvial nutrients and cations that ameliorate pH and nutrient availability (Adair et al. 2004, Kreiling et al. 2015, Olde Venterink et al. 2006). Floodplain forest succession consequently unfolds on a heterogeneous relief with contrasting seedbeds and variable flood exposure.

The floodplain forest successional sequence on meandering rivers typically begins with the colonization of pioneers on a point bar (Egger et al. 2015, Salo et al. 1986, Shelford 1954, Walker et al. 1986). Much of what we know about the recruitment of pioneers on bars, however, comes from research on rivers in arid- and semi-arid western North America, where floodplains are generally dominated by only a few tree species, typically *Salix* spp. (willows) and *Populus* spp. (cottonwoods) (Eyre 1980). Research on these floodplain forests has emphasized the critical interactions between the magnitude and timing of the annual flood pulse, water-table recession, and sediment transport and scour in creating conditions suitable for recruitment of these species (Auble and Scott 1998, Harper et al. 2011, Mahoney and Rood 1998). Given that willow and cottonwood seedlings are initially only a couple of millimeters tall, they are highly susceptible to the surface soil drying, destruction by scour, and burial by sediments. This understanding has generated specific recommendations for management of flows and sandbar formation to improve cottonwood recruitment on regulated rivers (e.g., Rood et al. 2005). Nonetheless, it is unclear how much these prescriptions can be generalized to species-rich assemblages characteristic of floodplain forest in climates that are more humid, such as in eastern North America or Central Europe. In these regions, willows and cottonwoods are considered floodplain pioneers that are replaced as succession progresses by species that are more shade-tolerant and have larger seeds (Schnitzler 1995, Shankman 1993, Shelford 1954). Our intent is to describe these shifts in species dominance with succession.

Flooding is likely as important as succession in shaping the composition of floodplain forests. Floodplain inundation in humid climates can be several meters deep and can last for several weeks along the lower reaches of large meandering rivers, such as the Connecticut River (i.e., watersheds over 10,000 km^2 in area; Marks et al. 2014). A striking pattern in such wetter floodplains is species sorting along topographic gradients (Kramer et al. 2008, Sharitz and Mitsch 1993, Wittmann et al. 2010). This observation has led to an emphasis on species differences in flood tolerance (Glenz et al. 2006, Kozlowski 2002, Marks and Atia 2020). The combination of succession and flooding gradients may provide ample opportunities for habitat partitioning among floodplain forest species (Battaglia et al. 2004, De Jager et al. 2019). Specifically, the large microtopographic variability associated with meander scrolls implies that both more- and less-flood–tolerant tree species could survive floods at every successional stage. Here, we combine data on species' flood tolerances from earlier research (Marks et al. 2014) with the description of the successional sequence from the present study to explore this idea.

Site Descriptions

Vegetation

The floodplain forests of the Connecticut River (Fig. 1) are dominated by *Acer saccharinum* L. (Silver Maple; Metzler and Barrett 2006, Sperduto et al. 2011, Thompson and Sorenson 2000). *Ulmus americana* L. (American Elm) was co-dominant with Silver Maple in the canopy prior to the spread of Dutch elm disease (Nichols 1916). On the lower Connecticut River, *Fraxinus pennsylvanica* Marshall (Green Ash) can be another co-dominant floodplain species and *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood) can be important in young stands (Metzler and Barrett 2006). *Matteuccia struthiopteris* (L.) Todaro (Ostrich Fern), *Laportea canadensis* (L.) Weddell (Wood Nettle), and *Onoclea sensibilis* L. (Sensitive Fern) dominate the herb layer (Metzler and Barrett 2006, Sperduto et al. 2011, Thompson and Sorenson 2000). The Silver Maple–American Elm floodplain forest type is widespread, being typical of major rivers from the Great Lakes–Saint Lawrence region in Canada to Missouri and Maryland in the United States (Eyre 1980).

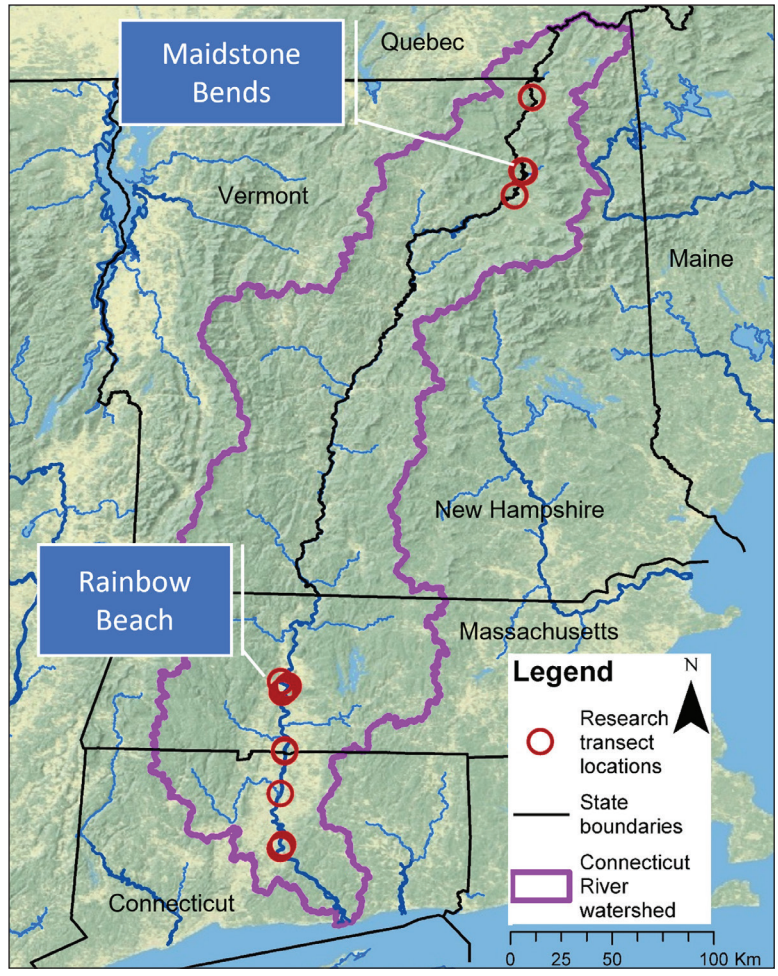

Figure 1. Map of the Connecticut River watershed. Red circles show the locations of the 19 research transects. Some transects are so close to each other that the circles are overlapping. The Maidstone Bends and Rainbow Beach sites where trees were cored to estimate ages are labelled (for a list of sites, see also Supplemental File 1, available online at n28-4-N1921-Marks-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1921.s1).

