



# Variation in Tree Growth along Soil Formation and Microtopographic Gradients in Riparian Forests

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## Abstract

Policy makers are interested in managing forests to store carbon. Optimizing this strategy requires understanding how carbon storage varies across environmental gradients. We explored variation in tree growth rate, tree longevity, and surface soil organic matter across 135 Connecticut River riparian forest plots. Tree growth rate did not vary significantly with climate but rather increased with sediment accretion rate, soil pH and decreased with plot elevation, where elevation was measured relative to the stage of the 2-year flood. By contrast, surface soil organic matter was negatively related to pH and tree growth rate. Tree species longevity were greater at higher elevations with coarser soils. The faster growth rates at lower elevations allow for restoring forest structure rapidly, whereas flood intolerant but longer-lived tree species allow more durable carbon sequestration at higher elevations. The close associations of growth rate, sediment accretion, and pH suggest that riverine nutrient inputs are important to maintaining the exceptionally high productivity of floodplains. Environmental assessments of river dams should consider impacts of intercepting sediments and reducing flooding on downstream floodplain fertility and productivity. Restoration of riparian locations with high deposition of sediments and associated nutrients may be an opportunity to maximize both nutrient and carbon sequestration.

**Keywords** Alluvial soils · Bottomland forest · Carbon sequestration · Floodplain forest · Productivity · Sediment accretion rate · Soil fertility · Soil organic matter

## Introduction

Forest restoration has been proposed as a strategy to help mitigate rising atmospheric carbon dioxide (CO<sub>2</sub>) concentrations (Canadell and Schulze 2014; Griscom et al. 2017), and several countries have already made ambitious reforestation pledges under the United Nations Environment Program's

Bonn Challenge and the New York Declaration on Forests (UN Climate Summit 2014). Initial research on this conservation strategy has focused on mapping the land that could be reforested around the globe (Nave et al. 2018; Bastin et al. 2019). The potential for restored forests to capture carbon dioxide from the atmosphere varies by forest type and geographic setting, which implies a need to prioritize sites for

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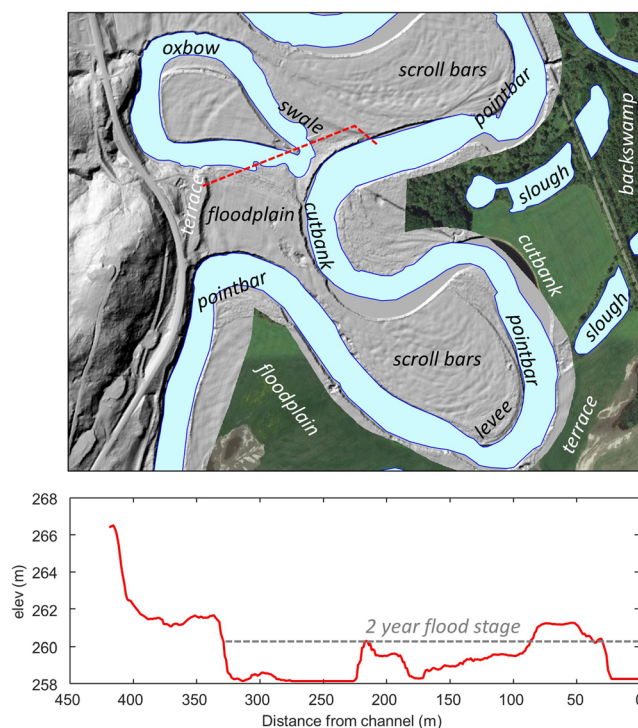
forest restoration (Hoover and Smith 2012). Knowing how forest carbon sinks vary along environmental gradients can help inform such strategic planning in the next stage of developing forest carbon sequestration as a conservation strategy (Hoover and Smith 2012). The response of forest productivity to topographic gradients has been investigated in uplands (e.g. Fralish et al. 1978; McNab 1993; Bolstad et al. 2001; Takyu et al. 2003; Homeier et al. 2010; Smith et al. 2016; Reed and Kaye 2020), but has received less attention in floodplains and other riparian forests.

Floodplains are attractive locations for enhancing ecosystem carbon storage through reforestation because floodplain forests combine high productivity with other valuable ecosystem services such as flood attenuation and improvement of water quality (Dybala et al. 2019). Further, the continual burial of organic matter by repeated sedimentation events allows for long-term carbon storage (Ricker et al. 2013; Bätz et al. 2015; Ricker and Lockaby 2015; Scott and Wohl 2018; Hupp et al. 2019). Indeed restoration of floodplains and riparian forest buffers is already a conservation priority in many countries such as under Brazil's Forest Code (Soares-Filho et al. 2014), the European Habitats Directive (Hughes et al. 2012), or the Natural Resource Conservation Service's incentive programs in the United States (Cox 2006).

Three key measures of forest carbon storage are tree growth rates, tree longevities, and soil organic matter (SOM). Tree growth rates and SOM are important because tree boles and the soil are the largest carbon pools in forests (Gough et al. 2008; Fahey et al. 2010). Tree longevity is also important because it regulates when a planted forest transitions from sequestering carbon in growing trees to releasing carbon from decomposing trees (Körner 2017; Büntgen et al. 2019). Our goal is to explore the broad patterns of covariation among these three dimensions of forest carbon sequestration along soil formation and microtopographic gradients in riparian forests to help prioritize sites for reforestation.

Topographically diverse riparian landforms are built by spatially and temporally variable rates of erosion and sediment deposition (Bridge 2003; Ellery et al. 2003; Steiger and Gurnell 2003; Heitmuller et al. 2017). On meandering lowland rivers such as the Connecticut River in northeastern North America, frequently flooded landforms include floodplains, channel bars, point bars, oxbow lakes, meander scrolls, swales, levees, sloughs, and backswamps (Fig. 1, top panel). Riparian areas also include higher terraces and lower hill slopes that rarely or never flood. Flooding varies with elevation across this topography (Fig. 1, bottom panel).