Climate and flood regime

The 660-km-long Connecticut River flows from north to south (Fig. 1). The temperate climate varies from an average annual extreme minimum temperature of -37.2 to -34.4 °C (USDA plant hardiness zone 3b) in the headwaters to -20.6 to -17.8 °C (hardiness zone 6b) in the tidal estuary (Agricultural Research Service 2012). Average annual precipitation varies from 1000 to 1500 mm/year (NRCC 2021). Winter snowfall accumulates at higher elevations (Green Mountains of Vermont and White Mountains of New Hampshire) and in the northern part of the watershed. Melting of the accumulated snowpack and spring rainfall causes some floodplain inundation in most years. Late summer hurricane rainfall events can cause infrequent larger floods (Jahns 1947, Wolman and Eiler 1958, Yellen et al. 2016).

There are over a thousand dams within the Connecticut River watershed, most of which are obsolete mill dams on small tributaries (Zimmerman and Lester 2006). There are 65 large dams in the watershed that continue to operate for hydroelectric power generation, water supply, and flood control (Zimmerman and Lester 2006). Following major flood disasters on the Connecticut River in 1936 and 1938, the US Army Corps of Engineers built a system of 14 flood-control dams on tributaries (Julian et al. 2015). These flood-control dams have dramatically reduced downstream flooding on the affected tributaries, but their impact on the Connecticut River has been more modest (Marks et al. 2014). On the Connecticut River, the magnitude of large flood flows (10-year return interval flow or greater) has been reduced by about 20% since flood-control operations began, but smaller flow peaks (5-year return interval flow or less) are about the same as before flood control (Marks et al. 2014). Of all the flow metrics, fluvial geomorphologists believe that the 2-year recurrence interval flow contributes the most to geomorphic change because it has enough energy to move ample sediments, yet occurs frequently enough to have a large cumulative effect (Wolman and Leopold 1957). The continuation of the 2-year recurrence interval high flow ensures that the 2 processes that drive floodplain ecology—flooding and geomorphic change—are still functioning in the unimpounded reaches of the Connecticut River.

Geomorphic chronosequences

Where a river meander has migrated in the same direction for many decades, a chronosequence of forest stands is established from pioneer tree saplings on the point bar to progressively older forest stands with increasing distance from the riverbank (e.g., Fig. 2). Indeed, such meander chronosequences have been used to study floodplain forest succession on numerous rivers around the world, including the Mississippi River and its tributaries (Dietz 1952, Hosner and Minckler 1963, Shelford 1954), the Sacramento River in California (Greco et al. 2007), the Amazon River and its tributaries (Foster et al. 1986, Salo et al. 1986), rivers in the temperate coastal rainforest of northwestern North America (Cline and McAllister 2012, Van Pelt et al. 2006), rivers in boreal forests (Nanson and Beach 1977, Van Cleve and Viereck 1981, Walker et al. 1986), rivers on the northern Great Plains of North