Flooding and sediment deposition or lack thereof might affect carbon sequestration via several pathways. Flood stress could reduce tree growth directly (Kozlowski 1984; Burke and Chambers 2003; Kreuzwieser et al. 2004), but floodwaters also contain dissolved nutrients that could ultimately enhance growth. Still more nutrients may be adhering to silt



**Fig. 1** Example of diverse riparian landforms on the Connecticut River in Maidstone, Vermont (top panel) illustrated with hillshaded LiDAR in grey. Vegetation is shown in green with an aerial photo. A cross-section illustrating some of the topographic variability from the dashed line is illustrated with the red line (bottom plot)

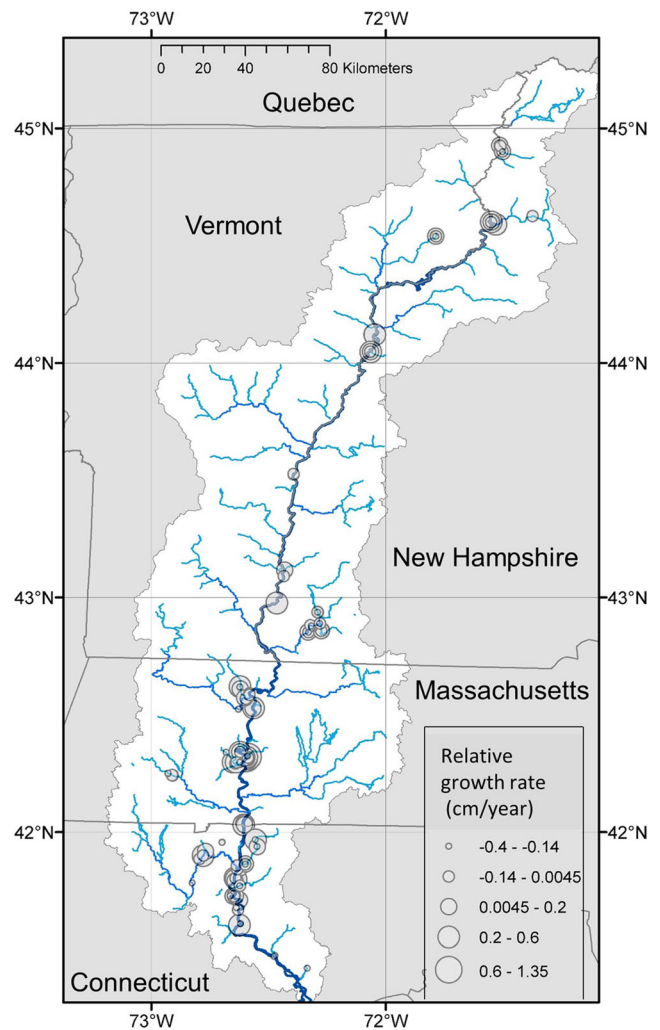
particles in sediment deposits (Kronvang et al. 1998; Steiger and Gurnell 2003; Adair et al. 2004; Olde Venterink et al. 2006; Kronvang et al. 2009; Kroes et al. 2015; Noe et al. 2019). High rates of sediment deposition also affect soil organic matter (SOM) because leaf litter and other organic matter will be buried under sediments thereby enhancing carbon sequestration in the deep soil (Ricker et al. 2013; Ricker and Lockaby 2014; Bätz et al. 2015; Ricker and Lockaby 2015; Scott and Wohl 2018; Hupp et al. 2019). By contrast, where sediment accretion rates are low, organic matter mainly accumulates in an O-horizon above the mineral soil, as is typical of upland forests (Binkley and Fisher 2013). This accumulation of carbon in an O-horizon sequesters carbon but it can reduce tree growth rates over time because the nutrients that are tied up in undecomposed organic matter are unavailable for new plant growth (Gower et al. 1996; Prescott et al. 2000). For example, the rate of nitrogen mineralization from plant litter is closely related to forest productivity (Pastor et al. 1984; Reich et al. 1997; Schuur et al. 2001; Takyu et al. 2003; Wolf et al. 2011). Riparian landforms that rarely or never flood may also lose fertility due to nutrient leaching (Gaines and Gaines 1994; Crews et al. 1995; Richardson et al. 2004; Wardle et al. 2004). However, fine-textured soils are less susceptible to nutrient leaching than coarse soils because clay and silt particles more strongly bind nutrients to their surfaces than sand particles (Binkley and Fisher 2013). These possible

relationships of tree growth rates with flooding, soil texture, SOM, and sediment accretion rate are based on assumptions about how nutrients move through riparian ecosystems.

An alternative hypothesis is that riparian tree growth rates are limited more by climate than by soil fertility. Although climate is the best predictor of productivity at continental scales (e.g. Schuur 2003; Running et al. 2004; West 2020), it is still unclear how much variation in productivity can be explained by climate at smaller spatial scales. Productivity may also be less responsive to climate in riparian forests than in upland forests because riparian trees sometimes have access to alluvial groundwater which could reduce their dependence on rainfall (Kolb et al. 1997; Rood et al. 2003).

Maximizing forest productivity may be at odds with maximizing the durability of the forest carbon sink. As forests age, they eventually reach a point when dead and dying trees release as much or more carbon as is being taken up by growing trees (Körner 2017; Büntgen et al. 2019). When this point is reached depends on tree longevity. Unfortunately, there may be a tradeoff between growth rate and tree longevity because traits that increase longevity such as defense against decay require diverting resources from growth (Loehle 1988; Wright et al. 2010; Stephenson et al. 2011; Reich 2014; Marks and Canham 2015; Büntgen et al. 2019). Differences in how tree growth rates and longevity respond to environmental gradients is thus of importance to managing forests for carbon sequestration.

Our objectives for the present research include the following: 1) explore the broad patterns of how tree growth rate, longevity, and SOM vary along environmental gradients in riparian forests, 2) link these patterns to processes such as flooding and sediment deposition that have been altered on regulated rivers, 3) provide insights for optimizing forest management strategies for carbon sequestration. Specifically, we explored patterns of covariation among tree growth rate, longevity of species, and soil properties in 135 research plots in riparian forests distributed throughout the Connecticut River watershed (Fig. 2). We expected tree growth rates to be positively related with minimum temperature, soil pH, percent soil fines, flooding, and sediment accretion rate. By contrast, we expected to find a negative correlation between surface SOM and productivity which could indicate a potential tradeoff in maximizing sequestration in these two forest carbon compartments. Likewise, we expected to find a tradeoff between growth rate and tree longevity. Optimizing tree planting and forest management plans for carbon sequestration will need to carefully consider potential tradeoffs among maximizing different aspects of forest carbon storage. Our results point to the coincidence of high tree growth rates, deep burial of organic matter, and high rates of alluvial nutrient inputs in riparian locations that have high rates of sediment accretion. These riparian locations may be an opportunity for restoring a frequently degraded habitat that also maximizes both carbon sequestration and nutrient sequestration rates.