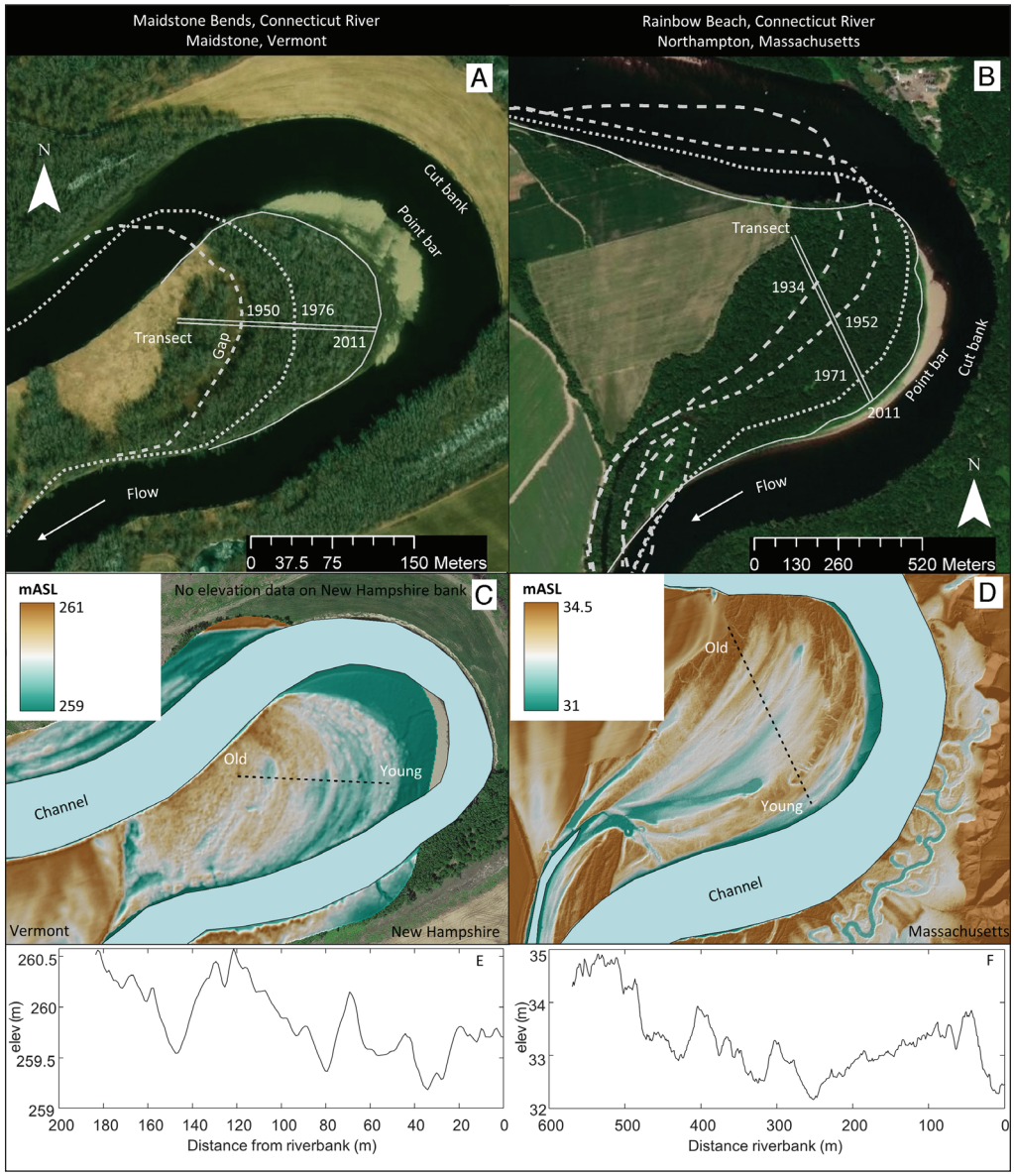

Figure 2. Aerial photos of the northern (Maidstone Bends) and southern (Rainbow Beach) Connecticut River dendrochronology research sites (A and B, respectively). The point bars have expanded in the same direction for decades at an average rate of 2 m/yr at the northern (upstream) site, and 5 m/yr at the southern (downstream) site. White lines with years indicate the locations of the riverbank in the past. Old riverbank locations were mapped in georeferenced historical aerial photos. The double lines show the research transects where trees were cored. Maps of microtopographic relief (C and D) and transect elevation profiles derived from LiDAR-based DEMs (E and F) illustrate the characteristic ridges and swales of meander scrolls. Older parts of the point bar tend to have accumulated more sediments than younger parts closer to the riverbank, but there is much variation.

America (Egger et al. 2015, Everitt 1968, Johnson et al. 1976, Philipsen et al. 2021), and the Kol River in southwestern Kamchatka (Morris et al. 2011).

The chronosequences approach has been criticized in some other contexts for assuming that the communities of the younger locations are currently developing in a temporal pattern that resembles how the older locations developed (Johnson and Miyanishi 2008, Walker et al. 2010). To test if this space-for-time substitution is reasonably accurate in the case of floodplain meander chronosequences, we estimated the age of different parts of the point bar with tree-ring counts of the oldest trees and confirmed it with riverbank locations in historical aerial photographs (Fig. 2). In additon, we used historical aerial photographs to exclude any forests that arose on abandoned fields to avoid land-use legacies confounding the natural successional sequence. We also intentionally excluded sites with avulsions where it would be difficult to order sampling locations chronologically. In total, we included 19 transects from a network of Connecticut River floodplain research sites (Fig. 1; see also Table S1 in Supplemental File 1, available online at n28-4-N1921-Marks-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1921.s1). The research transects that we included are concentrated in reaches on the upper river and on the lower river because that is where most of the remaining floodplain forests are located (Fig. 1). In the middle reaches of the Connecticut River, floodplains have been lost due to a series of hydroelectric dam impoundments as described above.

Methods

Successional sequence

Vegetation data on the 19 chronosequence transects were collected as part of a previously published study (Marks et al. 2014), in which we recorded the species of plants on 6-m-wide belt transects. We recorded all living woody plants with trunks that were at least 10 cm circumference at breast height (1.37 m). We also used the tree-circumference data to analyze structural change over succession. We recorded the dominant herb layer species in a circular area with a radius of 1 m around the base of each tree. The 19 transects analyzed for the present study included a total of 1448 woody plants. A total of 12 tree species and 9 herbaceous species were common enough to plot their distributions on transects. Botanical nomenclature follows the USDA plants database (USDA NRCS 2020). Species distributions on the chronosequences are illustrated with piecewise cubic splines fitted to the occurrence data along the transect. We used the 'smooth.spline' function in the statistical software package R to fit splines (Version 4.0.3; R Core Team 2013). We increased the number of knots in the splines for longer transects so that splines could have multiple abundance peaks, having observed multiple abundance peaks only on long transects and only in some species. We used dates from historical aerial photos to estimate the year that different parts of the transect were first colonized by plants to create chronosequences. We averaged the species abundances over these 19 chronosequences to obtain a generalized representation of the successional sequence.

Tree cores

We collected tree cores and estimated tree ages at 2 of our research sites: a northern site (Maidstone Bends transect 3; 44°36'0.6876"N, 71°32'59.73"W) and a southern site (Rainbow Beach transect 5; 42°19'12.108"N, 72°35'14.1108"W) (Figs. 1, 2). Cores were mounted on wood, sanded, and analyzed under a compound microscope following standard dendrochronology protocols (Speer 2010). We compared the ages of the oldest trees to riverbank locations in historical aerial photos to help validate these ages.

Soil and sediment measurements

We measured soil properties at several locations along each transect. These locations typically included some near the riverbank as well as some further inland (see plots in Supplemental File 1 for soil sampling locations on transects). We fit a logistic curve to these points to model the average effect of distance-to-riverbank on soil properties.

We used the well-established artificial marker horizon technique for measuring sediment accretion in floodplains (Baumann et al. 1984, Cahoon and Turner 1989, Conner and Day 1991, Heimann and Roell 2000, Hupp and Bazemore 1993, Kleiss 1996). Specifically, we spread a thin layer of red potters clay on the soil surface which provides a clear color contrast to the pale beige of Connecticut River sediments. We installed these marker layers between May 2012 and July 2014. We returned to these locations between June 2014 and July 2015. We used the clay as a marker for measuring the thickness of sediments that had accumulated in the intervening time. The thickness divided by the number of days and multiplied by 365 gives the average annual sediment accretion rate. The sediment accretion measurements are representative of most years because the annual peak flows during this period were below the 5-year recurrence interval flow (US Geological Survey 2015). With an average annual sediment yield of roughly 30 T/km^2/year (Patton and Horne 1992), the Connecticut River is relatively sediment rich compared with other rivers in New England (Yellen et al. 2014). However, sediment yield is variable in the region, but generally low compared to tectonically active areas (Milliman and Farnsworth 2013).

We collected samples at each soil measurement location during the summer field season. We took samples from the top 1-cm layer of soil. We excluded any fresh litter on top of the soil from the sample. We dried and weighed samples in the laboratory. We approximated soil organic matter by loss-on-ignition (LOI), a measure of percent reduction of dry sample mass after combustion for 4 hours in a 550 °C oven (Dean 1974). We wet-sieved the remaining mineral soil to determine various measures of texture. Here we report only the percent fines (i.e., particles < 0.0625 mm) because all the measures of texture were highly correlated.

Flooding gradients

Species distribution limits on flooding gradients were estimated in a previous study of Connecticut River floodplain forests (Marks et al. 2014). To avoid statistical problems with taking the most extreme individual, the distribution limit was

estimated by the individual tree in the 90th percentile instead (i.e., the wet end of the distribution). Survival rates in experiments that completely submerged seedlings for varying durations explained over 90% of the variance in these distribution limits (Marks and Atia 2020). It appears that the combination of depth and duration of flooding determines seedling flood survival (Marks and Atia 2020). In the field, depth and duration of flooding are correlated because they are both related to elevation. We are reporting depth of flooding during the 2-year recurrence interval flood because depth is easier to map than duration. The stage of the 2-year recurrence interval flood is a standard reference elevation used by fluvial geomorphologists.

Results

The chronosequences on the upper and lower Connecticut River reveal similar successional sequences (compare Figs. 3 and 4). On the upper river, *Salix eriocephala* Michx. (Heart-leaved Willow) and *Salix nigra* Marsh. (Black Willow) are first, followed by *Acer negundo* L. (Boxelder), Eastern Cottonwood, Silver Maple, American Elm, *Fraxinus nigra* Marsh. (Black Ash), and *Juglans cinerea* L. (Butternut). On the lower river, Heart-leaved Willow and Black Willow are first, followed by Eastern Cottonwood, Silver Maple, American Elm, Green Ash, Boxelder, and *Quercus palustris* Münchh (Pin Oak). The main difference between these sequences is that Green Ash is replaced by Black Ash on the upper river. Another difference is that Boxelder tended to occur in the pioneer stage on the upper

Figure 3 (see following page). Summary of successional trends in floodplain forest chronosequences at the northern research sites on the Connecticut River (see Supplemental File 1 for individual site data). Trends in tree diameter at breast height (DBH) and tree density are plotted in panel A. Logarithmic functions are fitted to the soil data in panel B. Soil data include sediment accretion rate (Sed. accre.), and the percentages of fines (Fines) and organic matter (Org.). The relative abundances are approximated by the frequency of trees of that species. Cubic splines were fitted to the species data to illustrate their changing abundance over time (C–E). Full names of species are included in the text (see also Table S2 in Supplemental File1). The average soil elevation relative to the stage of the 2-year recurrence interval flood is plotted in panel F (Rel. elev.). We chose that stage because it is a benchmark for generalizing across sites that is commonly used by fluvial geomorphologists.

Figure 4 (see page 587). Summary of successional trends in floodplain forest chronosequences at the southern research sites on the Connecticut River (see Supplemental File 1 for individual site data). Trends in tree diameter at breast height (DBH) and tree density are plotted in panel A. Logarithmic functions are fitted to the soil data in panel B. Soil data include sediment accretion rate (Sed. accre.), and the percentages of fines (Fines) and organic matter (Org.). The relative abundances are approximated by the frequency of trees of that species. Cubic splines were fitted to the species data to illustrate their changing abundance over time (C–E). Full names of species are included in the text (see also Table S2 in Supplemental File1). The average soil elevation relative to the stage of the 2-year recurrence interval flood is plotted in panel F (Rel. elev.). We chose that stage because it is a benchmark for generalizing across sites that is commonly used by fluvial geomorphologists.

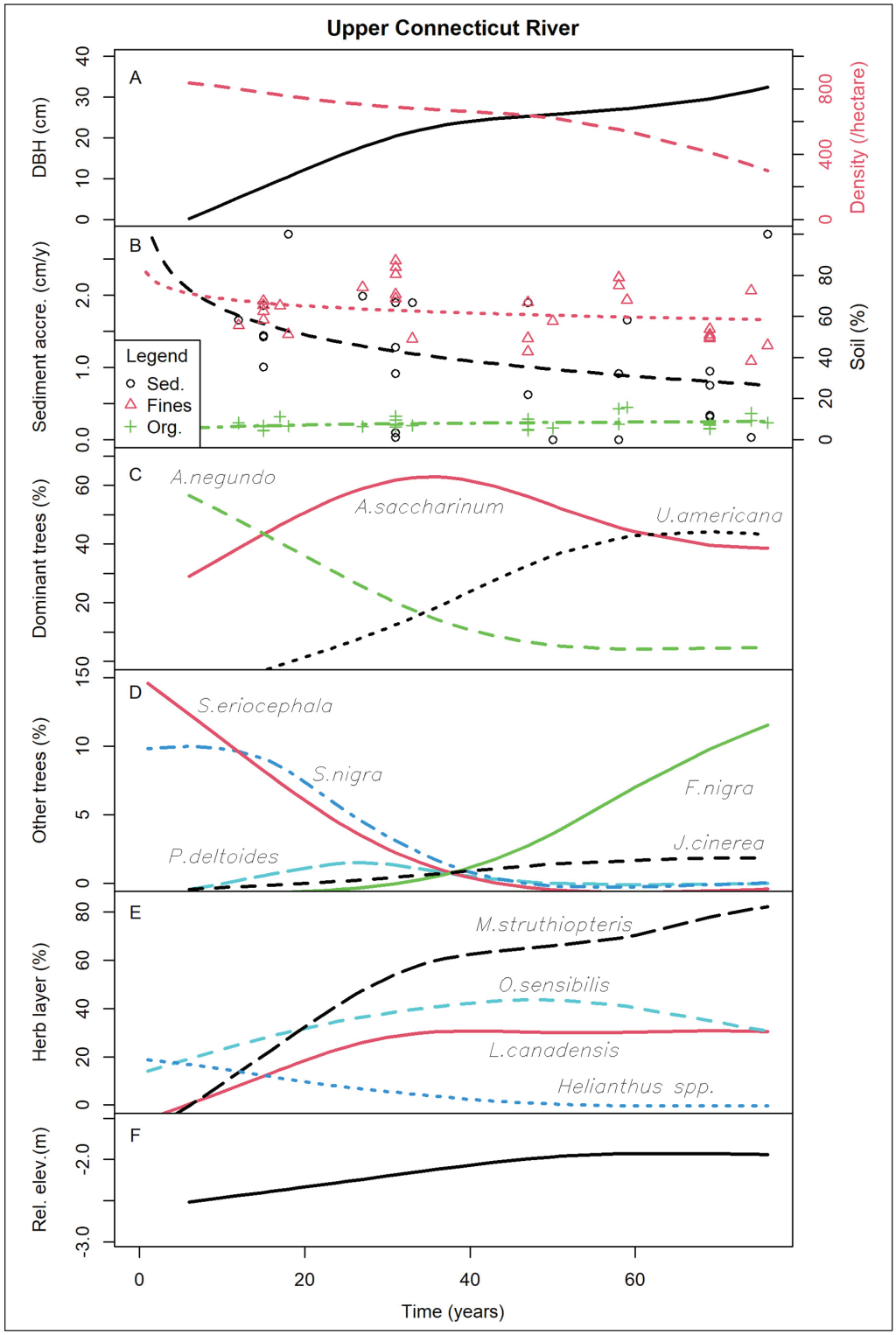

Figure 3. [Caption on preceding page.]