**Fig. 2** Map of Connecticut River watershed showing the locations of the 135 riparian forest research plots. The size of the symbols is proportional to the average relative growth rate of trees on the plot. Notice that the local variation in growth rate along edaphic and microtopographic gradients is greater than the regional variation along climatic gradients. The greater sampling on parts of the mainstem Connecticut River reflects the greater extent of floodplains in those reaches

## Methods

### Study Area

The 660 km long Connecticut River mainstem is a 7th order river when it enters Long Island Sound. Its 28,000 km<sup>2</sup> watershed has a cold temperate climate with annual extreme minimum temperatures that range from  $-37^{\circ}\text{C}$  (USDA plant hardiness zone 3b) in the headwaters to  $-21^{\circ}\text{C}$  (hardiness zone 6b) in the tidal estuary (Agricultural Research Service 2012). Average annual precipitation varies from 1000 to 1500 mm/year, a substantial fraction of which falls as snow, especially in the headwaters and at higher elevations. In most years, the Connecticut River experiences a snowmelt-driven spring freshet that brings floodwaters and sediments onto

floodplains (Marks et al. 2014). Less frequent larger floods are associated with late summer and early fall hurricane rainfall events (Jahns 1947; Wolman and Eiler 1958; Yellen et al. 2014). The pH of soils and sediments can vary depending on the parent materials. The eastern tributaries of the Connecticut River drain watersheds that have relatively acidic parent materials and coarser textured soils, whereas some of the western tributaries have watersheds with more calcareous parent materials, particularly those draining the Waits River Formation in Vermont (US Geological Survey 2015a).

The tree species that is most frequently dominant in Connecticut River floodplain forests is *Acer saccharinum* L.. Other important floodplain tree species in the watershed include *Acer negundo* L., *Fraxinus pennsylvanica* Marsh., *Populus deltoides* Bartram ex Marsh., *Platanus occidentalis* L., *Quercus bicolor* Willd., *Quercus palustris* Münchh., *Salix nigra* Marsh. and *Ulmus americana* L. (Kearsley 1999; Thompson and Sorenson 2000; Metzler and Barrett 2006; Sperduto and Kimball 2011). At higher floodplain elevations, where flooding is infrequent and generally less than 1 day in duration, there is a transition from these floodplain tree species to upland tree species (Marks et al. 2014). Upland tree species that can be dominant in Connecticut River Valley forests include the following: *Abies balsamea* (L.) Mill., *Acer rubrum* L., *Acer saccharum* Marsh., *Betula lenta* L., *Fagus grandifolia* Ehrh., *Pinus strobus* L., *Prunus serotina* Ehrh., *Quercus rubra* L., and *Tsuga canadensis* (L.) Carrière (Thompson and Sorenson 2000; Metzler and Barrett 2006; Sperduto and Kimball 2011). There are also some tree species that thrive in the rich alluvial soils with limited flooding in the transition zone, which include *Carpinus caroliniana* Walter, *Carya cordiformis* (Wangenh.) K. Koch, *Carya ovata* (Mill.) K. Koch, *Celtis occidentalis* L., *Juglans cinerea* L., *Tilia americana* L., and *Ulmus rubra* Muhl. (Marks et al. 2014). Species differences in flood tolerance promote coexistence of this wide array of species (Marks & Atia, in this special feature of *Wetlands*), which makes floodplain forests some of the most species rich forests in the Connecticut River watershed.

## Data Collection

In the tradeoff between expending research effort on greater accuracy at a few sites versus greater generality across many sites, most past studies of floodplain forest productivity have opted for accuracy. Instead, we needed a dataset that includes many plots even if measurements were not as detailed as possible because our goal was to describe the broad patterns of covariation among tree growth rates, tree species longevities and soil properties. To that end, our study took advantage of prior research on the Connecticut River which established 234 belt transects that traversed the topographic relief from riverbanks and bars through the floodplain forest into the adjoining upland forest at 103 research sites (Marks et al. 2014; Marks

and Canham 2015). Sites were selected to encompass a broad range of floodplain geomorphology, flood regime, climates, and species composition. Each site had 1 to 5 transects, with more transects in larger floodplain sites. The original study took the belt transect approach because its objective was to quantify flooding thresholds associated with transitions in the vegetation. For the present study, we selected discrete segments of the transects that were relatively uniform in both elevation and vegetation as sampling plots. Plot sizes were designed to encompass a minimum number of 10 trees with growth data. Therefore, plots with mature trees which are more widely spaced were larger in area than plots with dense stands of young trees. A total of 135 plots across 56 sites met our criteria for reasonably uniform and sufficiently large plots. The levels of environmental variables are represented with roughly the frequency with which they occur in the floodplain. In the case of elevation (measured relative to the 2-year recurrence interval flood, as explained later), the range of values are equally represented, but in the cases of sediment accretion rate and SOM there are more plots with low to medium values than plots with high values. From the perspective of analyzing relationships statistically, it would have been better to have equal replication across all levels and combinations of environmental variables. However this ideal would have been difficult to achieve even if the study locations had been selected for this purpose because some combinations of environmental variables are rare or do not occur at all (e.g. high surface SOM and high sediment accretion rate is an impossible combination because river sediments are mostly inorganic). Nevertheless, the among plot variation encompasses a broad range of elevations, climate, and soil properties (Table 1). Furthermore, this dataset includes a relatively large number of plots and sites (135 plots across 56 sites). By comparison, past research of floodplain forest productivity has typically included only a few plots from a single site.

## Measurements

The following data were measured on every plot:

- 1.1. *Sediment accretion rates*: 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 Jr. 1991; Hupp and Bazemore 1993; Kleiss 1996; Heimann and Roell 2000). Specifically, we spread a thin layer of red potters clay on the soil surface near the center of each plot between May 2012 and July 2014. Connecticut River floodplain sediments are a pale beige providing a clear color contrast with the red clay. Upon returning to the plots between June 2014 and July 2015, we used the clay as a marker for measuring the thickness of the layer of fresh sediments that had accumulated in the

**Table 1** Summary statistics of environmental variables measured on the 135 riparian forest plots. Elevation refers to plot ground elevation relative to the stage reached by the 2-year recurrence interval flood. Accretion rate is the average rate of sediment accretion on the plot over the study period. The soil samples for measuring pH, percent organic, and percent fines were taken from the top 1 cm of the soil/sediment deposits. Growth rate is the diameter growth rate compared to the average tree of that diameter

	Elevation relative to 2Y RI flood (m)	Soil pH	Soil Organic Matter (%)	Soil Fines (%)	Sediment Accretion rate (cm/year)	Tree growth rate (cm/year)	Typical tree longevity (years)	Daily Min. Temp (°C)
Min.	-4.05	4.33	0.59	2.79	0.00	-0.381	40	-4.46
1st Qu.	-1.95	5.08	4.84	38.24	0.00	-0.136	100	-0.57
Median	-0.90	5.34	7.42	56.32	0.32	-0.056	110	0.91
Mean	-1.16	5.49	13.13	54.79	1.18	0.006	124	0.17
3rd Qu.	-0.19	5.98	13.80	75.24	1.44	0.118	136	1.67
Max.	2.14	6.48	97.19	96.08	21.47	1.315	268	2.84

(see methods). Thus, plots with negative values have trees that grow slower than the average tree of that size, whereas plots with positive values have trees that grow faster than the average tree of that size. Typical tree species longevities are based on published values. Relative growth and typical longevity are average values for the plot. Daily minimum temperatures are averaged over the period 1981–2010

intervening 2 or 3 years. The thickness divided by the number of days between sampling dates and multiplied by 365 gives the average annual sediment accretion rate during the period. USGS stream flow gage records indicate that the annual peak flows in these years did not exceed the 2-year recurrence interval flow nor did they include any prolonged droughts (US Geological Survey 2015b). The accretion rates are thus representative of the amount of sediment deposition that is typical of most years.