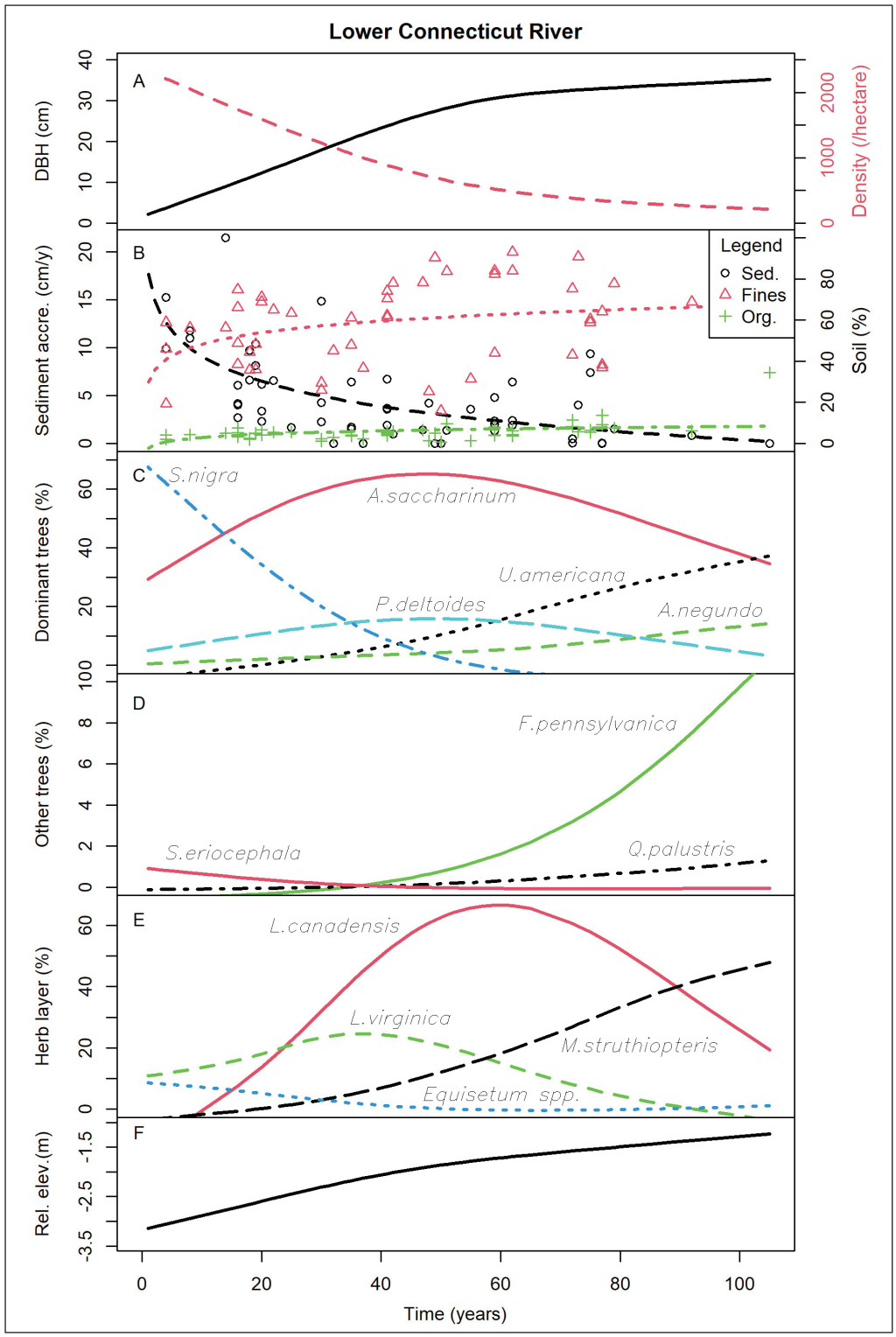

Figure 4. [Caption on page 585.]

river, whereas on the lower river, it was more typical as a canopy gap colonizer late in succession. However, at some sites on the lower river, Boxelder also occurred during the pioneer stage (see Figs. S1.10 and S1.11 in Supplemetnal File 1) and at some upper river sites, it also occurred as a gap colonizer late in succession (see Figs. S1.4 and S1.5 in Supplemental File 1). Thus, Boxelder appears to have a bimodal distribution on both the upper and lower river. Although Butternut was not recorded on research transects on the lower river, we have observed Butternut as a canopy gap colonizer on the lower river. Butternut is a relatively rare floodplain tree species and therefore liable to be missed by research transects. Similarly, *Quercus bicolor* Willd. (Swamp White Oak) is relatively rare. When we observed Swamp White Oak, it consistently occurred together with the more common Pin Oak. The ranges of neither of these oaks extends sufficiently far north to occur on the upper Connecticut River. Similarly, Eastern Cottonwood is relatively rare on the upper river, but when found there, occurs at the same point of succession as on the lower river.

The dendrochronology results from the upper Connecticut River site (Maidstone Bends) and the lower Connecticut River site (Rainbow Beach) confirm the successional sequence from the chronosequences, although with more variability (Fig. 5). At a given distance from the riverbank, one can read the successional sequence in the plot (Fig. 5) from the oldest trees at the bottom to progressively younger trees vertically above it. Reading the plots in this way reveals that the initial wave of pioneer recruitment occurs over about a decade. The pioneer wave includes Black Willow, Boxelder, Eastern Cottonwood, and Silver Maple. Willows are short-lived and disappear once the more shade-tolerant Silver Maple becomes dominant in the canopy. Therefore, the parts of the transect further from the riverbank where pioneer recruitment started more than 35 years ago typically do not have any Black Willow left that could be cored because they would have died already. By contrast, Eastern Cottonwood persists longer but only as emergent trees above the Silver Maple canopy (i.e., Eastern Cottonwood is older than Silver Maple at any given point on the transects in Fig. 5). American Elm, Green Ash, and Black Ash recruit later in the forest understory and over a much longer period than the initial wave of pioneer recruitment.