- 1.2. *Soil metrics:* We took at least one soil sample on every plot, but most plots only had one soil sample taken. Sampling locations were chosen randomly within plots and included enough soil (~500 ml) to fill a sandwich-size zip lock bag halfway. Fresh litter on top of the soil was excluded and soil samples were homogenized before analyses. We analyzed the following soil properties: pH, soil organic matter (SOM) content, and percent fine particles (i.e. silt and clay <0.0625 mm sieve). Part of the soil sample was used to measure pH at the University of Massachusetts Soil and Plant Nutrient Testing Laboratory. The other part of the soil sample was dried and weighed in the Geosciences Laboratory at the University of Massachusetts Amherst to measure SOM and percent fines. SOM was approximated by loss on ignition (LOI), a measure of percent reduction of dry sample mass after four hours in a 550 °C oven (Dean 1974). The remaining mineral soil was wet-sieved, with the retained soil's dry mass representing the coarse fraction. We averaged values if there was more than one soil sample measured on a plot.
- 1.3. *Elevation:* The soil surface elevations measured at every tree during the previous study (Marks et al. 2014) were averaged for each plot. These elevations were not relative to sea level but rather relative to the stage of the 2-

year recurrence interval peak flow. Thus, elevations are also a measure of depth of flooding. Depth of flooding is highly correlated with frequency and duration of flooding and therefore other measures of flooding were considered redundant and not included in the final analyses. The stage of the 2-year recurrence interval peak flow was calculated with hydraulic models and USGS stream gage data in the previous study (see Marks et al. 2014 for details). A plot with a negative elevation would be under water during the peak flow that occurs every two years on average, whereas a plot with a positive elevation would be above water at that time.

- 1.4. *Climate:* We used the PRISM 30-year normals (1981–2010) of average daily minimum temperature for each research plot location (PRISM Climate Group 2012). We did not include other measures of temperature such as annual growing degree days because different measures of temperature are highly correlated. We did not include precipitation in the analysis because there is too little variation in precipitation among the research locations.
- 1.5. *Productivity:* We focused on trunk diameter growth rate as our index of plot productivity. While this method does not capture production of short-lived tissues like fine roots and leaves, it is a suitable proxy for productivity in our study because we are interested in longer term carbon sequestration in wood. We calculated diameter growth rate from repeated tree circumference measurements recorded in an earlier study (Marks and Canham 2015). We used diameter tapes to measure circumference rather than growth bands or coring trees because this method is less costly and less labor intensive which allowed us to measure many more trees. We marked the height of circumference measurements with an aluminum nail and tag number to reduce relative

errors in circumference measurements. The repeat measurement was taken about three years later to have a larger change in diameter and thereby reduce relative measurement errors. Moreover, diameter measurement errors were normally distributed and therefore tended to cancel each other when averaging growth across multiple trees on a plot.

Diameter growth is size-dependent and a comparison among trees should attempt to account for this effect. Specifically, diameter growth rates on plots with larger trees could be greater than on plots with smaller trees due to this size effect rather than due to a difference in plot fertility (Fig. 3). We avoided this confounding effect by calculating tree growth rate relative to the average tree of the same size. Specifically growth rate ( $G$ ) of the average tree was modelled as a power function of tree diameter ( $D$ ) as follows using data for all trees regardless of species (Marks and Canham 2015):

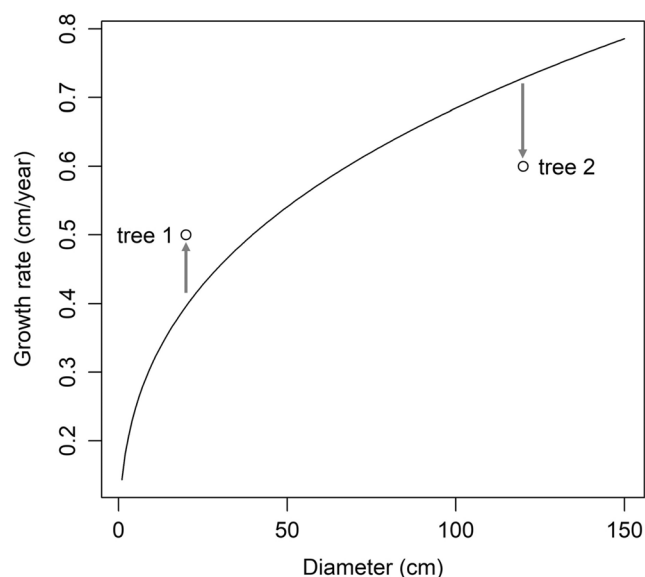
$$G = 1.43 * D^{0.34}$$

where  $G$  is in cm/year and  $D$  is in cm. We calculated the difference between the measured diameter growth rate of individual trees and the average growth rate predicted by this function (see examples in Fig. 3). We averaged these deviations in growth rate across the trees on the plot as our index of plot productivity. Positive values of this relative growth rate indicate that the trees on the plot are growing faster than average trees, whereas negative values indicate that they are growing more slowly than average.

Plots also differ in species composition, which is significant because species have inherent differences in growth rate. Specifically, fertile sites tend to be dominated by fast-growing species while infertile sites tend to be dominated by slow-growing species. Thus, differences in growth rates among plots due to differences in fertility tend to be amplified by differences in species composition. To consider this species effect, we repeated all analyses using only growth data from the most common floodplain forest tree species, *Acer saccharinum*. We used the following size-dependent growth function specific to *Acer saccharinum* to compute relative growth rates in the analyses that included only *Acer saccharinum* trees (Marks and Canham 2015):

$$G = 2.25 * D^{0.23}$$

In the initial analyses, we included only plots where we had growth data for at least 10 trees to have a reliable estimate of growth rate. There were 135 plots that met this criterion. We needed to lower this requirement to a minimum of 6 trees per plot for the *Acer-saccharinum*-only analyses to have enough plots. Specifically, 75 plots met this criterion in the *Acer-saccharinum*-only analyses.