Forest structure also changes predictably over floodplain succession (Figs. 3A, 4A). Initially dense stands of pioneer tree seedlings gradually thin out as they grow larger. These dense stands allow little light to reach the ground thereby suppressing recruitment of new tree seedlings. As the pioneer trees mature, they gradually allow more light to reach the understory. The thickest Silver Maple trees at these research sites have trunk diameters >1.5 m, and the tallest Eastern Cottonwood trees are over 40 m in height. When these large pioneer trees die, they create large canopy gaps with high light availability. These changes in structure with successional stage are easy to recognize in the forest (Fig. 6; also see photos in Supplmental File 1).

The herb layer is more variable among transects but still follows a predictable sequence (Figs. 3D, 4D). A few patches of tall wildflowers such as *Helianthus decapetalus* L. (Thin-leaved Sunflower) occur in full sunlight on the point bar by

the riverbank, but most of the sandbar is bare of herbaceous vegetation. A grass species, *Leersia virginica* Willd. (Whitegrass), is common in the forest understory early in succession on the lower Connecticut River. It is followed by Wood Nettle

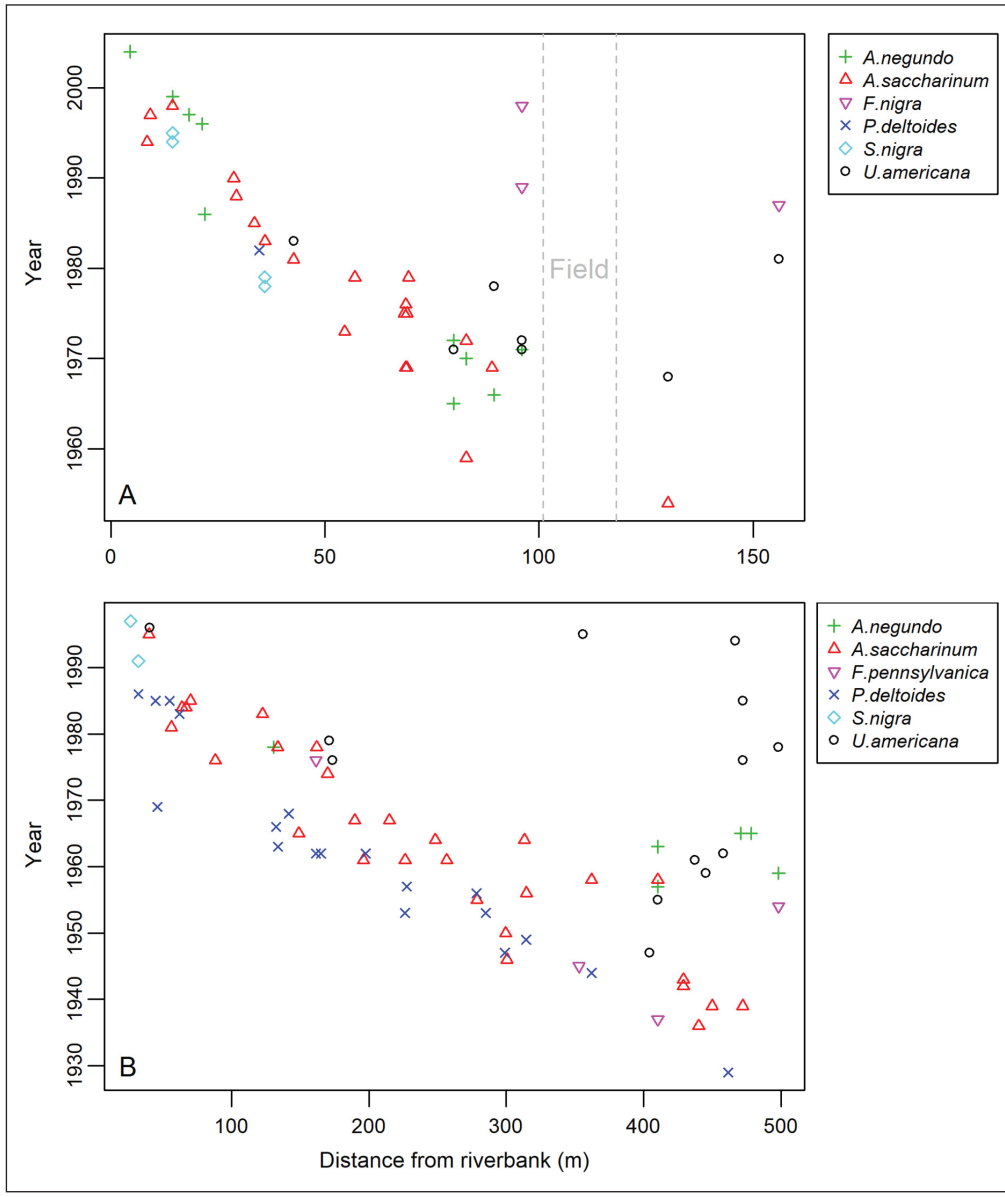

Figure 5. Plots of estimated tree recrutiment year and its location along the chronosequence from the riverbank on the left to older surfaces on the right for a more northern Connecticut River site, Maidstone Bends (A) and a more southern Connecticut River site, Rainbow Beach (B). Associated with the latitudinal difference in climate is a change in *Fraxinus* (ash) species. Each dot represents a single tree that was cored. The Maidstone Bends transect includes a gap where it crosses a narrow field before continuing into an older patch of floodplain forest (see aerial photo in Fig. 2).

and Ostrich Fern, which are usually co-dominant in most of the herb layer, but Ostrich Fern tends to be later in succession than Wood Nettle. Sensitive Fern is also common, but does not appear to follow a pattern with respect to succession. We observed that Sensitive Fern tends to be associated with swales that may be too wet for Wood Nettle and Ostrich Fern.

Soil formation also followed some repeatable trends, but soil properties and microtopography were variable at all stages of succession. Specifically, lateral channel migration and point-bar growth are episodic, which builds a highly variable meander scroll topography (Fig. 2 CD, D). If one averages this variability out over multiple transects, some consistent trends in soil properties emerge (Figs. 3, 4). Specifically, the sediment-accretion rate was highest on the point bar (>10 cm per year in some willow-dominated locations on the lower Connecticut River) and tended to decrease with increasing distance from the riverbank (Figs. 3B, 4B). Most of this decline occurs within the first few meters. The average soil elevation tended

Figure 6. Photos of Connecticut River floodplain forests to illustrate the stages of succession as follows: stand initiation (A), stem exclusion (B), understory re-initiation (C), and old growth (D). (See Supplemental File 1 for additional photos that illustrate the successional stages in Connecticut River floodplain forests with more detailed descriptions.)

to increase with age of the floodplain location as sediments accumulate (Figs. 3F, 4F), but there was much microtopographic variability around this average elevation (Fig. 2E, F). Sediment texture (% fines) did not show a consistent trend with distance from the riverbank (Figs. 3B, 4B). The point bar initially consisted of mostly inorganic sediments. Leaf litter was buried in these locations by high rates of sediment deposition. Where there is less sediment deposition, organic matter can gradually accumulate on the soil surface. Consequently, trajectories of sediment accretion rate and organic matter on the soil surface followed opposite trends (Figs. 3B, 4B).

These consistent results from the chronosequences and dendrochronology data allowed us to summarize a general successional sequence for Connecticut River

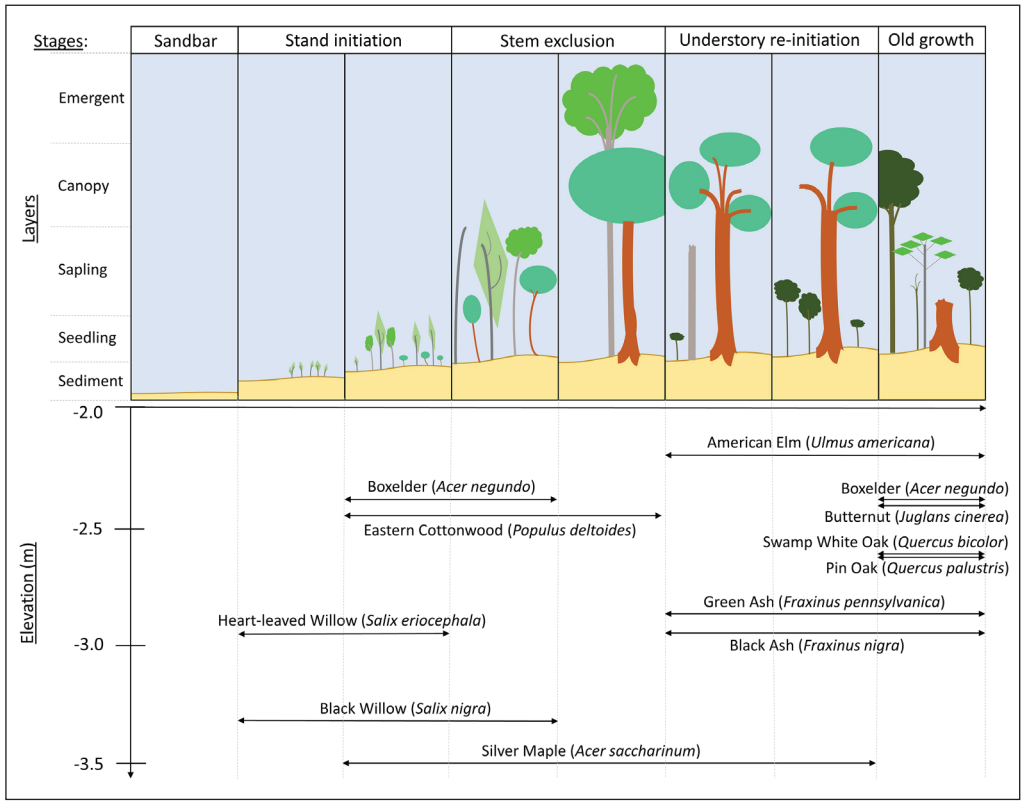

Figure 7. Diagram illustrating the generalized succession sequence observed in Connecticut River floodplain forests from left to right. The species lower elevation-distribution limit on riparian microtopographic gradients is measured relative to the 2-year recurrence interval flood peak. For example, the water depth at the lowest elevation for Silver Maple trees is 3.5 m during the 2-year recurrence interval flood peak whereas that depth is only 2.19 m at the lowest elevation for American Elm trees. Duration of flooding is also correlated with these elevations. The stage of the 2-year recurrence interval flood has the advantage that it is easier to calculate and map than flood duration. The successional sequence is a synthesis of the chronosequence species abundance data (Figs. 3, 4). The sequence was further validated by the dendrochronology data (Fig. 5). Note that, Pin Oak, and Swamp White Oak do not occur on the colder upper Connecticut River, and Green Ash is replaced by Black Ash.

floodplain forests (Fig. 7). The diagram divides succession into the following 4 general physiognomic stages that were first developed as a model to describe succession in various North American upland forest types (Oliver 1980): (1) "stand initiation" when trees first colonize the newly opened up space after a major disturbance, (2) "stem exclusion" when the canopy closes and intense competition for light reduces the density of stems in the stand, (3) "understory reinitiation" when mature overstory trees let enough light through to the forest floor for tree seedlings of shade tolerant species to establish, and (4) "old growth" when individual overstory trees die thereby creating canopy gaps which allow recruitment of younger trees with a variety of shade tolerances. We also plotted the species distributional limitations on flooding gradients in this diagram to illustrate how local microtopographic differences and the accumulation of sediments might affect the successional sequence.

Discussion

Floodplain forest succession on Connecticut River meanders has a predictable sequence (Fig. 7), as follows: (1) a stand-initiation stage when pioneers such as Heart-leaved Willow, Black Willow, Eastern Cottonwood, Boxelder, and Silver Maple colonize new sandbars in full sunlight;(2) a stem-exclusion stage wherein dense stands of young, fast-growing pioneers gradually thin out; (3) an understory re-initiation stage when seedlings of species that are more shade tolerant such as American Elm, Green Ash, and Black Ash recruit in the understory; and (4) an old-growth stage when large canopy gaps form as the now huge pioneer trees start breaking apart and dying. The structural diversity and associated variable light availability in the old-growth stage allows both shade-tolerant species such as American Elm and shade-intolerant, gap-colonizer species such as Butternut to recruit, thereby increasing the species diversity. Coexistence of diverse species is further promoted by topographic relief that provides habitat for both species that are more flood tolerant species (e.g., Black Willow, Silver Maple, Green Ash, Pin Oak) and less flood tolerant (e.g., Eastern Cottonwood, Boxelder, American Elm, Butternut) at every stage of succession (Fig. 7). If sediment accumulation has raised the elevation of the soil surface and reduced flood exposure, succession progresses toward American Elm, which is less flood tolerant but more shade tolerant. Alternatively, where there has been little sediment accretion, succession proceeds toward species that are more flood tolerant but less shade tolerant, such as Green Ash and Pin Oak. Thus, variation in flooding severity over time and among different microtopographic positions can modify the successional sequence.