**Fig. 3** Plot illustrating the size-dependence of growth rate in trees. The curve represents the average growth rate for Connecticut River riparian trees as a function of size. Although the absolute growth rate of tree 2 is greater than for tree 1, it is a relatively slower growing tree than tree 1 when we compare their growth rates to the growth rates of the average tree of that size. Using this relative growth rate as an index of plot ability to support rapid growth avoids the confounding effects of tree size associate with plot differences in stand age

- 1.6. *Stand density*: Silvicultural treatments and natural disturbances that thin a stand of trees to give each tree more growing space and light can enhance growth rates. We calculated the density of trees (trees/ha) in each plot to insure that stand density is not confounding our analysis. However, we do not expect density to have any significant effect because the stands of trees in all our plots were fully stocked with closed canopies. We intentionally selected research sites on protected land that is not subject to silvicultural treatments such as stand thinning. Furthermore, our plots do not include locations where trees are dying from permanently raised water levels from beaver impoundments or from rising sea levels in the estuary. We also excluded tributary sites with channel bars where extremely fast flows from Tropical Storm Irene had stripped away much of the vegetation in August 2011. Moreover, our approach of correcting growth rates for size-dependence also helps avoid confounding effects of stand density because tree size and density tend to be correlated.
- 1.7. *Tree longevity*: We obtained typical longevities of tree species from a published list (Loehle 1988). We used these typical longevities to calculate a mean for each plot weighted by the number of trees of that species on the plot. Thus, we investigated the longevity of tree species in the plot rather than the actual age of the trees in the plot. In other words, differences among plots in longevity reflect differences in species composition

such as changes in composition associated with succession or microtopography. Species not in the longevity dataset were excluded from calculating the plot mean. The analysis only included plots where longevity data were available for at least half the trees in the plot. The results were not sensitive to this arbitrary cut-off because we had longevity data for all canopy tree species. The species which lacked longevity data were large shrubs or small understory trees. Therefore, our tree longevity data refer to the canopy tree species in the plot.

## Data Analyses

We implemented all analyses with the statistical package R (R Core Team 2013). We explored the covariation of growth rate, tree longevity, floodplain elevation, sediment accretion rate, SOM, soil pH, percent fines, and average daily minimum temperature in the following ways: variograms, correlations, principal components analysis (PCA), and multiple regression. These analyses are intended to complement each other and increase confidence in the results where the different analyses agree.

### 1.1. Variograms

We plotted variograms of semi-variance versus distance among plots for each environmental variable to explore spatial dependence and check for spatial autocorrelation. We used the function “*variog*” from the package “*geoR*”. Distances among plots were calculated from the latitude and longitude of plot centers.

### 1.2. Correlations

We calculated a correlation matrix of Pearson’s *r*-values among growth rate, longevity and environmental variables. We used the function “*rcorr*” from the “*Hmisc*” package in R. We highlight correlations that were significant at the  $p < 0.01$  level.

### 1.3. Principal Components Analysis

We implemented a PCA with the function “*prcomp*” in R. We log transformed the growth rate, SOM, and sediment accretion data to more closely approximate a normal distribution. The data were scaled to have unit variance before implementing the PCA (i.e. *prcomp* used the correlation matrix rather than the variance-covariance matrix). We plotted the results of the PCA with the function “*autoplot*” from the package “*ggfortify*”. We illustrated the first two principal components in the plot because they accounted for over half of the variation.

### 1.4. Regression

We analyzed the relationship of environmental variables and stand density with growth rate using multiple regression models. We implemented the multiple regression analysis with the function “*lm*” in R. We used a stepwise regression approach wherein the final model that we report here included only the variables that significantly improved the fit (i.e. difference in  $\text{adj.}r^2 \geq 0.01$ ). We used the square root of the variance inflation factor (“*vif*” function in the library “*car*”) to estimate co-linearity (values for variables included in the final multiple regression were below 1.06, well below the 2.0 threshold for concern over co-linearity). We plotted residuals (with the “*plot(modelname)*” function in R) to check linearity, homoscedasticity, and normality. The data also met these assumptions reasonably well. We normalized the data to *z*-scores prior to regression to be able to compare coefficients easily.

## Results

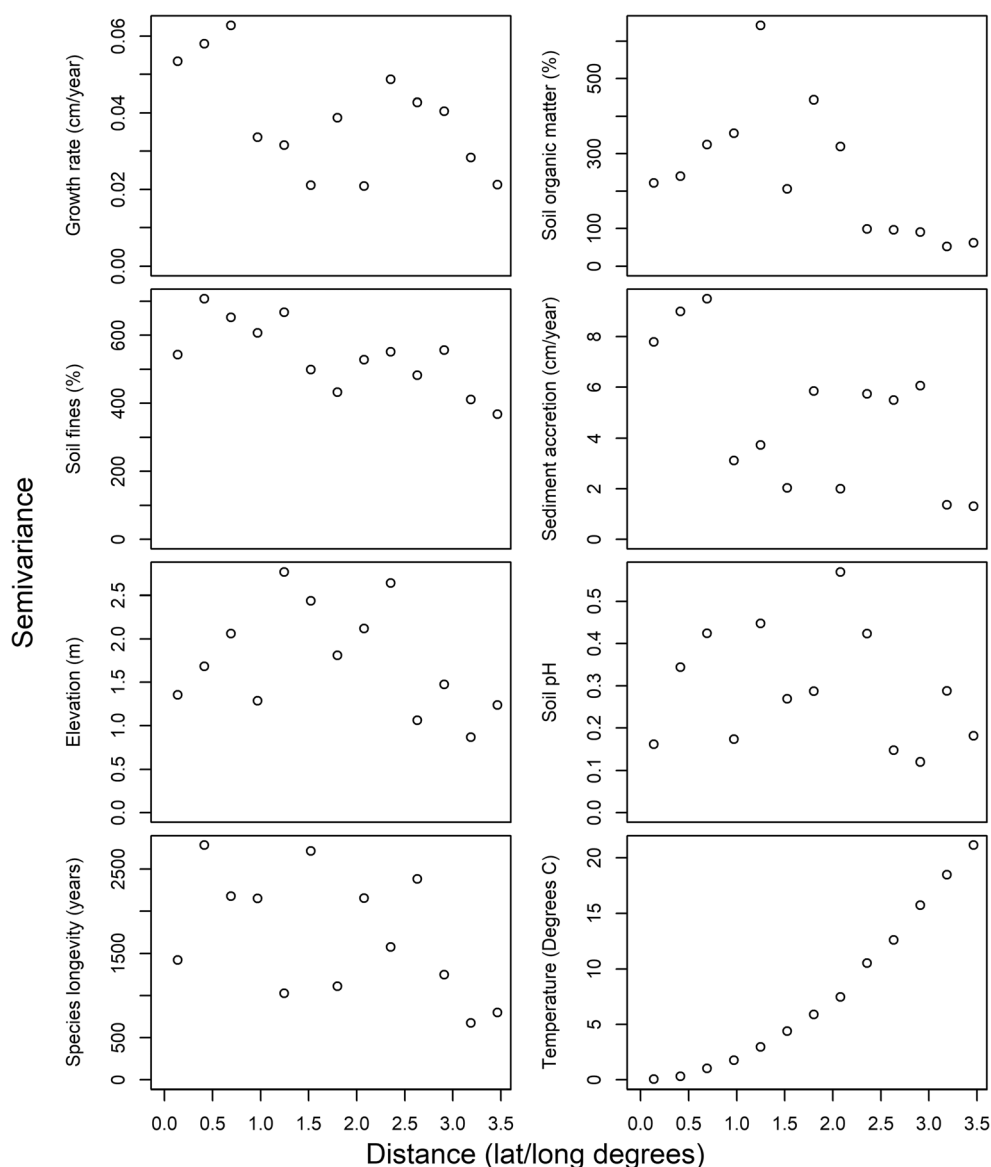
Tree diameter growth rates varied by almost 1.7 cm/year among plots (Table 1) but did not show a latitudinal trend across the Connecticut River watershed (Fig. 2). Variance in tree growth rates and other measured variables declined with distance between plots (Fig. 4). The exception was temperature which varies with latitude on this North to South flowing temperate river. The high variance in growth rate and soil properties over short distances illustrates the great habitat diversity in topographically heterogeneous riparian forests on meandering rivers.

Growth rate was most closely correlated with sediment accretion rate, while surface SOM was most closely related with soil pH, and tree longevity was most closely related to floodplain elevation and percent fines (Table 2). Growth rate was negatively related to SOM and tree longevity (Table 2). These negative correlations suggest that growth, SOM, and tree longevity are maximal in different places on edaphic gradients. Specifically, growth rate was maximal where sediment accretion rate was high whereas tree species longevity were greatest at higher elevations with coarse soils (Fig. 3).

These correlations were reflected in the results from the PCA (Fig. 5). The first two axes of the PCA indicate that growth rate is primarily related to sediment accretion rate and secondarily to pH. Soil pH tends to be lower where there is more SOM in the top 1 cm of soil. The PCA also indicates that long-lived tree species tend to occur at higher elevations with coarser soils.

Stepwise regression also indicated that floodplain tree growth is most strongly related to sediment accretion rate (Table 3). Sediment accretion rate, SOM, and elevation

**Fig. 4** Variograms plotting the change in semivariance with distance among 135 riparian research plot locations for each of the environmental variables included in the analyses



(relative to the stage of the 2-year recurrence interval flood) together explained 44% of the variation in growth rates (Table 3). The other variables such as stand density and minimum daily temperature were not significantly related with growth rate and were therefore dropped from the final regression model. Sediment accretion rate alone could explain 39% of the variation in growth rates. However, excluding the plots with sediment accretion rates over 0.5 cm/year reduced the variance explained by roughly half. This sensitivity suggest that sediment accretion rates must differ by cm/year rather than mm/year to show a statistically significant difference in growth rates. Using a more precise method for measuring tree growth than diameter tapes likely might have increased the variance explained by these variables.

Repeating the analyses with the dataset where only *Acer saccharinum* was used to calculate growth rate generally showed the same trends (Table 4, Fig. 5b). Specifically, growth rate increased with sediment accretion rate, whereas surface SOM increased with soil fines and decreased with soil pH. The strength of the correlation between sediment accretion rate and growth rates across analyses implies that this correlation is not merely a consequence of differences in species composition among plots. By contrast, the trend for growth rate to decline with surface SOM and elevation in the single species dataset was weaker than in the dataset that included all species (compare Tables 3, 4), which suggests that differences in plot species composition may be partially responsible for these correlations.



**Table 2** Correlations in the dataset using all tree species to estimate growth rate (A) and in the dataset using only *Acer saccharinum* to estimate growth rate (B). Correlations that are statistically significant at the  $p \leq 0.01$  level are highlighted in bold font. Variables include the

A)	growth	organic	fines	accretion	elevation	pH	temperature	longevity
growth	1	<b>-0.26</b>	0.04	<b>0.63</b>	<b>-0.34</b>	<b>0.27</b>	0.03	<b>-0.25</b>
organic	<b>-0.26</b>	1	0.2	-0.15	0.01	<b>-0.51</b>	0.05	-0.03
fines	0.04	0.2	1	0.04	<b>-0.51</b>	0.04	0.2	<b>-0.33</b>
accretion	<b>0.63</b>	-0.15	0.04	1	<b>-0.3</b>	<b>0.34</b>	0.07	<b>-0.25</b>
elevation	<b>-0.34</b>	0.01	<b>-0.51</b>	<b>-0.3</b>	1	<b>-0.3</b>	-0.09	<b>0.36</b>
pH	<b>0.27</b>	<b>-0.51</b>	0.04	<b>0.34</b>	<b>-0.3</b>	1	-0.14	-0.04
temperature	0.03	0.05	0.2	0.07	-0.09	-0.14	1	0.08
longevity	<b>-0.25</b>	-0.03	<b>-0.33</b>	<b>-0.25</b>	<b>0.36</b>	-0.04	0.08	1
B)	growth	organic	fines	accretion	elevation	pH	temperature	
growth	1	-0.27	-0.11	<b>0.65</b>	-0.14	0.16	0.1	NA
organic	-0.27	1	<b>0.4</b>	-0.26	-0.12	<b>-0.32</b>	0.1	NA
fines	-0.11	<b>0.4</b>	1	-0.23	<b>-0.41</b>	0.04	0.21	NA
accretion	<b>0.65</b>	-0.26	-0.23	1	0.01	<b>0.39</b>	0.08	NA
elevation	-0.14	-0.12	<b>-0.41</b>	0.01	1	-0.02	-0.05	NA
pH	0.16	<b>-0.32</b>	0.04	<b>0.39</b>	-0.02	1	-0.05	NA
temperature	0.1	0.1	0.21	0.08	-0.05	-0.05	1	NA

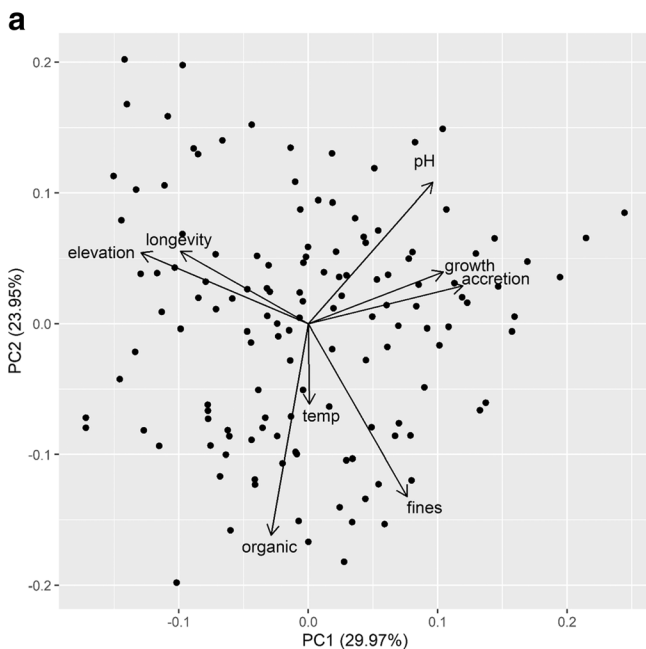
following: tree growth rate, typical tree longevity, daily minimum temperature, surface soil organic content, soil fines, plot elevation (relative to the stage of the 2-year recurrence interval flood), soil pH, and the sediment accretion rate