Recruitment in the stand-initiation stage tends to be in the following order: willows first, followed by Eastern Cottonwood, Boxelder, and Silver Maple. Differences in microtopographic relief among locations and flooding among years can favor recruitment and survival of Black Willow and Silver Maple (both more flood tolerant) or Eastern Cottonwood and Boxelder (both less flood tolerant). Species differences in flood tolerances interact with species differences in timing of seed dispersal (Dixon 2003, Merritt and Wohl 2002, Niiyama 1990). Boxelder and

Silver Maple seeds disperse earlier in the spring than Black Willow and Eastern Cottonwood seeds (C.O. Marks, unpubl. data). Seed dispersal that coincides with the recession of floodwaters favors successful recruitment (Auble and Scott 1998, Harper et al. 2011, Mahoney and Rood 1998). Floodwaters recede later from lower floodplain surfaces. Since younger land is often lower in elevation (Figs. 3F, 4F), the later dispersal of willow and cottonwood favors their recruitment on the newest land. Variable seedling survival of subsequent flooding and scour can modify the composition of patches of young pioneer seedlings on bars (Dixon 2003, Friedman and Auble 1999, Wintenberger et al. 2019). Despite this variability in pioneer seedling recruitment and survival, Black Willow and Eastern Cottonwood tend to precede Silver Maple and Boxelder in the succession sequence (Figs. 3–5). Black Willow and Eastern Cottonwood can only establish on bars if they arrive prior to Silver Maple and Boxelder because Black Willow and Eastern Cottonwood have extremely low shade tolerance (Burns and Honkala 1990). Even where Black Willow and Eastern Cottonwood succeed in colonizing bars ahead of Silver Maple and Boxelder, their presence may be short lived if *Castor canadensis* Kuhl (North American Beaver) settle at the site because Beavers preferentially cut and consume salicaceous species (Marks and Canham 2015). This precariousness of Black Willow and Eastern Cottonwood recruitment may help explain the widespread dominance of Silver Maple in Connecticut River floodplain forests.

The typical succession sequence in Connecticut River floodplain forests at the level of genera (*Salix* [willow]–*Populus* [poplar]–*Acer* [maple]–*Ulmus* [elm]–*Fraxinus* [ash]–*Quercus* [oak]) has been observed across a wide range of floodplain-forest studies and locations. This order of succession appears to be characteristic wherever the Silver Maple–American Elm floodplain forest type occurs in northeastern North America (Eyre 1980). Examples include the Allegheny River in Pennsylvania (Cowell and Dyer 2002), the Wabash River in Indiana (Phillippe and Ebinger 1973), and the Upper Mississippi River and its tributaries (Barnes 1997, Curtis 1959, Hosner and Minckler 1963). On the Missouri River in the Dakotas, the successional sequence is the same, except that Silver Maple and Pin Oak do not occur that far west (Johnson et al. 1976, Wilson 1970). The sequence will be familiar to European floodplain ecologists as well, given floodplain forest succession in Central Europe follows a similar sequence of genera, except that it is missing the *Acer* (maple) phase (Carbiener and Schnitzler 1990, Karpati and Toth 1961, Loiseau 1997, Margl 1973, Passarge 1956, Schnitzler 1995). Succession in southeastern North American floodplain forests also follows this general sequence, but with additional genera such as *Liquidambar* (sweetgum), and more species of ash, elm, and especially oak in the old-growth stage (Robertson and Augspurger 1999, Shankman 1993, Shelford 1954). This resemblance at the generic level suggests that floodplain succession in the northern hemisphere was likely already similar when the deciduous forest floras of Europe, Asia, and North America became separated.

Non-native pests and pathogens are now threatening ash and elm species in both North America and Europe. Dutch elm disease has reduced survival rates of elm trees on the Connecticut River to the point where they now rarely live long

enough to reach the forest canopy (Marks and Canham 2015). The recent invasion of *Agrilus planipennis* Fairmaire (Emerald Ash Borer) is threatening to do the same to ash trees (Knight et al. 2013). Butternut is also declining due to Butternut canker disease (Schlarbaum et al. 1998). The demise of these genera could alter the structure and composition of late-successional floodplain forests in northeastern North America. The development of disease-tolerant selections of American Elm and the release of biological controls of Emerald Ash Borer could help reverse the decline (Duan et al. 2012, Townsend et al. 2005). Restoration of floodplain forests in northeastern North America will thus need to consider holistic approaches that emphasize both physical factors, such as flooding and sedimentation, as well as biotic factors, such as invasions by non-native species.

Periodic flooding and associated bank erosion and sediment deposition are critical to maintaining distinct and diverse floodplain forests on large meandering rivers (Dufour et al. 2015, Florsheim et al. 2008, Shankman 1993, Wohl et al. 2015). Sporadic deposition of sediments by floods builds an uneven floodplain microtopography and new sandbars needed for the recruitment of pioneers. Riverbank location change in georeferenced historical aerial photographs of Connecticut River floodplain forests provide a first estimate of an average bank migration rate of at least 1.30 m/year for sites where Black Willow is more likely to occur than not occur, and 0.58 m/year for Eastern Cottonwood sites (C.O. Marks, unpubl. data). Population declines in floodplain pioneers, such as Black Willow and Eastern Cottonwood, have been reported from numerous regulated rivers in northeastern North America (Barnes 1997, Cook 2005, Hale et al. 2008, Johnson et al. 2012, Johnson and Waller 2012, Knutson and Klaas 1998), including the Connecticut River (Marks and Canham 2015). Ensuring that the twin drivers of geomorphic change, lateral channel migration and flooding, are not hindered by riverine development, such as dams, levees, channel straightening, and riverbank hardening, is necessary to sustain diverse floodplain forest assemblages that include pioneer species.

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