## Discussion

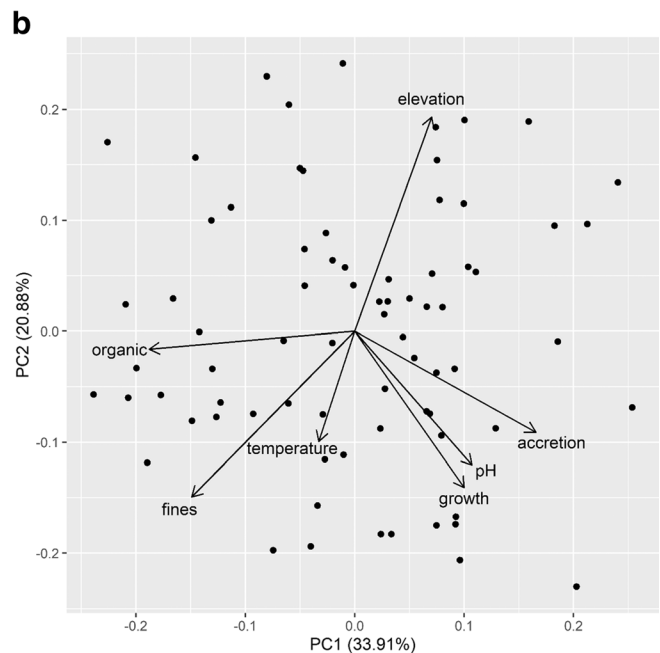
### Correlates of Floodplain Forest Productivity

Despite a significant gradient in annual minimum temperature across the study region (USDA plant hardiness zone 3b to 6b),

flooding and soil forming processes like sediment accretion and the development of an O-horizon appear more strongly related to riparian forest productivity than climate (Table 2 & Fig. 5). The close positive correlations among sediment accretion rate, soil pH and growth rate (Tables 2–4, Fig. 5) suggests that riverine inputs of nutrients and alkalinity associated with



**Fig. 5** Principal component analysis (PCA) of the dataset including all tree species to estimate growth rate (A) and of the dataset including only *Acer saccharinum* to estimate growth rate (B). Arrows draw eigenvectors



on the first two axes of the PCA model. The percentages indicate the amount of variance explained by that principal component axis

sediments are important to governing riparian forest productivity. This interpretation is consistent with research on other temperate rivers that have shown large nutrient inputs to floodplains associated with sediments (Kronvang et al. 1998; Steiger and Gurnell 2003; Adair et al. 2004; Olde Venterink et al. 2006; Kronvang et al. 2009; Kroes et al. 2015; Noe et al. 2019). Besides introducing substantial amounts of new nitrogen and phosphorus, sediment deposition stimulates mineralization of in situ organic nitrogen and phosphorus (Noe et al. 2013; Shrestha et al. 2014). The greater floodplain forest productivity on rivers with large sediment loads (“whitewater” rivers or “várzea”) compared to rivers with few sediments and water stained by humic acids (“blackwater” rivers or “igapó”) (Worbes 1997; Parolin and Ferreira 1998; Schöngart et al. 2010) also supports the view that nutrients associated with sediments boost floodplain forest productivity.

Our results imply that riparian forest productivity may be limited by nutrient availability similar to productivity in upland forests in the region, which are typically nitrogen-limited (Reich et al. 1997; Norby et al. 2010; Reich 2012), with a possible supporting role for calcium or pH (Bigelow and Canham 2007). The difference between floodplains and uplands is that nutrients and alkalinity are eroded and leached away from upland soils (Crews et al. 1995; Richardson et al. 2004; Wardle et al. 2004), whereas riparian soils are enriched by floods (Kronvang et al. 1998; Steiger and Gurnell 2003; Adair et al. 2004; Olde Venterink et al. 2006; Kronvang et al. 2009; Kroes et al. 2015; Noe et al. 2019) and riparian groundwater flows (Lowrance et al. 1984; Peterjohn and Correll 1984; Haycock and Pinay 1993; Vellidis et al. 2003; Hoffmann et al. 2009; Hoffmann et al. 2011; Hill et al. 2014). The increases in tree growth at lower elevations (relative to the stage of the 2-year recurrence interval flood) and with increasing sediment accretion rate suggest that these soil enrichment processes could be important in governing riparian productivity (Tables 3, 4, Fig. 5).

**Table 3** Summary of multiple linear regression model of riparian tree growth against sediment accretion rate, soil organic matter, elevation (relative to stage of 2-year RI flood), and daily minimum temperature. Variables were converted to z-scores prior to regression. Residual standard error: 0.7495 on 131 degrees of freedom. Multiple R-squared: 0.4509, Adjusted R-squared: 0.4383. F-statistic: 35.85 on 3 and 131 DF, *p* value: 2.2e-16

Predictor	Estimate	Std. Error	t value	Pr(> t )	Significance
Accretion	0.5476	0.0687	7.97	<0.0001	***
Organic	-0.1772	0.0656	-2.70	0.008	**
Elevation	-0.1761	0.0679	-2.59	0.01	*

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘.’ 1

**Table 4** Summary of multiple linear regression model of *Acer saccharinum* growth against sediment accretion rate, soil organic matter, elevation (relative to stage of 2-year RI flood), and daily minimum temperature. Residual standard error: 0.7547 on 71 degrees of freedom. Multiple R-squared: 0.4535, Adjusted R-squared: 0.4304. F-statistic: 19.64 on 3 and 71 DF, *p* value: 2.244e-09

Predictor	Estimate	Std. Error	t value	Pr(> t )	Significance
Accretion	0.6158	0.0909	6.78	<0.0001	***
Organic	-0.1257	0.0915	-1.37	0.17	.
Elevation	-0.1596	0.0884	-1.81	0.08	.

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘.’ 1

The relationship between tree growth rate and sediment accretion rate could be in part due to differences in species composition among plots. For example, pioneer species such as *Salix nigra* and *Populus deltoides* that colonize sandbars where sediment accretion rates are greatest have inherently faster growth rates than more late successional species (Marks and Canham 2015). However, our finding of a relationship between sediment accretion rate and *Acer saccharinum* growth rate indicates an effect that is independent of species differences among plots.

The amount of surface SOM could be affected by both tree species and the physical environment. For example, the plots with the highest SOM in our study were dominated by eastern white pine (*Pinus strobus* L.), an evergreen conifer species whose needles are known to decompose slowly (McClagherty et al. 1985). Regardless of the cause, the development of a thick O-horizon indicates that organic matter is decomposing more slowly than it is being produced and thereby becoming a sink for nutrients and carbon. Studies of upland forests have shown a positive relationship between organic matter mineralization rate and productivity (Pastor et al. 1984; Reich et al. 1997; Norby et al. 2010). A negative relationship between accumulation of SOM in an O-horizon and productivity has been observed in boreal forests (Vioreck et al. 1983; Simard et al. 2007). Similarly, productivity, decomposition rates, and nitrogen availability decline with increasing precipitation in tropical montane forests whereas SOM increases (Schoor et al. 2001; Wolf et al. 2011). These consistent results across biomes suggest that the negative relationship between forest productivity and SOM in an O-horizon may be a general one for forests.

Elevation is often treated as a relatively easily measured proxy for floodplain processes like flooding but is not easily interpreted when considering productivity. Specifically several studies have found a peak in productivity at intermediate floodplain elevations (Megonigal et al. 1997; Rodríguez-González et al. 2010; Lucas et al. 2014), but others found higher productivity, higher nitrogen availability, and higher pH at lower elevations (Clawson et al. 2001). We found that

sediment accretion rate and surface SOM were better at explaining variation in tree growth rates than elevation (Tables 2–4, Fig. 5), which may explain some of the inconsistent results in past research. The type of parent materials and land cover from which sediments are derived in different watersheds could also cause differences among studies (Furch and Junk 1997). We propose that future research on floodplain forest productivity should focus more on sediment accretion rate and associated nutrients than on elevation to investigate differences in riparian forest productivity.

### Implications for Managing Forests for Carbon Sequestration

The idea of managing forests to help mitigate rising atmospheric carbon dioxide levels is enticing to many conservation organizations but should consider site conditions to optimize outcomes (Cao et al. 2011). Tree growth rates are exceptionally high in riparian forest plots with ample sediment deposition, but species also tend to be short lived (Table 2 & Fig. 5). These riparian forests will reach the point where they emit as much carbon from decaying trees as they absorb in growing trees sooner than upland forests with slower-growing and longer-lived species. Upland forests are more suitable for carbon storage in long-lived trees. For example, regionally common upland species such as *Acer saccharum*, *Fagus grandifolia*, *Quercus alba*, or *Tsuga canadensis* typically live for three centuries, whereas the most common floodplain trees such as *Acer negundo*, *Acer saccharinum*, *Fraxinus pennsylvanica*, *Populus deltoides*, *Quercus palustris*, and *Ulmus americana* typically live less than half as long. However, the spread of non-native pests and pathogens may undermine strategies to sequester carbon in long-lived trees both in floodplain and upland forests, with four of the above genera already impacted in eastern North America (*Fagus*, *Fraxinus*, *Tsuga*, *Ulmus*). Carbon sequestration may be more durable in soils than in trees. In upland forest soils, much carbon sequestration is typically in an O-horizon, whereas in the floodplain, organic matter may be buried underneath layers of sediments (Ricker et al. 2013; Ricker and Lockaby 2014; Bätz et al. 2015; Ricker and Lockaby 2015; Scott and Wohl 2018; Hupp et al. 2019). For example, sediment cores collected by one of us (BCY) revealed that SOM remains elevated within the top meter of the soil profile in Connecticut River floodplains, thus resulting in higher total carbon inventories in floodplain soils. This buried SOM allows floodplains to act as long-term carbon sinks.

Sediment loads have been dramatically reduced in many of the world's large rivers because of dam construction (Syvitski et al. 2005), including on Connecticut River tributaries (Renshaw et al. 2014). Floodplain inundation and sediment deposition have also been reduced by levees (Tobin 1995), channelization (Brooker 1985), and channel incision (Shields Jr et al. 2010). This decline is a concern for the capacity of floodplains to sequester carbon because deposition

of sediments and nutrients by regular flooding is associated with the exceptionally high productivity of riparian forests (Tables 2–4 & Fig. 5) and long-term storage of SOM in deep soil profiles. Furthermore, the enhancement of tree growth by rising atmospheric CO<sub>2</sub> concentrations is constrained by soil nutrient availability (Reich et al. 2006; Norby et al. 2010). Strategies for managing forest carbon sequestration should consider these interactions in an era when the number of large dams in the world is projected to more than double (Zarfl et al. 2015; Latrubesse et al. 2017). Specifically, conservation of processes such as flooding and sediment deposition may be as important as reforestation to longer term carbon sequestration in floodplains. Indeed, studies of projects that reconnected floodplains to river channels have shown that restoring flooding and sediment deposition not only increased soil nutrients (Kronvang et al. 1998; Kronvang et al. 2009; Hoffmann et al. 2011; Noe et al. 2019) but also floodplain productivity (Robertson et al. 2001).

An ideal conservation outcome would restore processes and vegetation to the full range of riparian landforms with their high associated biodiversity and productivity, but there may be frequent resistance to reforesting the well-drained parts of floodplains because their rich alluvial soils are prized for agriculture (Frimpong et al. 2007). Our results suggest a compromise for floodplain properties where landowners are only willing to give up a small part of their agricultural fields for conservation. Specifically, we showed that the geomorphic features along riverbanks that receive some of the most sediment deposits such as natural levees and point bars also support the fastest growing trees. Planting buffers of trees along streambanks in crop fields is already a best management practice for intercepting excess nutrients and reducing erosion (Hoffmann et al. 2009; Stutter et al. 2012). Our results suggest that these buffers could also be exceptionally valuable for augmenting carbon sequestration. The coincidence of hotspots for nutrient sequestration and hotspots for carbon sequestration in floodplains could be an opportunity for combining two ecosystem services to motivate and fund restoration of these critical ecosystems.

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**Authors Contributions** Christian O. Marks conceived of field research, performed all analyses and wrote and revised the draft manuscript.

Brian C. Yellen supervised and trained interns in soil sample analyses and soil sampling techniques in the field, contributed idea of analyzing

SOM in soil samples, provided expertise in river sedimentology for the project, helped edit draft manuscript.

Stephen A. Wood contributed idea of investigating relationship between SOM and productivity, provided statistical advice on analyses, provided expertise on SOM dynamics, helped edit draft manuscript.

Erik H. Martin prepared the climate data, helped edit draft manuscript.

Keith H. Nislow helped conceive floodplain forest ecology research project with a broad interdisciplinary perspective, helped edit draft manuscript.

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